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The importance of various types of littoral habitats for fish in reservoirs

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Anotace

Cílem práce bylo zjistit habitatové preference běžných druhů našich ryb na třech typech litorálních habitatů (pláže, sutě, pařeziny). Shromážděný materiál pochází ze čtyř českých nádrží. Tato studie ukázala, že se jednotlivé habitaty liší jak biomasou a početností ryb, tak druhovým složením. Ačkoliv měly nádrže odlišné druhové složení, trendy v biomase, početnosti a rybích preferencích zůstávaly stejné.

Annotation

The aim of this study was to evaluate fish habitat preferences in three various types of littoral habitats (beaches, rubble slopes and stumps). Data originated from four Czech canyon-shaped reservoirs. This study showed that habitats differed in biomass and abundance of fish as well as in species compositions. Patterns in biomass, abundance and species preferences were the same even under different community structures of sampled reservoirs.

Tato práce je psána ve formě manuskriptu a bude odeslána do časopisu Ecology of Freshwater Fish, nakladatelství Wiley Blackwell, Oxford, UK.

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Obsah

Úvodní komentář

Tato práce je zaměřena na význam různých litorálních habitatů pro společenstvo ryb přehradních nádrží. Litorál představuje výrazně heterogenní prostředí (Brosse et al. 2001, 2007; Kratochvíl et al. 2012). Ačkoliv má litorál v kaňonovitých nádržích díky strmým břehům minoritní zastoupení (Čech et al. 2005; Kratochvíl et al. 2012), jeho přítomnost je nesmírně důležitá pro společenstvo ryb - během jarního tření je na tento habitat vázán reprodukční cyklus mnoha druhů ryb (Hladík & Kubečka 2003). Ve vegetační sezóně je zde početnost a biomasa ryb nejvyšší ze všech habitatů nádrže (Prchalová et al. 2008, 2009). Motivace pro výskyt ryb v litorálu jsou různé a liší se druh od druhu: noční refugium před predátory (Bohl 1980; Kubečka 1993), urychlení růstu důsledkem vyšší teploty vody (Gardner et al. 1998), vyhledávání potravy (Diehl 1988; Kobler et al. 2008; Říha et al. v tisku) a odpočinek v průběhu noci (Imbrock et al. 1996; Říha et al. v tisku).

Navzdory významu litorálu pro ryby v nádržích víme stále velmi málo o preferencích ryb pro jednotlivé typy habitatů. Jen málo studií se zabývalo vymezením habitatů v rámci litorálu a studiem rybích společenstev na nich žijících (Eklöv 1997; Fischer & Eckmann 1997). Další studie zabývající se habitatovými preferencemi byly zaměřeny buď jen na omezený výběr druhů v experimentálních podmínkách (Diehl 1988; Rendón et al. 2003; Dieterich et al. 2004), nebo na studii mělkých habitatů převážně tohoročních ryb (Brosse et al. 2001, 2002, 2007; Kratochvíl et al. 2012). Rozsáhlý průzkum litorálních habitatových preferencí celých společenstev v rozsahu několika nádrží však doposud chyběl.

Standardní průzkum rybích společenstev nádrží bývá mnohdy založen na tenatních úlovcích (Vašek et al. 2004; Prchalová et al. 2008, 2009). Lov tenaty je pasivní metoda, jejíž úlovek odráží aktivitu ryb v daném habitatu (Holmgren 1999; Olin & Malinen 2003). Lov se standardizuje pomocí evropské směrnice (European Standard Document EN 14 757). Tenata se instalují do vody dvě až tři hodiny před setměním a vytahují se s úlovkem dvě až tři hodiny po úsvitu, čímž jsou pokryty vrcholy rybí aktivity po dobu expozice tenat (Prchalová et al. 2010). V rámci minimalizace poškození tenat bývá situován průzkum litorálu na pláže, kde je nejmenší šance na zachycení tenat o podvodní překážku a následného poškození při vytahování. Na kaňonovitých nádržích přitom pláže nepřevládají mezi litorálními habitaty; v kaňonovitých nádržích bývají dominantním habitatem sutě (Kratochvíl et al. 2012). Třetím významným habitatem jsou pařeziny po vykácených lesích. Cílem této práce bylo zjistit, zda se společenstva ryb liší mezi těmito třemi typy habitatů vzhledem k biomase a početnosti ryb, případně zda se liší i společenstva ryb obývajících tyto habitaty. Design sběru a zpracování dat dále umožnil popsat preference jednotlivých habitatů na druhové úrovni.

Průzkum probíhal v letech 2010 a 2011; na přehradní nádrži Římov probíhal po oba roky, na nádržích Vír, Vranov a Žlutice probíhal v roce 2011. Na podélné ose nádrží se stanovily čtyři lokality (tři v případě Žlutic s malou vzdáleností mezi přítokem a hrází); v rámci každé z nich jsme nalezli nejméně dva ze tří habitatů vybraných pro tento průzkum. Habitat pařeziny byl dostupný v potřebném rozsahu pouze na přehradní nádrži Římov – na ostatních nádržích probíhal tedy pouze průzkum pláží a sutí. Minimální délka vhodného habitatu byla dána délkou jednoho panelu tenat, tj. 30 metrů; na každé lokalitě jsme nainstalovali tři panely tenat na každý habitat.

Habitaty se mezi sebou lišily v biomase i početnosti tohoročních ryb i ryb starších. Největší početnosti a biomasy dosahoval habitat pláže, pařeziny měla tyto hodnoty nižší a nejnižší biomasa a početnost ryb byla na sutích. Druhová data byla analyzována RDA analýzou v programu Canoco. Výsledky ukázaly, že habitaty s mírným sklonem dna (pláže a pařeziny) preferoval z ryb jednoletých a starších cejn velký *Abramis brama*, cejnek malý *Abramis bjoerkna* a plotice obecná *Rutilus rutilus*. Sutě vyznačující se velkým sklonem dna preferoval okoun říční *Perca fluviatilis*, ježdík obecný *Gymnocephalus cernuus*, bolen dravý *Aspius aspius* a štika obecná *Esox lucius*. Z tohoročních ryb preferoval pláže cejn, cejnek, ouklej obecná *Alburnus alburnus*, ježdík, a candát obecný *Sander lucioperca*. Jedinou tohoroční rybou preferující sutě byl okoun. Preference ryb na jednotlivých nádržích byly podobné celkovým preferencím ryb. Z výsledků vyplývá, že průzkum litorálního habitatu založený na úlovcích z pláží může být zavádějící pro obrázek rybího společenstva celé nádrže.

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Manuscript

The importance of various types of littoral habitats for fish in reservoirs

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Keywords: habitat preferences, gillnet, reservoir, structural complexity, slope steepness, community structure

Abstract

Fish preferences for different types of littoral habitats were studied in four Czech canyon-shaped reservoirs in years 2010 and 2011 by gillnet sampling. Three habitats – beaches, stumps and rubble slopes were defined and sampled along the longitudinal axis of reservoirs. Effects of habitat, locality and reservoir on fish community biomass, abundance and species structure were tested for juvenile and adult fish separately. Hierarchical ANOVA revealed that habitats differed significantly in fish biomass and abundance. Redundancy analysis revealed that all environmental variables had significant influence on community structure. Most variability in fish community structure was explained by reservoir, than by combination of habitat and slope steepness and locality had smallest influence on community. For both adult and juvenile fish, the most inhabited habitat was beaches; rubble slopes were the least inhabited. Among adults, bream *Abramis brama*, white bream *Abramis bjoerkna* and roach *Rutilus rutilu*s preferred beaches and stumps, whereas perch *Perca fluviatilis*, ruffe *Gymnocephalus cernuus*, asp *Aspius aspius* and pike *Esox lucius* preferred rubble slopes. Among juveniles, beaches were preferred by bream, white bream, bleak *Alburnus alburnus*, ruffe and pikeperch *Sander lucioperca*, whereas the only juvenile with preference to rubble slopes was perch. We showed distinct preferences of most common species and differences in utilization of various littoral habitats in general. These findings could improve gillnet sampling design and bring new insight into fish community assessment of whole reservoir.

Introduction

Littoral zone of reservoirs and lakes are fundamental for fish inhabitants (Kubečka 1993; Jennings et al. 1999; Winfield 2004; Järvalt et al. 2005; Hautala 2008). Reproductive success of most fish species is dependent on quality of littoral habitats within littoral zone (Kennedy & Fitzmaurice 1970; Kahl et al. 2008). Many young of the year fish utilize the littoral zone of reservoirs (Brosse et al. 2001, 2007; Vašek et al. 2006; Kratochvíl et al. 2012) to maximize growth and minimize predation pressure (Fernando & Holčík 1991; Gardner et al. 1998; Kahl et al. 2008). For reasons such as feeding, resting or searching refugee from predators (Kubečka 1993; Říha et al. submitted), adult fish utilize the littoral zone of reservoirs as well (Järvalt et al. 2005; Prchalová et al. 2008; 2009). Therefore the littoral zone is the most important habitat of the all available reservoir habitats (Fernando & Holčík 1991; Winfield 2004).

Littoral zone of the reservoir is scarcely uniform (Brosse et al. 2001, 2007; Kratochvíl et al. 2012) and as such, importance of littoral for fish may differ habitat from habitat. Many authors mention crucial role of littoral structural complexity for fish (Beauchamp et al. 1994; Imbrock et al. 1996; Jennings et al. 1999; Winfield 2004; Poulet et al. 2005). At least two distinct habitats are formed in typical canyon-shaped reservoir – rubble slopes and beaches (Kratochvíl et al. 2012). In respect with functions of reservoirs, the water level usually varies in time (Winfield 2004; Krolová et al. 2011). This fact together with freezing erosion during winter results in formation of these habitats. When the slope steepness is considerably high, rubble slopes are usually being developed in a few years after filling the reservoir. When the slope is mild, the substrate usually stays on the bottom or only fine particles are being washed out, which results in sandy or muddy beaches (Li et al. 2001; Krolová et al. 2011). Considering the fact that reservoirs were often filled in forested valleys, habitats densely embedded with stumps are not exception in younger reservoirs (Kratochvíl et al. 2012). However, stumps are secondarily missing in older reservoirs due to decomposition of roots. Submerged aquatic vegetation has great influence on distribution of fish in littoral (Diehl 1988; Rossier et al. 1996; Brosse et al. 2007). Unfortunately, the steep banks of canyon-reservoirs together with water level fluctuation prevent grow of large formations of submerged aquatic vegetation as well as eutrophication does (Winfield 2004). In the most of reservoirs their presence is usually restricted to tributaries, where quite constant water level is (Krolová et al. 2011). Rocks are the last common littoral habitat in reservoir (Kratochvíl et al. 2012). This habitat is usually scarce. The bottom is commonly below the depth threshold of littoral zone and that obstruct benthic gillnet sampling.

Only few studies targeted fish littoral habitat preferences in lentic waters of Europe (Eklöv 1997; Fischer & Eckmann 1997; Brosse et al. 1999, 2001, 2002, 2007), but the results usually described either one particular species or ontogenetic group only. Thus, here is a lack of knowledge about littoral habitat preferences, especially of adult fish community.

Reservoirs are inhabited mainly by generalist species (Fernando & Holčík 1991; Vašek et al. 2004; Freeman & Marcinek 2006; Loureiro-Crippa & Hahn 2006). These species are able to occupy various habitats within a river, lake or reservoir (Molls 1999; Aarts & Nienhuis 2003; Hladík et al. 2008). Abundance of these species in littoral is changing diurnally (Bohl 1980; Kubečka, 1993; Říha et al. 2011). This pattern usually results in higher abundance at night for adults. The aim of such behavior is not clear; some species are seeking refuge from predators (Kubečka, 1993; Říha et al. 2011), nocturnal species feed there and day-active species probably use littoral as resting habitat (Říha et al. submitted). The opposite pattern was found for young of the year cohorts (Bohl 1980; Jůza et al. 2009). Some habitat preferences of common species have been revealed mostly by laboratory experiments. Fine sediment or mud was favorable feeding ground for bream *Abramis brama,* roach *Rutilus rutilus,* juvenile tench *Tinca tinca* and ruffe *Gymnocephalus cernuus* (Diehl 1988; Rendón et al. 2003; Dieterich et al. 2004), whereas coarse substrate or structured habitat was favorable feeding environment for both juvenile and adult perch *Perca fluviatilis* and pike *Esox lucius* (Diehl 1988; Dieterich et al. 2004; Kobler et al. 2008).

The aim of this study was to describe pattern of fish distribution in different littoral habitats in reservoirs. Three habitats – beaches, rubble slopes and stumps were sampled using benthic gillnets in four canyon-shaped reservoirs. We expected that because of different characteristics of these three habitats, fish communities inhabiting them would be different as well as overall biomass and abundance. We anticipated that the preferences for different littoral habitats would be species-specific with possible grouping of higher taxonomical groups with similar ecological requirements.

Study areas

The research was conducted in four canyon-shaped Czech reservoirs: Římov, Vír, Vranov and Žlutice. Basic characteristics of these reservoirs are summed up in Table 1.

Methods

Gillnet sampling

The samplings were carried out in two consecutive years 2010 and 2011. During the first year the Římov Reservoir was chosen for pilot sampling of structured habitats. Once assumed as possible, other three reservoirs besides the Římov Reservoir were sampled in the year 2011. Late summer was chosen as the best time for extensive sampling of the reservoir fish community as juveniles of a majority of fish species are large enough to be sampled using gillnets and identified (Prchalová et al. 2009). Also no spawning or wintering migrations take place during this part of the year in Czech reservoirs (Hladík & Kubečka 2003).

Benthic gillnets (Pokorný-sítě, Brloh, Czech Republic) were used to sample littoral habitats. Benthic gillnets were constructed according to European Standard Document EN 14 757 (2005; 1.5 x 30 m height x length, 12 mesh sizes). Gillnets were set overnight (installed two hours before sunset and lifted the next day two hours after sunrise; Prchalová at al. 2010) at depths between 2 and 3 meters. The placement depth was measured by an acoustic depth gauge. Gillnets were set at four (three at the short Žlutice Reservoir) localities along the longitudinal axis of the reservoirs.

At each locality, two to three littoral habitats were sampled according habitat presence: beaches, rubble slopes, stumps; the slope steepness was measured on each habitat by inclinometer (Leica DISTO D5) with at least ten independent measurements on each habitat. Beaches were defined as gently sloped shore (9.9° ± 3.6°, mean steepness ± SD) with fine sediment on the bottom and without occurrence of any underwater structures. All rubble slopes were formed in steep-sloped parts of the bank (31.5° ± 4.4°). Average boulder size was 25 centimeters in diameter. Stumps were presented and sampled only in the Římov Reservoir, and were gently sloped (8.2° ± 0.3°) with fine substrate on the bottom. The maximum distance between different habitats sampled on the same locality was approximately one kilometer. Each habitat was sampled independently three times by setting benthic gillnets parallel to the shore.

All fish caught were measured to the nearest 0.5 cm standard length (SL) and weighted to the nearest 1 g. Juvenile fish were measured to nearest 0.1 cm standard length. Altogether, 7231 fish individuals with a total weight of 437 kg were caught during the study.

Term adult fish is there used for fish older than one year; younger fish are being referred as juvenile fish in the whole text. The threshold size separating juvenile and adult fish was set according to the length-frequency distribution supported by the scale reading for each species.

Data analysis

The results were expressed as the biomass per unit of effort (BPUE) and as number per unit effort (NPUE) of adult and juvenile fish (kg/number 1000 m^{-2} $night^{-1}$; 'biomass' or 'abundance' in the further text) separately and as a per cent share of particular species in the total biomass/abundance.

Hierarchical ANOVA was used for testing influence of littoral habitat on the adult fish biomass in the program Statistica (Statistica, Inc., StatSoft, Tusla, Oklahoma). Data of both biomass and abundance had lognormal distribution, so we transformed them into logarithmic scale before analysis. In the data analysis, the variable locality was nested in variable reservoir, influence of variables year and habitat was added without any effect. Post hoc Tukey HDS test was used to reveal differences among habitats.

Direct gradient redundancy analysis (RDA) was used to test effects of slope steepness, habitat, locality, reservoir and year of sampling on fish community structure using multivariate statistics (Canoco software, Biometris – Plant Research International, Wageningen, The Netherlands). Using per cent share in Canoco analysis was assumed to be better choice when describing differences in communities among habitats, localities and reservoirs. The length of gradient in the detrended correspondence analysis indicated, that we have to use linear method with Euclidean distances for comparing samples (Lepš & Šmilauer 2003). The environmental (explanatory) variables were: The quantitative variable - slope steepness and the qualitative dummy (i.e. 0 or 1) variables for the habitat (beach, rubble slopes and stumps), locality (1 - 4), reservoir (Římov, Vír, Vranov, Žlutice) and for year of sampling (2010 - 2011). Excluding the number of species, the data were log – transformed ($y'=\log_{10}(y+1)$) and centered by species. Scaling was focused on inter-species correlations, species scores were divided by the standard deviation and samples were standardized by norm. Statistical significances were analyzed by Monte Carlo permutation tests. The unrestricted type of permutation tests was performed with blocks defined by covariates to quantify the effect of a given environmental variable (the samples were permuted only within blocks and never across blocks; Lepš & Šmilauer 2003). We tested environmental variables habitat, locality and reservoir independently, to estimate their marginal effect. The not tested environmental variables were used as covariates, because we did not want to interpret them and simultaneously take their effect into account. The responses of dependent variables to individual environmental variables were fitted using general linear models (GLM; CanoDraw software, Petr Šmilauer, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic). Similar results in both RDA analyses and CanoDraw figures were obtained using pure abundance and biomass. The possibility, that some species could have actually same biomass/abundance in all habitats, but their per cent share could vary with respect to overall caught biomass in particular habitat, was therefore rejected.

Results

Differences between littoral habitats

The total biomass and abundance differed considerably between littoral habitats (Table 2, Fig. 1). The highest biomass and abundance were recorded on beaches. The rubble slopes provided markedly the lowest biomass and abundance estimates. This pattern of habitat differences was similar in adults and juveniles (Fig. 2). The biomass and abundance estimates recorded on individual habitat differed from each other in most cases in both adults and juveniles (Table 3). Exceptions were adult abundance in rubble slopes and stumps, and adult biomass and juvenile biomass and abundance in beach and stumps.

Species preferences

The community structure was significantly influenced by the habitat and the slope steepness (Table 4). Following species of the adult fish community preferred beaches together with stumps: bream, white bream *Abramis bjoerkna* and roach (Fig. 3). Juvenile bream and white bream preferred beaches as well together with juveniles of bleak *Alburnus alburnus*, ruffe and pikeperch *Sander lucioperca* (Fig. 4). There were no obvious preferences for stumps among juveniles. One basic characteristic had stumps and beaches in common – gentle slope steepness (the average steepness was 9.5°). The slope steepness explained considerable part of variability in community structure of adults and juveniles (7.5 and 7.3 %, respectively), as well as the habitat did (6.1 and 6.2 %, respectively; Table 4). Habitat as well as slope steepness described patterns in communities better together than alone and therefore, the interpretation of habitat fish preferences was more accurate while using both environmental variables (explained variability 12.0 and 11.2 % in adult and juvenile communities, respectively).

Rubble slopes were preferred by four species of the adult fish community: perch, ruffe, pike and asp *Aspius aspius* (Fig. 3). The only juvenile species with preference of rubble slopes was perch (Fig. 4).

Effect of reservoir and locality

The reservoir had substantial effect on community structure (Table 4). The reservoir explained 20.2 % of the variability in the community structure of adults and 22.8 % in the community structure of juveniles. The fish community of the Vranov Reservoir was dominated by bleak, white bream and bream, whereas roach was the main species in the Římov Reservoir. The community structure showed unusual high proportion of perch in the Vír Reservoir, and the Žlutice Reservoir was the only reservoir with high occurrence of European catfish *Silurus glanis* and tench (Fig 5).

We tested habitat preferences also within each reservoir separately. Although only the Římov Reservoir had large enough data to be significant ($F = 3.433$, $p = 0.045$; Vranov $F = 1.654$, $p = 0.38$; Vír $F = 1.380$, $p = 0.459$; Žlutice $F = 3.033$, $p = 0.263$), all ordination diagrams in CanoDraw showed very similar species preferences as demonstrated by the total model of all reservoirs together (Fig. 3 and 4).

The adult biomass on particular littoral habitat was not only function of the habitat, but also of position of locality on longitudinal axis of reservoir (Table 4). Majority of species were more abundant in tributary parts of reservoirs, namely ruffe, bream, white bream, tench and pike (Fig. 6). The different pattern was revealed for perch, European catfish and asp. Perch and European catfish were most abundant in the dam part of reservoirs. Asp tended to occupy middle part of reservoirs. The locality preferences were rather unclear for juveniles, which could be caused by generally lower catches of juveniles than adults.

Discussion

We proved species-specific preferences for various littoral habitats during this study. Habitats beach, stumps and rubble slopes differed in relative abundance and biomass of fish as well as in species composition. Parameters of fish communities differed also along longitudinal axis of reservoirs and among reservoirs.

Generally, more is known about habitat preferences of juvenile fish than about these of adults (Fischer & Eckmann 1997; Brosse et al. 1999, 2001, 2002, 2007). Studies of Brosse and colleagues are targeted on shallow littoral with and without vegetation up to one meter depth. In these studies, the most common species were roach, rudd and perch, which occupied habitat with macrophytes predominantly. However, shallow habitats defined in this study were different from our definition of littoral habitats and besides; there is a lack of macrophytes in most reservoirs due to steep-sloped banks (Winfield 2004; Krolová et al. 2011). According to Jennings et al. (1999), rubble slopes, which occurrence is associated with steep-sloped banks, could enhance structural complexity of littoral and therefore could substitute in some extend macrophytes. Similar habitats as in our study were sampled by Fischer & Eckmann (1997) in Lake Constance. Juveniles of perch and ruffe occupied macrophytes, whereas adults were recorded on pebbles and boulders in the greatest abundance.

Cyprinids becoming more abundant in higher trophic state of water bodies and along the trophic gradient towards the tributary part – bream, white bream and roach (Olin et al. 2002; Vašek et al. 2004; Prchalová et al. 2008, 2009) also grouped predominantly together among habitats; they preferred gently sloped habitats – beaches and stumps. These species are known to prosper in turbid waters, where they can feed effectively on zooplankton (Persson et al. 1987, 1991). Cyprinids thrive also from reduced predation pressure, which is lower in case of more trophic waters (Persson et al. 1991; Říha et al. 2009). In our study, mentioned habitats showed also lesser abundance of predators in comparison with rubble slopes.

Species optimize their ecological niche in the environment; therefore, they try both to maximize growth (Gardner et al. 1998; Krause et al. 1998) and minimize predation pressure (Skov et al. 2008). Good indicator of ingesting rate is swimming speed (Priyadarshana et al. 2001). Diehl (1988) studied foraging of bream, roach and perch. Roach and bream were superior foragers on beaches, whereas in structured habitat their swimming speed and therefore also ingesting rate was lowered considerably. However, perch swimming speed was not affected by habitat structural complexity (Winfield 1986; Diehl et al. 1988; Jacobsen & Berg 1998). Perch as a visually oriented predator (Bergman 1988; Diehl 1988) is superior forager in structured habitats (Diehl et al. 1988), which are known to be inhabited more intensively by invertebrates (Webster et al. 1998). Perch was found to inhabit steeply-sloped structured habitats in Lake Constance and Degersjön (Imbrock et al. 1996; Eklőv 1997), which was in accordance with our study. We sampled two structured habitats – gently sloped stumps, and rubble slopes, which had both steepness and structural complexity - from which perch preferred only rubble slopes.

Beside perch, other three species preferred rubble slopes to other habitats – asp, ruffe and pike. Asp predominantly inhabits open water of reservoirs (Prchalová et al. 2008, 2009). Rubble slopes resemble to open water to large extend and open water starts just few meters from the shore due to steep banks. Thus, asp could utilize both open water conditions and higher concentration of prey in near shore habitats.

Ruffe, known to feed mainly on benthic invertebrates (Bergman & Greenberg 1994; Říha et al. submitted) at night (Schleuter & Eckmann 2006), was found to be better competitor on fine substrate than on coarse substrate (Dieterich et al. 2004). However, in our study ruffe clearly preferred rubble slopes and was less abundant in habitats with fine substrate. The potential explanation could be in predation pressure, which factor was not included in laboratory experiments of Dieterich et al. (2004). Structural complexity reduces foraging efficiency of predators (Eklöv 1992; Eklöv & Diehl 1994) and ruffe could avoid predators by finding shelter between boulders on rubble slopes.

Pike is generally known to inhabit structured littoral habitats (Cook & Bergersen 1988; Casselman & Lewis 1996; Kobler et al. 2008). We expected pike to inhabit predominantly stumps, but we found out that pike catches were the highest in rubble slopes. However, especially in the case of pike the gillnet catches might report on fish activity more than on real fish density (Holmgren 1999; Olin & Malinen 2003). Kobler et al. (2008) found out, that basically two major strategies of pike exist. First strategy is to occupy small home range in littoral parts of water bodies, whereas the second one is moving in considerable larger home range in the open water (Kobler et al. 2008). As was mentioned above, rubble slopes resemble to open water habitats and it is possible that rubble slopes were occupied besides littoral pike with small home range also by more actively swimming pelagic pike.

Recently, effect of placement of the sampling locality along the longitudinal gradient of water bodies was studied thoroughly with respect to fish biomass and community structure (Siler et al., 1986; Vašek et al., 2004, 2006; Draštík et al. 2008; Prchalová et al. 2008, 2009). Now it is evident that fish species are not distributed regularly within reservoirs. As well as trophic level, phytoplankton (Hejzlar & Vyhnálek 1998) and zooplankton abundance (Seďa & Devetter 2000) decrease along the longitudinal axis of a reservoir from tributary towards the dam part, the same overall pattern was found for fish biomass (Siler et al., 1986; Vašek et al., 2004, 2006; Prchalová et al. 2008, 2009). Fish preferring higher trophic conditions like bream, white bream, ruffe, pike and tench are more abundant in these productive tributary parts of reservoirs with higher food availability (Vašek et al., 2004, 2006; Prchalová et al. 2008). This pattern was seen also in our study. The opposite pattern was revealed for perch, which as visually oriented predator (Persson et al. 1988; Bergman 1991) prefer waters with mezotrophic conditions at the dam parts of reservoirs (Vašek et al. 2004; Prchalová et al. 2008).

Although fish communities differed markedly between sampled reservoirs and factor reservoir explained the biggest part of variability in community structure, species preferences were found constant across reservoirs. Also, sampled reservoirs differed in their trophy state with the least trophic Vír Reservoir with perch being very common and other reservoirs reaching higher trophy with community dominated by cyprinids. But even under conditions of different trophy and community structure, fish followed described patterns of species-specific preferences for individual littoral habitats.

Commonly, standard assessment of fish community in lakes and reservoirs is based on shore seining (Pierce et al. 1990; Kubečka 1993; Říha et al. 2011) thus targeting fish community of beaches only. Other method of littoral sampling is electrofishing, which is restricted by water conductivity (Hill & Willis 2004) and water transparency (Fischer & Eckmann 1997; Brosse et al. 2002, 2007). From this point of view, gillnets offer good alternative gear to already mentioned techniques. From advantages connected with gillnetting we can name sampling various habitats not limited by depth and structural complexity. However, gillnets are passive gear able to capture fish, which are actively moving only (Finstad et al. 2000). The rate of fish movement is influenced mainly by water temperature (Linløkken and Haugen, 2006) and peaks of fish activity (Cook & Bergersen 1988; Jacobsen et al. 2004; Prchalová et al. 2010). Also, in habitats with fallen trees, many stumps or rocks, gillnets can be severely damaged. Accordingly, littoral gillnetting is usually performed also on the beaches. Nevertheless, our study demonstrated that sampling only one type of several littoral habitats (and on only one locality within the reservoir) can bias fish community assessment markedly when these findings are extrapolated to whole-reservoir community.

Utilization of space is not easy to study in aquatic environment of lentic waters. To reveal causes of found patterns in niche segregation among species, many biotic and abiotic factors are needed to be monitored. Although we gained better knowledge about fish habitat preferences, further investigation can lead in precise assessment of niche segregation. Suitable experiment under controlled conditions of predation pressure, food availability and structural complexity could provide better insight in littoral fish communities. There is also place for using telemetry, since there is possibility of occurrence of some movements between these distinct littoral habitats.

To conclude, littoral habitats of sampled reservoirs differed considerably both in fish biomass and community structure. Common species were found to have habitat preferences that are stable in various reservoirs. Competition for food and avoidance of predators were hypothesized to be driving force for found patterns.

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Tables

Table 1. Basic characteristics of reservoirs Římov, Vír, Vranov and Žlutice.

Env. variables	Římov	Vír	Vranov	Žlutice
Length (km)	12.0	9.3	30.0	4.6
Surface (ha)	210	223	761	167
Average depth (m)	16.0	25.0	17.4	9.0
Maximum depth (m)	45	65	47	27
Retention time (days)	100	180	160	145
Elevation (m a. s. l.)	417	464	353	511
GPS location of the dam	48°50′ N, 14°29′ E	49°33′ N, 16°18′ E	48°54′ N, 15°49′ E	50°05′ N, 13°09′ E
Year of filling	1978	1958	1933	1968

Sources: http://www.pmo.cz/, http://www.pvl.cz/

Table 2. Differences between habitats in biomass and abundance of adult and juvenile fish tested in nested design ANOVA.

Adult fish	**DF**	**F statistics**	**P level**
biomass	2	28.457	< 0.001
abundance	2	26.636	< 0.001
Juvenile fish			
biomass	2	10.049	< 0.001
abundance	2	12.263	< 0.001

Table 3. Comparison of habitats using post hoc Tukey tests of biomass and abundance in adult and juvenile communities.

Adult fish	**Beach x Rubble slopes**	**Stumps x Rubble slopes**	**Beach x Stumps**
biomass	< 0.001	< 0.001	NS
abundance	< 0.001	NS	0.010
Juvenile fish			
biomass	< 0.001	0.002	NS
abundance	< 0.001	0.010	NS

Table 4. Response of both adult and juvenile fish to environmental variables (habitat, slope steepness, habitat + slope steepness, locality and reservoir) in terms of per cent of explained variability of the community structure.

Env. variables	**Explained variability (%)**	**F statistics**	**P level**
Adult fish			
Habitat	6.1	3.480	0.009
Slope steepness	7.5	5.026	< 0.001
Habitat & Slope steepness	12.0	6.251	< 0.001
Locality	8.9	3.034	0.023
Reservoir	20.2	7.328	< 0.001
Juvenile fish			
Habitat	6.2	4.041	0.030
Slope steepness	7.3	6.711	< 0.001
Habitat & Slope steepness	11.2	8.843	< 0.001
Locality	5.3	3.565	0.034
Reservoir	22.8	13.477	< 0.001

Figures and captions

Fig. 1. Means and 95 % confidence intervals of log transformed adult biomass caught in three different habitats (beach, stumps, rubble slopes) in all reservoirs together.

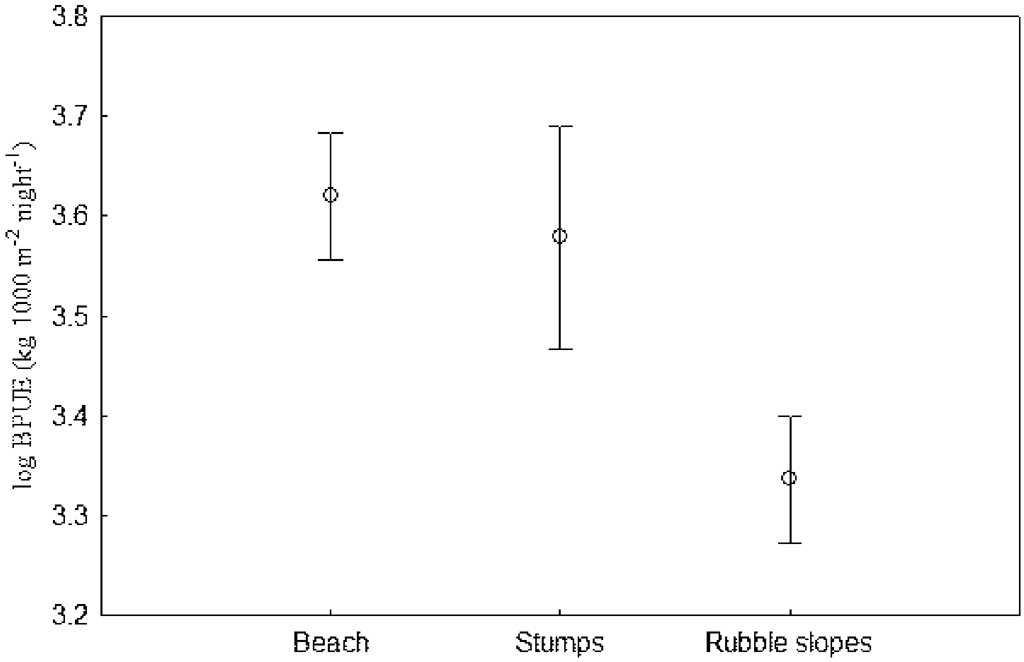

Fig. 2. Means and 95 % standard deviations of log transformed juvenile abundance caught in three different habitats (beach, stumps, rubble slopes) in all reservoirs together.

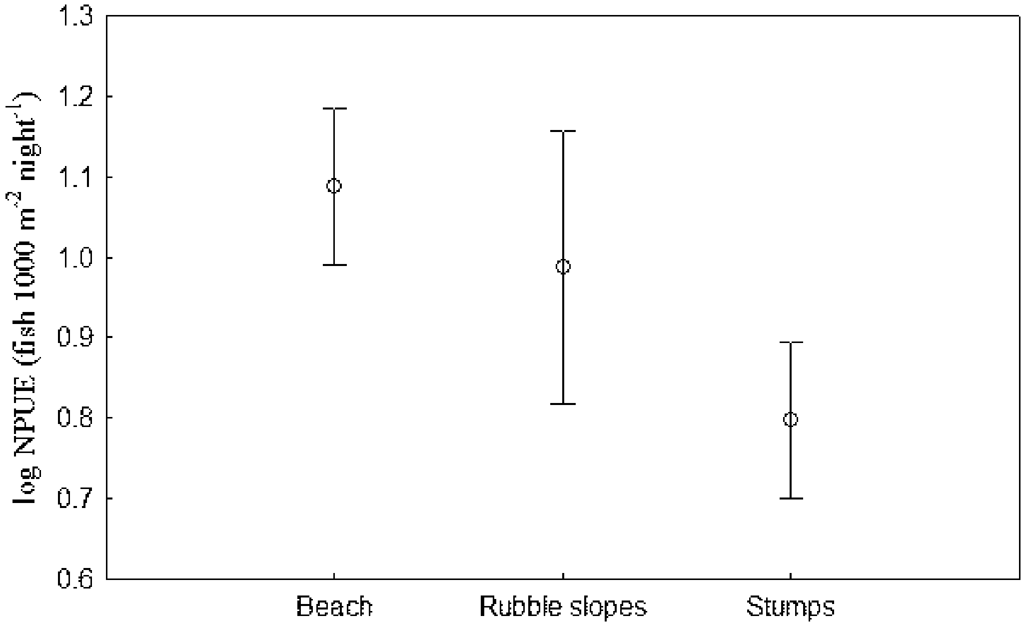

Fig.3. Biplot of the adult fish preferences for three littoral habitats and slope steepness. Black triangles represent three sampled habitats. Percentage of adult biomass increases in direction of the arrow of a given species. Rate of correlation is shown by an angle between species arrows and habitat triangles. *Abramis bj.* white bream, *Abramis br.* bream

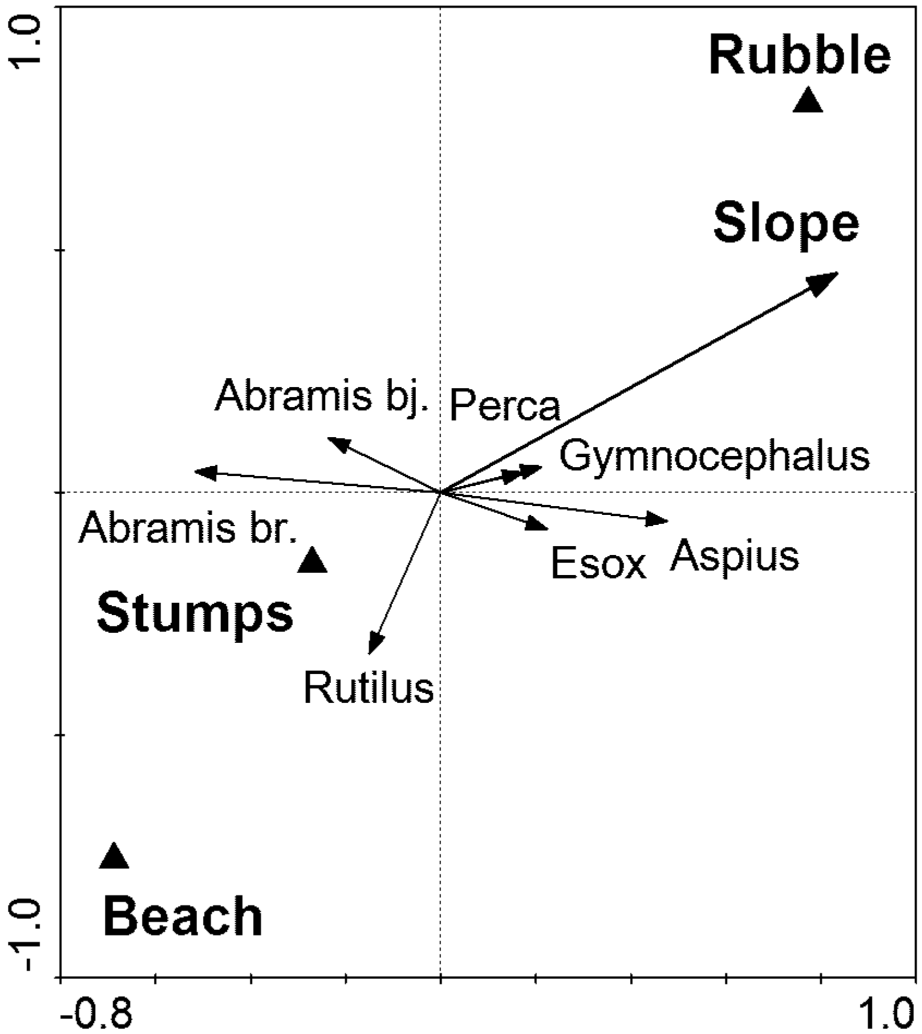

Fig.4. Biplot of the juvenile fish abundance for three sampled littoral habitats and slope steepness. See legend of Fig. 3 for biplot explanation.

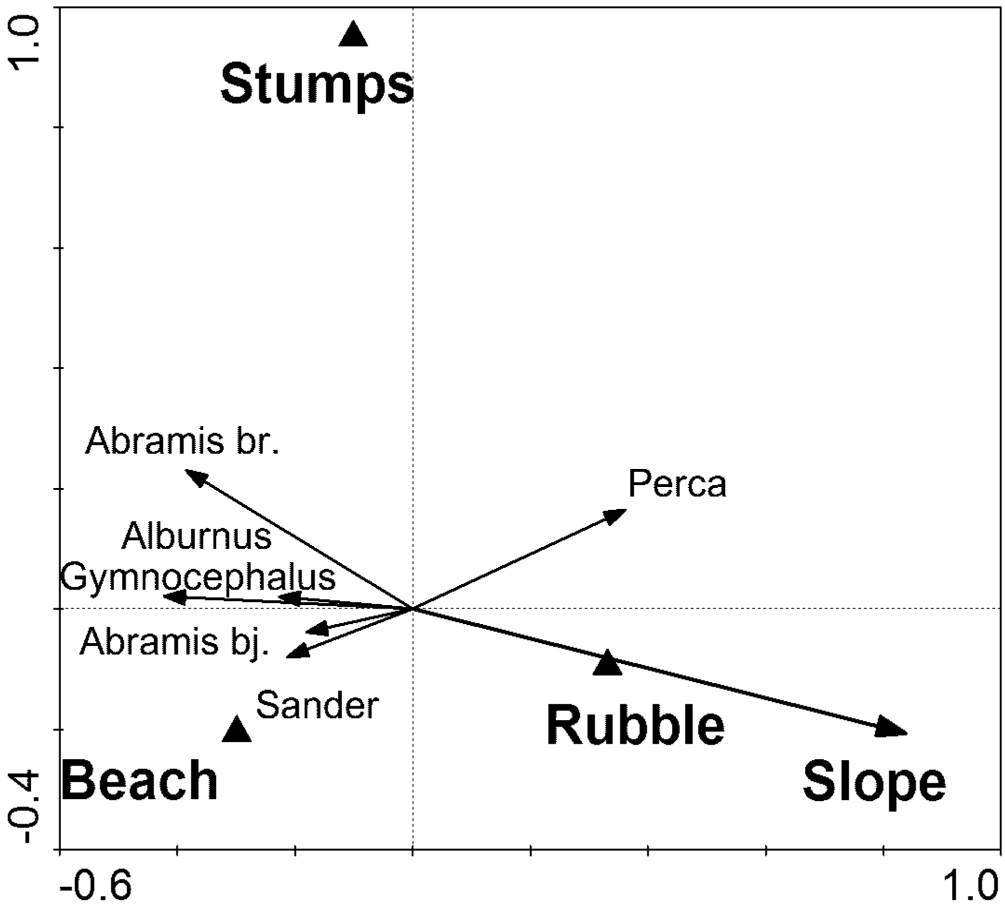

Fig.5. Biplot of differences among adult fish biomass in sampled reservoirs. See legend of Fig. 3 for biplot explanation.

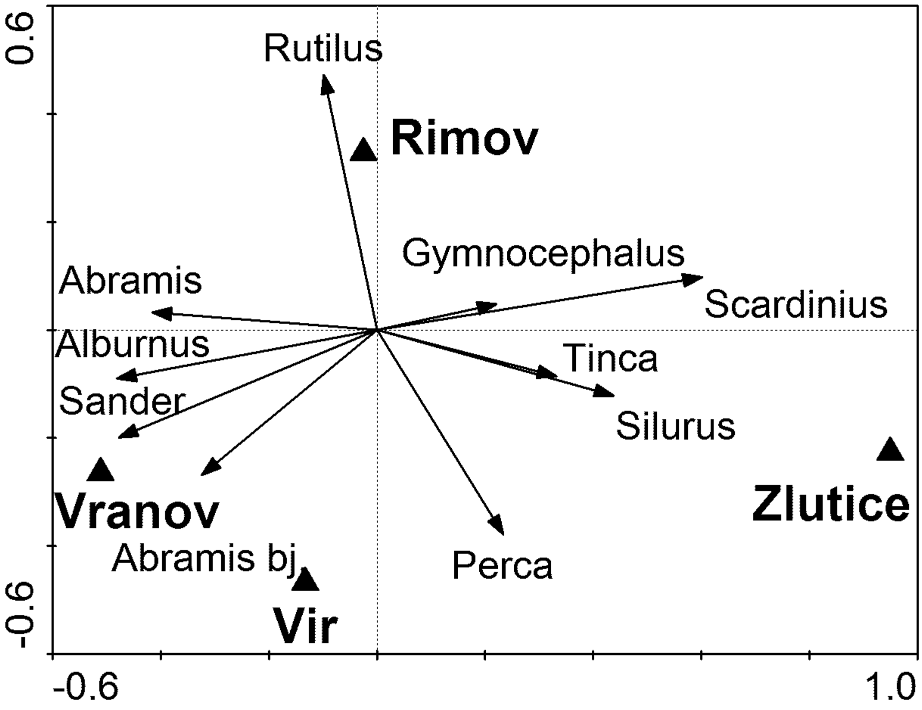

Fig.6. Biplot of the adult fish biomass of four localities in reservoirs (dam part, middle part, upper part, tributary part). See legend of Fig. 3 for biplot explanation.