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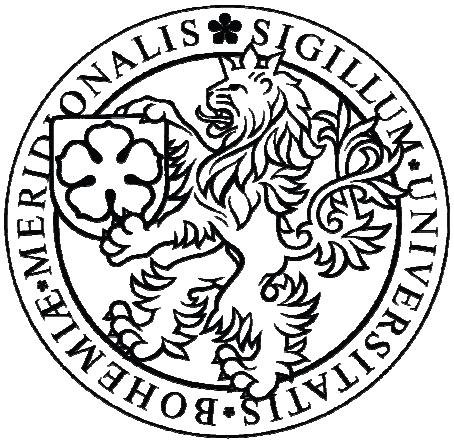

Dynamics of fish spatial distribution in reservoirs

Ph.D. Thesis

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Annotation

This dissertation thesis focuses on several aspects of fish ecology in reservoirs and the methodology of their sampling. It is divided to three parts. The first part focuses on the dynamics of fish distribution throughout the seasons and between day and night. The second part deals with the efficiency and the selectivity of the beach seine net, trawl and purse seine net. The third part describes the long-term development of fish populations in the Římov Reservoir.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Milan Říha

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DECLARATION OF ORIGINALITY

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

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Paper II
Říha M., Kubečka J., Prchalová M., Mrkvička T., Čech M., Draštík V., Frouzová J., Hohausová E., Jůza T., Kratochvíl M., Peterka J., Tušer M., Vašek M. (2011) The influence of diel period on fish assemblage in the unstructured littoral of reservoirs. *Fisheries Management and Ecology*, **18**, 339–347 34

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DYNAMIC OF FISH SPATIAL DISTRIBUTION IN RESERVOIRS

INTRODUCTION

Reservoirs are of crutial importance for the Czech Republic, because they represent the only large standing waters in the country. They serve many difference purposes such as flood protection, generation of hydropower, drinking water supply and recreation (Broža *et al.* 2005). Knowledge on how the reservoir ecosystem functions is necessary for optimization in achieving these objectives. It has been widely recognignized that fish play a major role in the structuring and function of the water ecosytems (eg. Hrbáček *et al.* 1961; Brooks and Dodson 1965; Carpenter *et al.* 1985) and therefore, scientist as well as managers need to know the quality, quantity and distribution of the fish stock in order to asses their impact on the reservoir ecosystem.

The majority of reservoirs in the Czech Republic have a canyon-shaped morphology (Duncan and Kubečka 1995). Such waterbodies have one or a few inflowing rivers, an elongated shape, steep shores and a relatively low mean depth (Duncan and Kubečka 1995; Kalff 2002). These reservoirs also exhibit pronounced longitudinal zonation since the running environment of the inflowing river changes substantially to a lentic environment in the tributary. Inflowing nutrients from the river make the tributary and the upper part of a reservoir the most productive reservoir parts with highest nutrient, chlorophyll a and zooplankton concentrations. All these parameters gradually decrease towards the dam (eg. Hejzlar and Vyhnálek 1998; Seďa and Devetter 2000; Mašín *et al.* 2003; Vašek *et al.* 2003; Rychtecký and Znachor 2011).

Beside this longitudinal aspect, the pelagic and littoral zone can be distinguished in a reservoir body. The littoral is defined as the near shore region of the waterbody where the bottom lies within the photic zone, and where shallow water flora are frequently dominated physically by macrophytes (Kalff 2002). Thus, the littoral is very poorly represented in canyon-shaped reservoirs due to the steep shores resulting from the former river valley. Furthermore, high water level fluctuation prevents macrophyte occurrence in the reservoir littoral (Duncan and Kubečka 1995). On the other hand, the pelagic zone represents the majority of water volume in these reservoirs (Duncan and Kubečka 1995). The pelagic zone is usually stratified due to large depth of reservoirs and three layers can be distinguished - the warmer and high oxygenated epilimnion, transient metalimnion and cold, low oxygenated hypolimnion (Duncan and Kubečka 1995; Prchalová *et al.* 2008a, 2009a).

Fish distribution varies spatially and temporary in canyon-shaped reservoirs. Profound regular changes in fish distribution were observed throughout the seasons (Wilkonska 1967; Goldspink 1978; Hladík and Kubečka 2003) or diel periods (Kubečka 1993; Čech *et al.* 2005; Vehanen *et al.* 2005). Seasonal migrations to different parts of the reservoir are caused by the distinct spawning or feeding ground requirements of various fish species, or different needs for winter refuges (Lucas and Baras 2001). Diel migrations of fish were documented on the vertical "hypolimnio-epilimnion" (Čech *et*

al. 2005) or horizontal "littoral - pelagial" (Kubečka 1993; Vehanen *et al.* 2005) axes. These diel migrations are mostly associated with resource availability, resource use and predator avoidance (Bohl 1980; Gliwicz and Jachner 1992; Gliwicz *et al.* 2006; Hölker *et al.* 2007).

Some species that colonize reservoirs are able to complete their entire life cycles in restricted parts of these waterbodies (Vostradovský 1968; Vostradovská 1974; Hladík and Kubečka 2003). However, other fish species have to migrate to extensive parts of the reservoirs, including inflowing rivers, due to their changing requirements throughout the seasons (Poddubny 1971; Lucas and Baras 2001; Hladík and Kubečka 2003). The recent studies of Milan Hladík and colleagues (Hladík and Kubečka 2003, 2004) documented the intensive spawning migrations of numerous species from a reservoir main body to the tributary. These migrating fish occupy the latter only for a short spawning period and migrate afterwards back to their feeding grounds in the reservoir or inflowing river. Vašek and coworkers (Vašek *et al.* 2003, Vašek and Kubečka 2004) and Prchalová and colleagues (2008a, 2009a) have shown that fish follow longitudional nutrient and vertical oxygen/temprature gradients during the summer feeding season. The highest fish densities were found in the nutrient-rich tributaries and upstream parts and in the warm, well-oxygenated upper parts of the water column. Despite these findings, there is a lack of information about how these two patterns, tributary migration and summer longitudional pattern of distribution, are connected. Whether the redistribution of tributary spawners is driven by specific conditions in the reservoir or predetmined species-specific patterns.

In my diseratation, I focused mainly on diel horizontal migration between the littoral and pelagic zones. This type of migration is a broadly documented phenomenon (e.g. Bohl 1980; Gliwicz and Jachner 1992; Brabrand and Faafeng 1993; Copp and Jurajda 1999; Wolter and Freyhof 2004; Romare *et al.* 2003). Studies dealing with this diel habitat shift predominantly focus on juvenile or small zooplanktivorous fish, especially in lakes (eg. Bohl 1980; Gliwicz and Jachner 1992; Romare *et al.* 2003; Lewin *et al.* 2004; Hölker *et al.* 2007) in which migration is driven by resource availability, and use plus predator avoidance (Bohl 1980; Gliwicz *et al.* 2006). Generally, small fish are associated with submerged macrophytes or woody structures within a littoral during day (Jacobsen and Berg 1998; Jacobsen and Perrow 1998; Lewin *et al.* 2004; Gliwicz *et al.* 2006). Day shelters reduce predation pressure on small fish but may also reduce their feeding rates because resources are limited in these locales (Gliwitz and Jachner 1992; Gliwicz *et al.* 2006). Predator-prey interaction is light dependent, and thus when the environment becomes darker during night, predation pressure is reduced (Cerri 1983) and small fish migrate to the pelagic zone where zooplankton prey is more abundant (Bohl 1980; Romare *et al.* 2003; Gliwicz *et al.* 2006).

Contrary to this broadly accepted pattern, the opposite migration, when fish move to the littoral zone at night, has also been documented. Such a behavior pattern was described particularly for subadult and adult fish in rivers (Kubečka and Duncan 1998; Wolter and Freyhof 2004; Eros *et al.* 2008), some lakes (Schulz and Berg 1987; Zamora and Moreno-Amich 2002; Jacobsen *et al.* 2004) and reservoirs (Kubečka 1993; Vehanen *et al.* 2005). The reasons behind this behaviour is very poorly understood so far. Several

different explanations have been proposed, such as avoidance against nocturnal offshore predators (Coop and Jurajda 1993; Jacobsen *et al.* 2004) or the changing of a given feeding habitat or activity (Schulz and Berg, 1987; Wolter and Freyhof 2004; Roach and Winemiller 2011; Zamora and Moreno-Amich 2002), but a convincing explanation is still missing.

Our understanding of the diel horizontal migration of subadult and adult fish remains poor also due to metodological problems and the unknown selectivity of the utilized sampling gears (Pierce et al. 2001; Wolter and Freyhof 2004; Eros et al. 2008). A reliable estimate of both fish density and its diel change call for quantitative sampling of both habitats. Quantitative sampling means that fish are captured with low sampling bias or with a known bias that allows for correction of the obtained results (Bonar 2009). Active sampling gears are better for quantitative sampling than passive (Kubečka *et al.* 2012), because they provide information about fish density in actual time, on an exactly determined area and generally their selectivity is lower. Trawling, purse seining and beach seining are active methods used for pelagial (trawling and purse seining) and littoral (beach seining) sampling. These methods are the most important for sampling of a marine environment (Gabriel *et al.* 2005) but knowledge about their proper use, performance and selectivity are virtually missing in freshwater environments.

Our understanding of the ecological processes and functions of different trophic levels requires complex research with knowledge of the history of ecosystem. The Hydrobiological Institute of the Academy of Sciences of the Czech Republic (ASCR) has been using the Římov Reservoir as an important model. This waterbody possesses many typical features of canyon-shaped reservoirs. It has one main tributary, steep shores, summer oxygen/temperature stratification, low ratio of littoral/pelagial areas, longitudinal nutrient gradients and no macrophytes occurrence in the littoral (Kubečka 1990; Seďa and Devetter 2000; Hejzlar and Vyhnálek 1998; Hladík and Kubečka 2004; Prchalova *et al.* 2009; Rychtecký and Znachor 2011). Different aspects of the reservoir ecosystem have been studied since reservoir filling (Kubečka 1990; Seďa and Kubečka 1997; Komárková *et al.* 2003) but an overview of reservoir fish stock succesion and stability has been missing for almost the last two decades.

This dissertation thesis is focuses on several aspects of fish ecology in reservoirs and the methodology of their sampling. It is divided into three parts. The first part focuses on the dynamics of fish distribution throughout the seasons (Paper I) and between day and night (Paper II and III). The second part deals with the efficiency and selectivity of beach seine (Paper IV) plus trawl and purse seine nets (Paper V). The third part describes the long-term development of fish populations in the Římov Reservoir (Paper VI).

RESULTS

This dissertation is composed of six papers – four papers already published (Papers II, IV, V, VI) and one is in press (Paper I) in international scientific journals; one paper is unpublished (Paper III). They are referred to in the text by their roman numerals.

PAPER I

Post-spawning dispersal of tributary spawning fish species to a reservoir system

Říha M., Hladík M., Mrkvička T., Prchalová M., Čech M., Draštík V., Frouzová J., Jůza T., Kratochvíl M., Peterka J., Vašek M., Kubečka J. (2012) Post-spawning dispersal of tributary spawning fish species to a reservoir system. *Folia Zoologica*. (in press)

The study investigated post-spawning dispersal of seven species spawning in the tributary of the Římov Reservoir during years 2000 - 2004. Fish were captured during spawning migration to the tributary by two giant traps, marked and released. Afterward distributions of marked fish were investigated in the reservoir and the inflowing river during three successive periods 1) early summer; 2) late summer and 3) next spawning season. Species were divided into two groups - obligatory tributary spawners (white bream *Blicca bjoerkna* (L.), chub *Squalius cephalus* (L.), bleak *Alburnus alburnus* (L.) and asp *Aspius aspius* (L.)) that spawned only in the tributary of the reservoir and generalists (bream *Abramis brama* (L.), perch *Perca fluviatilis* L. and roach *Rutilus rutilus* (L.)) that spawned in the tributary as well as on different sites in the main body of the reservoir. We hypothesized that obligatory tributary spawners distribute across the whole reservoir after spawning according to their species-specific preferences to feeding grounds. In spawning generalists we expected relatively low or erratic post-spawning dispersal. Results of the study revealed that the post-spawning dispersal of obligatory tributary spawners fulfilled our assumption and they dispersed according to their requirements to feeding grounds. The post-spawning dispersal of generalists showed that assumed low dispersal was relevant for bream and perch and erratic dispersal for roach.

PAPER II

The influence of diel period on fish assemblage in the unstructured littoral of reservoirs

Říha M., Kubečka J., Prchalová M., Mrkvička T., Čech M., Draštík V., Frouzová J., Hohausová E., Jůza T., Kratochvíl M., Peterka J., Tušer M., Vašek M. (2011) The influence of diel period on fish assemblage in the unstructured littoral of reservoirs. *Fisheries Management and Ecology*, **18**, 339- 347.

Diel changes in littoral fish assemblage were studied in four reservoirs in the Czech Republic (Central Europe). The sampling was performed by beach seining in an unstructured littoral. Species such as perch *Perca fluviatilis* L., roach *Rutilus rutilus* (L.), bream *Abramis brama* (L.), carp *Cyprinus carpio* L., ruffe *Gymnocephalus cernua* (L.), pikeperch *Sander lucioperca* (L.), eel *Anguilla anguilla* (L.) and the hybrid *Abramis brama* x *Rutilus rutilus*, had higher densities at night. Only bleak *Alburnus alburnus* (L.) had higher density at day. The number of species was higher in night hauls, when differences in mean body size for roach and bleak were found. Diel changes in fish densities were the cause for the change of species composition between day and night. The study has implication for the sampling design of littoral fish assemblages using a beach seine net and recommends night sampling for a representative assessment or sampling during both diel periods for an accurate assessment.

PAPER III

Diel horizontal migration of fish between littoral and pelagial in a model reservoir

Říha M., Vašek M., Prchalová M., Mrkvička T., Jůza T. Čech M., Draštík V., Muška M., Kratochvíl M., Peterka J., Tušer M., Seďa J., Bláha M, Kubečka J. (2012) Diel horizontal migration of fish between littoral and pelagial in a model reservoir. (Unpublished manuscript)

The study investigated diel migration of fish between the littoral and pelagial zones of the Římov Reservoir (Czech Republic, Central Europe). The aim of the study was to describe fish assemblage diel changes between those zones and determine the potential influence of predator presence and shifting feeding habitats on this behavior in certain species and age groups.

The sampling was performed during the summer season of three consecutive years in 2009-2011. The complex multigear approach was chosen. The diel change in the unstructured littoral was measured using sampling by beach seine net, while diel change between unstructured and structured littoral was gauged by electrofishing. The pelagial was sampled using a trawl net in both diel periods and purse seine net at night. In addition, analysis of the diets maintained by several dominant species captured in both zones and diel periods was performed. The sampling of zooplankton (Cladocerans) was also undertaken in both zones and different littoral habitats.

Our complex sampling revealed distinctive fish-distribution diel changes in the reservoir, which were highly species and age-dependent. Subadults and small species mostly avoided the pelagial during the day and occupied this habitat at night. The association of those fish with different littoral habitats was species dependent, but a surprisingly higher density of small fish of various species was found in the littoral also at night. Adults of bream (*Abramis brama*), roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*) preferred the pelagic zone during day and partly migrated to the littoral at night. Potential fish predators were present in both zones and periods, and their high occurrence was most likely responsible for small fish avoidance of the poorly structured littoral during day. On the other hand, we assumed that a higher availability of food in the littoral was probably the most important driver of the high occurrence of subadults and nocturnal species in that zone at night rather than higher predation pressure in the pelagial. The reasons for night inshore migration for adults of the aforementioned species is not obvious, but the homogenization of their distribution or resting in the littoral most likely could explain such behavior more that predation risk or a switch of feeding habitat.

PAPER IV

Dependence of beach seine net efficiency on net length and diel period

Říha M., Kubečka J., Mrkvička T., Prchalová M., Čech M., Draštík V., Frouzová J., Hladík M., Hohausová E., Jarolím O., Jůza T., Kratochvíl M., Peterka J., Tušer M.,Vašek M. (2008). Dependence of beach seine net efficiency on net length and diel period. *Aquatic Living Resources*, **21**, 411-418.

The aim of this study was to quantify the efficiency of different lengths of beach seine nets for each diel period. Only fish older than young-of-the-year were considered. Nets of 10, 20 and 50 m length ("in-nets") were tested in an enclosed area framed by a 200 m long net (block net). The net efficiency estimate was calculated as the ratio of fish catches with the in-net and block net divided by the ratio of their respective areas.

The net efficiency estimate was significantly different between day and night catches. At night, the efficiency estimate of nets depended on the size of the fish. The efficiency estimate of a 10 m long net decreased significantly in reverse correlation with fish size. A similar trend was found when using a 20 m long net. The efficiency estimate of a 50 m long net was independent of fish size. The variance in efficiency estimate between samples with a given net length was high, but decreased with longer nets. Of five species tested, only the efficiency estimate for catching bream (*Abramis brama*) increased significantly with the length of net. The biomass and abundance of larger fish was generally higher at night, although especially short nets exhibited a spuriously high efficiency estimate during the day, probably due to the concentrating (chasing) effect of the hauling ropes. We therefore recommend the use of a 50 m long net, since its nighttime efficiency estimate was about 0.9 in terms of both sampling abundance and biomass. A model relating the efficiency estimate and net length was developed with the data acquired.

PAPER V

The size selectivity of the main body of a sampling pelagic pair trawl in freshwater reservoirs during the night

Říha M., Jůza T., Prchalová M., Mrkvička T., Čech M., Draštík V., Muška M., Kratochvíl M., Peterka J., Tušer M., Vašek M., Kubečka J. (2012) The size selectivity of the main body of a sampling pelagic pair trawl in freshwater reservoirs during the night. *Fisheries Research*, **127-128**, 56-60.

The aim of this study was to test the selectivity of a trawl main body, especially for small fish, during night sampling. The tested trawl had a mesh size of 80/40/20 mm in the main body, a mouth opening of approximately 100 m^2, and a length of 48 m and was originally designed for sampling vendace, *Coregonus albula,* L. Trawl selectivity was determined by comparing the catch using this gear with that from a purse seine net (mesh size 6-10 mm, length 120 m, height 12 m) at the same sites and time. The size distributions of the total catch and densities of three dominant species (common bream, *Abramis brama* (L.), roach, *Rutilus rutilus* (L.) and bleak, *Alburnus alburnus* (L.)) were compared between the two types of gear. Densities of these species were divided into size groups before comparison: i) small fish (60 – 120 mm, standard length SL); ii) middle-sized fish (125 – 180 mm SL); and iii) large fish (>180 mm SL), which included only roach and bream. Significant differences in the fish density between the trawl and purse seine nets were found. Generally, the densities in all size categories of bleak and small roach were underestimated in trawl catches, whereas the densities of middle- and large-sized bream were underestimated in the purse seine catch. We conclude that both types of gear are size selective – small fish escaped through the mesh of the trawl main

body, whereas larger bream were able to escape from the purse seine before closing. The trawl with the given mesh sizes is recommended for quantitative sampling only of fish larger than 180 mm (SL) under low light-intensity conditions.

PAPER VI

Long-term development of fish populations in the Římov Reservoir

Říha M., Kubečka J., Vašek M., Seďa J., Mrkvička T., Prchalová M., Matěna J., Hladík M., Čech M., Draštík V., Frouzová J., Hohausová E., Jarolím O., Jůza T., Kratochvíl M., Peterka J.,Tušer M. (2009) Long-term development of fish populations in the Římov Reservoir. *Fisheries Management and Ecology*, **16**, 121-129

The inshore fish community of the Římov Reservoir in the Czech Republic was evaluated over 21 years using shore seining at night. The development of the fish community was divided into two separate phases: a highly dynamic and unstable phase dominated by perch, *Perca fluviatilis* L., was replaced by an extremely stable cyprinidphase dominated by roach, *Rutilus rutilus* (L.), and bream, *Abramis brama* (L.). The abundance of both these species oscillated during the cyprinid phase, but with decreasing amplitude. The proportion of piscivorous fish species such as asp, *Aspius aspius* (L.), pike, *Esox lucius* L., and pikeperch, *Sander lucioperca* (L.), increased slightly with time but remained low. The biomass of large Cladocera was negatively correlated with fish biomass only during the perch phase. The Shannon-Weaver index of diversity increased during the fish community succession, mainly because of greater evenness among the species.

GENERAL DISCUSSION, CONCLUSIONS AND PERSPECTIVES

Profound changes in fish distribution were found throughout the seasons as well as between day and night in a reservoir environment.

The significant spawning migration between the reservoir and the inflowing river was confirmed for many fish species. The intensity of this behavior varied according their boundary to the tributary spawning ground. The importance of the tributary spawning grounds was revealed for the whole reservoir populations of white bream, chub, bleak and asp. Such findings well corroborated with previous studies by Hladík and Kubečka (2003, 2004). The post-spawning dispersal of these species was most likely shaped by their feeding ground requirements. This behavior in generalists, species that spawn in the tributary and the reservoir main body, showed that low dispersal was the case for bream and perch but erratic for roach. This finding was very much in agreement with those described by previous studies in other water bodies (Poddubny 1971; Collette *et al.* 1977; Johnson 1978; L'Abée-Lund and Vollestad 1985), and confirmed that the post-spawning dispersals of these species are driven by species-specific behavioral patterns.

The previous studies of Milan Hladík (Hladík and Kubečka 2003, 2004) as well as Paper I were focused only on the distribution pattern of tributary spawning fish. Information about the inter-season migration of species that spawn predominantly in the reservoir body are still lacking. Subsequent research will focus on common species

such as bream and perch, which spawn in the whole reservoir. This research should expand our knowledge about their spawning site fidelity and inter-season movements (Říha *et al.* in prep.).

Diel changes of fish distribution are a common phenomenon in Czech canyon-shaped reservoirs. Paper II documented the night migration of fish to the shallow, unstructured littoral zone; such pattern was stable for some species or age groups of species (ruffe, pikeperch, bream and large roach) whereas small specimens of roach and perch exhibit plasticity in this behavioral trait. Paper III thoroughly described the diel migration of fish in the Římov Reservoir. Results from Paper III clearly demonstrate that distribution is highly dependent on the species and age of fish. Generally, adult fish (bream, roach and bleak) preferred the pelagial during the day whereas the day distribution of small fish was more complex and highly species dependent. The assumed day habitat of small specimens were at the edge of the littoral and pelagial zones (bleak of age 1+), structured littoral (small perch and roach of age 1+) and deeper benthic habitats (roach of age 1+, bream of age 1+ and ruffe). However, future research is needed to determine the day distribution of subadults and small species. Specimens of all sizes of the above-mentioned species occupied both zones at night, although the importance of the littoral/pelagial zones highly varied among species. The importance of the pelagial (and thus relative insignificance of the littoral) seems to be the case for bleak (all size categories) and adult bream, while there is a similar importance of both zones for bream of age 1+. A high importance of the littoral (low importance of the pelagial) for roach (all size categories) and large perch was also observed, while the occurrence only in the littoral (no individuals captured in the pelagial) for small perch and ruffe was reported. These findings very well demonstrated the ontogenetic change in littoral/pelagial preference in many species, which correspond to previous studies (Lammens *et al.* 1992; Duncan and Kubečka, 1995; Imbrock *et al.* 1996).

The high prevalence of predators was most likely responsible for fish avoidance of the poorly structured littoral during the day, whereas higher diet availability was probably the most important driver of high occurrence of subadults and nocturnal species in that zone at night. The reasons for the night inshore migration of bream, roach and bleak adults are not so obvious. Most likely, the homogenization of their distribution or resting in the littoral could explain such behavior rather more than predation risk or a switch of feeding habitats.

A full understanding of factors driving fish horizontal migrations needs futher study at least for some species. Such a notion is supported by the behaviour and distribution of age 1+ roach. Paper II documented the variability of roach distribution among different reservoirs. The density of age 1+ roach considerably increased in littoral catches of three of the four tested reservoirs at night, including that in Římov. Age 1+ roach highly prefered the littoral and occured only rarely in the pelagial of the Římov Reservoir at night. The Želivka Reservoir was the exception, where similar day and night densities of age 1+ roach were found in littoral catches (Paper II) and pelagic trawling in the reservoir revealed that age 1+ roach was one of the most dominant components of the pelagic community at night (Paper V). Obviously, the pelagic zone was very important habitat for age 1+ roach in the Želivka Reservoir in contrats to the Římov Reservoir.

However, the reasons for such a difference are not obvious. The reservoirs share some features, such as reservoir morphology, fish species composition, vertical and horizontal gradients of fish spatial distribution plus density of piscivorous predators (Prchalová et al. 2008a, 2009a, Vašek et al. 2012). On the other hand, they differ in one important characteristic. Submerged macrophytes are present only in the Želivka Reservoir. Littoral macrophytes provide shelter for small size fish against predation during the day (Lewin *et al.* 2004) but may also reduce small fish feeding rates because resources are limited in these shelters (Gliwitz and Jachner 1992; Gliwicz *et al.* 2006). Therefore migration to the more profitable pelagial could be proposed as the main driver of small roach preference of that zone at night (Gliwitz and Jachner 1992; Gliwicz *et al.* 2006). However, the difference between the littoral and pelagial prey availability has not been studied in the reservoir so far and further research is needed to understand the factors behind a diel habit switch of age of 1+ roach in the reservoir.

The active sampling methods used in presented thesis (beach seining, trawling and purse seining) gave very robust results and helped us to determine the diel changes of fish communities between pelagic and littoral zones. However, the understanding their selectivity was necessary for choosing the appropriate gear design and interpretation of the obtained results. The selectivity and efficiency of the beach seine net (Paper IV) and pelagic trawl (Rakowitz *et al.* 2012) differed between day and night. Fish exhibit higher avoidance reactions during the day than at night when either type of gear was used, and their reactions were species as well as size dependent (Paper IV, V; Rakowitz *et al.* 2012). The results of Paper IV showed that these avoidance reactions could be reduced by extending the net length of the beach seine during both diel periods. The same benefit can be expected for the trawl net as well (Jůza and Kubečka 2007), especially during the day when avoidance reactions are considerably high (Rakowitz *et al.* 2012). However, the actual testing of trawl dimension enhancement is complicated and difficult to achieve due to the drastically increased requirements of boat towing power in the confines of a canyon-shaped reservoir. Paper V highlighted the importance of trawl net design for night quantitative sampling in terms of the size selectivity of its main body mesh. The results of this paper showed that direct penetration by fish through main body of the trawl can obviously produce a substantial bias in the density and size-distribution estimates of small fish. Therefore, the trawl for night quantitative sampling must be must carefully take this finding into account.

In addition to a detailed description of fish ecology, it is currently required to have a representative sampling of fish community in a certain habitat, especially to conform to the Water Framework Directive or other sampling standards (CEN 2008; Bonard *et al.* 2009). Representative sampling gives information about fish quantity as well as the species and size structures occurring in certain waterbodies. Thus, the determination of the diel period in which fish occur in certain habitats and the influence of this phenomenon on sampling gears is of high importance. Our results demonstrate that night is a more appropriate diel period for representative sampling in the littoral and pelagial of reservoirs. Two reasons support this statement. The first is the reduction of avoidance reactions, which was demonstrated for the beach seine net (Paper IV), trawl (Rakowitz *et al.* 2012) and was documented also for electrofishing, another frequently

used active sampling method (Reynolds 1996; Pierce et al. 2001). The second reason is the higher occurrence of fish in easily accessible habitats such as the shallow littoral or pelagial epilimnion at night (Paper II, III). Obviously, day sampling of these habitats alone would not be representative at all, because it would detect only a proportion of species and size/age classes that really occupy these habitats, and also underestimate fish densities due to higher fish avoidance (Paper II, III; Rakowitz *et al.* 2012).

Despite recent progress in the understanding of active sampling gears selectivity, further research on this topic is necessary to approach getting the true picture of a fish community (Kubečka *et al.* 2009). As we pointed out in Paper V, certain questions remain regarding the trawl main body mesh size selectivity. For example, the mesh size in the trawl main body should be reduced for night quantitative sampling of smaller fish, but the appropriate mesh size has not been determined yet. Moreover, the species-specific reactions to the net indicated in Paper V must be further investigated. Clarifying these issues will highly improve the assessment of the pelagic community in future. Another important topic requiring our attention is the intercalibration of different sampling gears and conversion their results. Recently, gillnets are one the most important sampling gears (Kubečka *et al.* 2009), but the conversion of gillnet catch per unit effort (CPUE) to that of active gears has not been successfully achieved yet (Kubečka *et al.* 2009). As a next step, we would like to focus our attention to trawl development for night sampling as well as intercalibration of sampling gears. The first step has been already done in the case of beach seine net and gillnet intercalibration (Prchalová *et al.* 2008b; 2009b). A study dealing with a comparison of gillnet and trawl data will follow in the near future (Říha et al. in prep.). Moreover, a new approach that combines trawl and hydroacoustic data through apportionment methods (Yule *et al.* 2009) will be tested because this method seems to be very promising and could considerably refine assessment of pelagic fish stock.

Temporal patterns of variation in fish species composition are one of the most important topics for fish stock assessment of lake and reservoir fisheries, with long-term studies of reservoir fish communities and yields being necessary to establish a baseline for management recommendations (Jutagate *et al.* 2012). Paper VI described the long-term development of fish populations in the Římov Reservoir. The study period includes the end of the perch dominance phase and subsequent succession of the cyprinid dominance phase. During the cyprinid phase, roach and bream had similar abundance dynamics resembling dampened oscillations of decreased amplitude. Such a pattern leads to stabilization of fish numbers and their population structure in the reservoir. The data processed in Paper VI were obtained by night beach seining. It has not been known until recently whether beach seining is able to detect changes of population densities and structures. The results of Paper III answered this question and proved night beach seining as a robust tool for sampling of the whole fish community and detection of population changes of dominant species. Further research on the long-term development of the fish community will focus on species interactions, changes of fish growth rate and tracing history of certain year classes from their beginning. Such a study could help us to determine the main population drivers because they remain poorly understood (Paper VI; Jůza *et al.* 2009).

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PAPER I

POST-SPAWNING DISPERSAL OF TRIBUTARY SPAWNING FISH SPECIES TO A RESERVOIR SYSTEM

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Key words: migration, distribution, reproduction, feeding ground

ABSTRACT

This study investigated the post-spawning dispersal of seven species occurring in a tributary of the Římov Reservoir during the years 2000-2004. Fish were captured during spawning migration to the tributary, marked and released. The subsequent distribution of marked fish was followed in the reservoir and tributary during three successive periods 1) early summer, 2) late summer and 3) the next spawning season. Species were divided into two groups – obligatory tributary spawners (white bream *Blicca bjoerkna*, chub *Squalius cephalus*, bleak *Alburnus alburnus* and asp *Aspius aspius*) that did so predominantly in the tributary of the reservoir and generalists (bream *Abramis brama*, perch *Perca fluviatilis* and roach *Rutilus rutilus*) that usually spawned in the tributary as well as at different sites within the reservoir main body. We hypothesized that obligatory tributary spawners would distribute across the reservoir after spawning according to their species-specific preferences for certain feeding grounds. We expected a relatively low or erratic post-spawning dispersal for spawning generalists. The results of the study revealed that the post-spawning dispersal of obligatory tributary spawners is consistent with our hypothesis and they most likely dispersed according to their feeding ground requirements. The post-spawning dispersal of generalists revealed that the assumed low dispersal was relevant for bream and perch while erratic dispersal was observed in roach.

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PAPER II

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The influence of diel period on fish assemblage in the unstructured littoral of reservoirs

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Abstract Diel changes in littoral fish assemblage were studied in four reservoirs in the Czech Republic (Central Europe). The sampling was performed by beach seining in an unstructured littoral zone. Perch, *Perca fluviatilis* L., roach, *Rutilus rutilus* (L.), bream, *Abramis brama* (L.), carp, *Cyprinus carpio* L., ruffe, *Gymnocephalus cernua* (L.), pikeperch, *Sander lucioperca* (L.), eel, *Anguilla anguilla* (L.) and *A. brama* × *R. rutilus* hybrids exhibited higher densities at night. Only bleak, *Alburnus alburnus* (L.) exhibited higher densities during the day. The number of species was higher in night hauls, and mean body size of roach and bleak was also higher at night. Diel changes in fish densities resulted in the change in species composition between day and night. The study has implication for the sampling design to assess littoral fish assemblages using beach seine netting and recommends night sampling for a representative assessment or sampling during both diel periods for a robust assessment.

KEYWORDS: beach seining, diel migration, Římov Reservoir, sampling, species composition.

Introduction

The littoral zones of lakes, rivers and reservoirs are the most complex and productive parts of these water bodies (Winfield 2004). The majority of fish species use the littoral zone during at least a part of their ontogenetic development (Duncan & Kubečka 1995; Winfield 2004). Thus, representative assessment of littoral zone fish assemblages is desirable for ecological studies, such as spatial fish distribution, habitat preference or evaluation of the ecological status of the water body.

Beach seining is an effective method for capturing fish in the unstructured littoral zone of lakes and rivers. It is widely used for littoral zone sampling in marine and freshwater environments (Pierce *et al.* 1990; Cowx *et al.* 2001; Johnson *et al.* 2007). This method combines many advantages over other sampling methods, such as simplicity of use, low selectivity during the day and night, a large sampled area and

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PAPER III

DIEL HORIZONTAL MIGRATION OF FISH BETWEEN LITTORAL AND PELAGIAL IN A MODEL RESERVOIR

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Keywords: distribution, diel dynamic, quantitative sampling, predation, feeding rate

ABSTRACT

The study investigated diel migration of fish between the littoral and pelagial zones of the Římov Reservoir (Czech Republic, Central Europe). The aim of the study was to describe fish assemblage diel changes between those zones and determine the potential influence of predator presence and shifting feeding habitats on this behavior in certain species and age groups.

The sampling was performed during the summer season of three consecutive years in 2009-2011. The complex multigear approach was chosen. The diel change in the unstructured littoral was measured using sampling by beach seine net, while diel change between unstructured and structured littoral was gauged by electrofishing. The pelagial was sampled using a trawl net in both diel periods and purse seine net at night. In addition, analysis of the diets maintained by several dominant species captured in both zones and diel periods was performed. The sampling of zooplankton (Cladocerans) was also undertaken in both zones and different littoral habitats.

Our complex sampling revealed distinctive fish-distribution diel changes in the reservoir, which were highly species and age-dependent. Subadults and small species mostly avoided the pelagial during the day and occupied this habitat at night. The association of those fish with different littoral habitats was species dependent, but a surprisingly higher density of small fish of various species was found in the littoral also at night. Adults of bream (*Abramis brama*), roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*) preferred the pelagic zone during day and partly migrated to the littoral at night. Potential fish predators were present in both zones and periods, and their high occurrence was most likely responsible for small fish avoidance of the poorly structured littoral during day. On the other hand, we assumed that a higher availability of food in the littoral was probably the most important driver of the high occurrence of subadults and nocturnal species in that zone at night rather than higher predation pressure in the pelagial. The reasons for night inshore migration for adults of the aforementioned species is not obvious, but the homogenization of their distribution or resting in the littoral most likely could explain such behavior more that predation risk or a switch of feeding habitat.

INTRODUCTION

Diel horizontal migration between the littoral and pelagic zones is a well documented phenomenon (e.g. Bohl 1980; Gliwicz and Jachner 1992; Brabrand and Faafeng 1993; Copp and Jurajda 1999; Wolter and Freyhof 2004; Romare *et al.* 2003). Studies dealing with diel habitat shift predominantly focus on juvenile or small zooplanktivorous fish (eg. Bohl 1980; Gliwicz and Jachner 1992; Romare *et al.* 2003; Lewin *et al.* 2004; Hölker *et al.* 2007) in which migration is driven by resource availability and use plus predators avoidance (Bohl 1980; Gliwicz *et al.* 2006). Generally, small fish are associated with submerged macrophytes or woody structures in the littoral during day (Jacobsen and Berg 1998; Jacobsen and Perrow 1998; Lewin *et al.* 2004; Gliwicz *et al.* 2006). Day shelters reduce predation pressure to small fish, but may also reduce small fish feeding rates due to their having limited resources (Gliwitz and Jachner 1992; Gliwicz *et al.* 2006). The predator-prey interaction is light dependent, such that upon a decrease in light intensity, effect of structures to predation risk is reduced (Cerri 1983) and small fish migrate to the pelagic zone where zooplankton prey is more abundant (often referred to as night offshore migration; Bohl 1980; Romare *et al.* 2003; Gliwicz *et al.* 2006).

Contrary to this broadly accepted pattern, the opposite migration, when fish move to the littoral zone at night, has also been documented and dubbed night inshore migration (NIM). Such behavior was described particularly for subadult and adult fish in rivers (Kubečka and Duncan 1998; Wolter and Freyhof 2004; Eros *et al.* 2008), some lakes (Schulz and Berg 1987; Zamora and Moreno-Amich 2002; Jacobsen *et al.* 2004) and reservoirs (Kubečka 1993; Vehanen *et al.* 2005; Říha et al. 2011). The reason for such migration has been poorly understood so far and several different explanations were proposed. Controversially, several authors assumed predator avoidance to be an important driving force for NIM. They explained NIM as avoidance of nocturnal offshore predators (Coop and Jurajda 1993; Jacobsen *et al.* 2004). Other explanations given for NIM are the changing of feeding habitat or activity. The former was observed for example undertaken by the common bream (*Abramis brama*) in Lake Constance,

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PAPER IV

Aquatic Living Resources

Dependence of beach seine net efficiency on net length and diel period

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Abstract – The aim of this study was to quantify the efficiency of different lengths of beach seine nets for each diel period in freshwater reservoirs. Only fish older than young-of-the-year were considered. Nets of 10, 20 and 50 m length ("in-nets") were tested in an enclosed area framed by a 200 m long net (block net). The net efficiency estimate was calculated as the ratio of fish catches with the in-net and block net divided by the ratio of their respective areas. The net efficiency estimate was significantly different between day and night catches. At night, the efficiency estimate of nets depended on the size of the fish. The efficiency estimate of a 10 m long net decreased significantly in reverse correlation with fish size. A similar trend was found when using a 20 m long net. The efficiency estimate of a 50 m long net was independent of fish size. The variance in efficiency estimate between samples with a given net length was high, but decreased with longer nets. Of five species tested, only the efficiency estimate for catching bream (*Abramis brama*) increased significantly with the length of net. The biomass and abundance of larger fish was generally higher at night, although especially short nets exhibited a spuriously high efficiency estimate during the day, probably due to the concentrating (chasing) effect of the hauling ropes. We therefore recommend the use of a 50 m long net, since its nighttime efficiency estimate was about 0.9 in terms of both sampling abundance and biomass. A model relating the efficiency estimate and net length was developed with the data acquired.

Key words: Beach seine net / Net length / Efficiency estimate / Size selectivity / Freshwater fish / European reservoir

Résumé – L'efficacité des sennes de plage dépend de la longueur du filet et de la période du jour et de la nuit. L'objective de cette étude est de quantifier l'efficacité de sennes de plage de différentes longueurs et à différentes périodes de la journée (nuit-jour). Seuls les poissons âgés d'un an et plus sont considérés ici. Des filets de 10, 20 et 50 m de longueurs sont testés dans un enclos fermés par un filet-barrage de 200 m de long. L'estimation de l'efficacité du filet testé est calculée par le rapport des captures de poissons dans le filet sur celles du filet-barrage divisé par le rapport de leur surface respective. L'estimation de l'efficacité du filet est significativement différente entre les captures effectuées de jour et celles de la nuit. De nuit, l'estimation de l'efficacité dépend de la taille du poisson. L'efficacité d'un filet de 10 ou de 20 m de long est inversement corrélée avec la taille des poissons. L'efficacité d'un filet de 50 m est indépendante de la taille des poissons. La variance de l'estimation de l'efficacité entre les échantillons est grande pour un filet de longueur donnée mais la variance décroît avec des filets plus longs. Des 5 espèces testées, seules les captures de brèmes (*Abramis brama*) augmentent significativement avec la longueur du filet. La biomasse et l'abondance de poissons de grandes tailles sont généralement plus élevées la nuit, bien que des filets courts présentent faussement une grande efficacité de jour, probablement due à la concentration des cordages de halage. Ainsi, nous recommandons l'usage de senne de 50 m de long, l'efficacité de captures nocturnes est estimée à 0,9 en terme d'abondance et de biomasse. Un modèle reliant l'estimation de l'efficacité et la longueur du filet est développé à partir des données acquises.

1 Introduction

Beach seining is a very effective method for sampling the assemblage of littoral fish, as it has several advantages over other techniques (Pierce et al. 1990; Prchalová et al. 2008a). Although seine nets have been used by fishermen since antiquity, and for scientific and management purposes for more than a century, most researchers still do not know the relationship

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PAPER V

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Short communication

The size selectivity of the main body of a sampling pelagic pair trawl in freshwater reservoirs during the night

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ABSTRACT

The aim of this study was to test the selectivity of a trawl main body, especially for small fish, during night sampling. The tested trawl had a mesh size of 80/40/20 mm in the main body, a mouth opening of approximately 100 m^2, and a length of 48 m and was originally designed for sampling vendace, *Coregonus albula* L. Trawl selectivity was determined by comparing the catch using this gear with that from a purse seine net (mesh size 6–10 mm, length 120 m, height 12 m) at the same sites and time. The size distributions of the total catch and densities of three dominant species (common bream, *Abramis brama* (L.), roach, *Rutilus rutilus* (L.) and bleak, *Alburnus alburnus* (L.)) were compared between the two types of gear. Densities of these species were divided into size groups before comparison: (i) small fish (60–120 mm, standard length SL); (ii) middle-sized fish (125–180 mm SL); and (iii) large fish (>180 mm SL), which included only roach and bream. Significant differences in the fish density between the trawl and purse seine nets were found. Generally, the densities in all size categories of bleak and small roach were underestimated in trawl catches, whereas the densities of middle- and large-sized bream were underestimated in the purse seine catch. We conclude that both types of gear are size selective – small fish escaped through the mesh of the trawl main body, whereas larger bream were able to escape from the purse seine before closing. The trawl with the given mesh sizes is recommended for quantitative sampling only of fish larger than 180 mm (SL) under low light-intensity conditions.

1. Introduction

Trawls designed for fish sampling rarely consist of only one mesh size. Generally, meshes of larger size are in the part of the trawl body near the opening, and smaller mesh sizes are used toward the rear part of the trawl body (Gabriel et al., 2005). The trawl netting promotes the herding effect in fish (Glass et al., 1995). The fish rarely swim through the mesh located in the part of the trawl body near the opening (Gabriel et al., 2005). The smaller mesh at the rear part of the trawl serves as a mechanical sieve to prevent fish of similar and larger girth from escaping. The use of a large mesh provides advantages such as the reduction of required engine power and lower fuel consumption (Gabriel et al., 2005).

Nighttime is considered preferable to daytime for quantitative fish sampling in the open-water habitats of large inland bodies of freshwater (Kubečka et al., 2012; McKenna, 2008). Informative quantitative sampling should ideally represent all species and sizes according to their actual proportions and numbers in the sampled habitat. However, there are indications that the herding effect caused by netting is reduced under low light intensities (Glass and Wardle, 1989; Suuronen et al., 1997). This reduction of the herding effect could cause small fish to pass through the large mesh present in the main trawl body, thus causing the underestimation of their proportions and densities in a trawl catch during night sampling.

The aim of this study was to describe the size selectivity of a trawl main body during fish sampling at night. We used an indirect method to compare the size distributions and fish densities obtained by different types of gear applied simultaneously. Trawling and purse seining were conducted simultaneously to demonstrate the size selectivity of the gear. The trawl used in the study was originally designed for sampling small fish, specifically vendace (*Coregonus albula* L.) (Kühlmann, 1997; Schmidt et al., 2007). The purse seine was found appropriate for the quantitative

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PAPER VI

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Long-term development of fish populations in the Římov Reservoir

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Abstract The inshore fish community of the Římov Reservoir in the Czech Republic was evaluated over 21 years using shore seining at night. The development of the fish community was divided into two separate phases: a highly dynamic and unstable phase dominated by perch, *Perca fluviatilis* L., was replaced by an extremely stable cyprinid phase dominated by roach, *Rutilus rutilus* (L.), and bream, *Abramis brama* (L.). The abundance of both these species oscillated during the cyprinid phase, but with decreasing amplitude. The proportion of piscivorous fish species such as asp, *Aspius aspius* (L.), pike, *Esox lucius* L., and pikeperch, *Sander lucioperca* (L.), increased slightly with time but remained low. The biomass of large Cladocera was negatively correlated with fish biomass only

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