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Flood duration determines the reproduction success of fish in artificial oxbows in a floodplain of a potamal river

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Abstract – Fish reproduction was studied in six man-made water bodies (borrow pits) adjacent to the channelised Dyje River (Danube basin) over five seasons. Terrestrial vegetation provided spawning and nursery habitats when inundated by raised water levels in the borrow pits (hereafter referred to as ‘floods’). The diversity of 0+ fish and the density of 0+ cyprinids (mainly *Abramis bjoerkna, Scardinius erythrophthalmus* and *Rutilus rutilus*) in June–October were positively correlated with flood duration in previous months. The density of 0+ P*erca fluviatilis* was independent of the flood duration. The density of spawners and predators did not influence the diversity of 0+ fish and the density of 0+ cyprinids. Receding flood and associated lack of shelters resulted in decreasing density of 0+ cyprinids, numbers sometimes decreasing to zero. Prolonged floods facilitated the survival of 0+ fish and resulted in high 1+ cyprinid density in the following season. Specific hydromorphological conditions (e.g., the presence of shallow littoral zone or flooded vegetation) are necessary to enable successful spawning and provide shelters for 0+ fish in artificial water bodies.

Key words: young-of-the-year; flood pulse concept; regression; recruitment; reproductive guilds

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Introduction

Floodplains provide spawning and nursery habitats in both tropical (e.g., Welcomme 1979; Agostinho et al. 2004) and temperate (e.g., Copp 1989; Sparks et al. 1998; King et al. 2003) river systems. Floodplain water bodies play an essential role in these systems. Both parapotamic backwaters (connected permanently with the main channel) and plesiopotamic oxbows (connected with the main channel only during inundation periods) are important nursery areas (e.g., Sheaffer & Nickum 1986; Scott & Nielsen 1989; Grift et al. 2001; Penczak et al. 2003), primarily for fish that spawn on vegetation (i.e., phytophilic species *sensu* Balon 1975).

The channelisation and diking of floodplain rivers has decreased the physical diversity of these river systems, with much of the surrounding flood plain and water bodies separated from the main channel and its flood (Neumann et al. 1996; Cowx & Welcomme 1998). Loss of lateral connectivity adversely affects the reproduction of many (primarily phytophilic) fishes (Nunn et al. 2007b). Artificial floodplain water bodies are suggested as convenient substitute biotopes, performing the same ecological role as natural water bodies that have been lost following river regulation (e.g., Staas & Neumann 1994; Nunn et al. 2007b).

Floodplain borrow pits excavated during dike construction could serve as such surrogates for natural plesiopotamic oxbows (Sabo & Kelso 1991). These permanent plesiopotamic water bodies in the floodplain may play a crucial role for 0+ fish survival after flood waters have receded (Halyk & Balon 1983). Former research has demonstrated the importance of borrow pits for the presence (Halačka et al. 1998) and reproduction (Bartošová et al. 2001) of phytophilic and phyto-lithophilic fish. However, fish reproduction can be significantly restricted in some borrow pits that

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lack shelters and shallow littoral zone (Jurajda et al. 2004; Ryšavá-Nováková et al. 2009). Flooded terrestrial vegetation seems to be particularly important for the reproductive success at these sites (Jurajda et al. 2004). The degree to which the flood regime and other mechanisms affect fish assemblage dynamics is still unknown at these sites. Deeper knowledge of these mechanisms is necessary for the proper assessment of importance of borrow pits.

Here, we evaluated the importance of several factors supposed to influence fish reproduction in borrow pits in the floodplain of a Dyje River (Czech Republic, Danube basin). We considered factors that were reported to influence 0+ fish assemblages in rivers and natural floodplains: flood regime (flood duration, flood timing, flood coincidence with high water temperatures; e.g., King et al. 2003; Schramm & Eggleton 2006), physical characteristics of water bodies (Sabo & Kelso 1991; Tales & Berrebi 2007) and density of spawners and predators (e.g., Copp 1989; Bailly et al. 2008).

The main aim of the study was to evaluate the importance of the flood regime (mainly flood duration) and the influence of site physical characteristics on 0+ fish density and diversity. Flood at the studied sites was important mainly because flooded terrestrial vegetation provided spawning substrate for phytophilic and phyto-lithophilic fish and shelters for 0+ fish, in contrast to habitat conditions within the borrow pits. Therefore, we hypothesised that the density and diversity of 0+ fishes from June to October and the density and diversity of 1+ fishes the following year (recruitment effect) would be positively correlated with flood duration and the number of spawners and negatively correlated with the number of predators.

Material and methods

Study area

Study sites were situated in the lowest section of the floodplain of the River Dyje in the Czech Republic (0.0–10.0 river km; Fig. 1). Most water bodies available to fish as nursery areas were lost after channelisation of the River Dyje during the 1970s, and natural floods in the study area were eliminated because of the construction of reservoirs 45 km upstream of the study sites during the 1980s. All six borrow pits under study were created in 1983–1985 when flood protective dikes were built from excavated floodplain material. The sites are 320–930 m away from the river bank, five of them in the active floodplain (in front of protective dikes) and one (Špicmaus) in the passive floodplain (behind the protective dikes) (Fig. 1; Table 1). All sites (0.2–1.4 ha) have a regular shape (square, rectangular or round), steep banks and a sand-gravel bottom with a thin layer of organic mud and mean depth of 2 m. In these permanent water bodies, the depth never fell below 1 m, even in the driest periods. Aquatic vegetation was almost absent from the borrow pits.

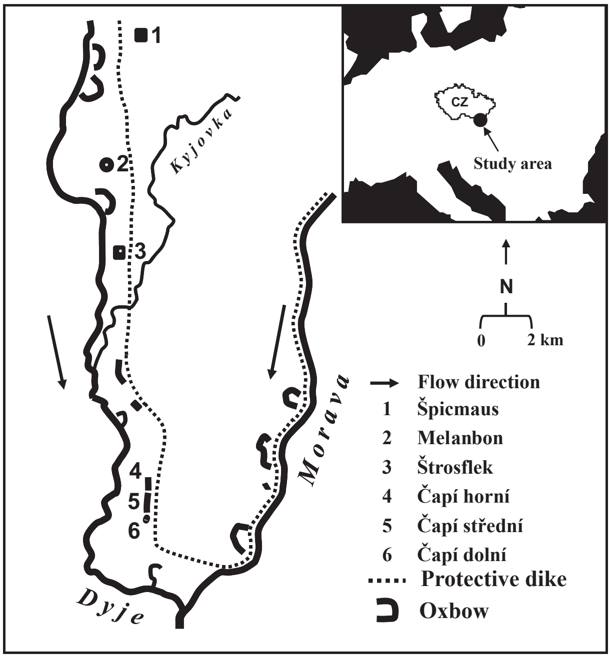

Fig. 1. Map of the study area with sampling sites indicated. CZ indicates the Czech Republic.

During the investigation period, connection of the five borrow pits in the active floodplain with the main channel occurred very rarely when the Dyje discharge exceeded 130 $m^3 \cdot s^{-1}$ (Lusk et al. 2004). Such connection with the main channel occurred briefly three times during the 5 years of study: in August 2002 (connected for 8 days, mean river temperature 21.7 °C) and at the end of March 2004 and 2006 (connected for 8 and 12 days, mean river temperature 7.6 and 8 °C, respectively). No surface water connections with the main channel occurred at the site situated in the passive floodplain (Špicmaus). The water level in the borrow pits corresponded with the discharge in the adjacent Dyje River, because water could permeate through the gravel subsoil. Therefore, whether surface connection with the main channel occurred or not, rising water levels in the borrow pits inundated a strip of adjacent meadows (hereafter referred as 'flood' for these sites), several metres wide. The flood occurred usually in spring (March/April) and persisted for a variable period of time (until April/until October). The brief intensive overspill of the river in August 2002 and the associated rise in water level in borrow pits inundated adjacent meadows until the October sampling period.

Table 1. Physical characteristics and fish assemblage parameters of the studied sites. Range (min–max) is shown for flood duration during the whole season (i.e., until October samplings), number of 0+ species in October (0+ S), density of 0+ C-Phyt fish in October [0+ fish catch per unit effort (CPUE)], density of non-0+ (mostly 2+ and older) C-Phyt fish able to spawn (spawners CPUE), density of non-0+ fish able to predate 0+ fish (predators CPUE) and mean density of 0+ fish able to predate 0+ fish (0+ predators CPUE).

Site	Čapí dolní	Čapí střední	Čapí horní	Melanbon	Špicmaus	Štrosflek
Physical characteristics						
Latitute coordinates – N	48°37′39″	48°37′47″	48°37′58″	48°40′32″	48°42′00″	48°39′50″
Longitude coordinates – E	16°55′59″	16°56′01″	16°56′03″	16°55′28″	16°55′48″	16°55′39″
Area (ha)	0.3	1.4	0.65	1.4	1.2	1.2
Maximal depth (m)	2.8	3.2	2.3	3	3	2.7
Shoreline length (m)	400	1100	670	499	373	469
Distance from river (m)	670	650	650	400	930	320
Floodplain	Active	Active	Active	Active	Passive	Active
Flood duration (days)	47–171	25–171	23–171	6–146	0–131	0–116
Fish assemblage parameters						
0+ S	1–13	0–15	0–12	1–12	1–9	0–11
0+ CPUE (inds·m^{-1})	0–3.69	0–3.74	0–3.82	0–3.43	0–2.19	0–3.07
Spawners CPUE (inds per 100 m^2)	13–26	25–61	31–103	1–2	9–14	10–12
Predators CPUE (inds per 100 m^2)	2–13	1–3	1–4	4–18	1–21	1–11
0+ predators CPUE (inds·m^{-1})	0.03–1.55	0.03–1.33	0.03–0.82	0.05–0.90	0.05–4.10	0–3.34

Data collection

For 5 years (2001–2004 and 2006), water level and temperature were measured approximately every 14 days from May to October. Estimates of water level and temperature for intervening days were obtained by interpolation. The accuracy of such estimates was checked and confirmed using values derived from daily measured water level and temperature in the adjacent Dyje River, published by the Morava River Authority (http://www.pmo.cz/portal/sap/cz). Thus, we were able to estimate on which days, the borrow pit was or was not flooded and on which days, the water temperature reached the threshold necessary for spawning for all species at the site (16 °C; Baruš & Oliva 1995). Consequently, we estimated the number of flooded days having a temperature ≥16 °C, subsequently referred to as 'flood duration'.

Non-0+ (1 year and older) fish were sampled once a year in October 2001–2004 using a beach seine (40 m length, 10 mm mesh size) at 2–12 locations (according to site size) in each borrow pit (Table 2). The area covered by each seine was estimated, and non-0+ fish density was expressed as number of fish per hectare. Fish were identified to species, measured to the nearest 1 mm (standard length, SL) and released back into the borrow pit from which they were taken.

The 0+ fish were sampled in June, July, August and October 2001–2004 and 2006 (Table 2). A small beach seine (5 m long, 1 mm mesh size) was primarily used for 0+ fish sampling. Two larger beach seines (10 m long, 1 mm mesh size and 15 m long, 4 mm mesh size) were used in July–October in response to possible movement of older 0+ fish to deeper water (Table 2). The number of hauls conducted with each seine net in a particular month did not differ among years and was similar among the sites. Data for semi-quantitative comparisons (number of 0+ specimens per 1 m seine) were treated as catch per unit effort (CPUE). The 0+ juvenile fish were euthanized with anaesthetics (clove oil), preserved in 4% formaldehyde and identified and measured to the nearest 1 mm (SL) in the laboratory. Fishes were classified according to the reproductive guild as suggested by Balon (1975).

Data analysis

Length–frequency distributions (combined with literature comparisons, Baruš & Oliva 1995) were used to separate 0+, 1+ and ≥2+ age groups of fish in seine samples. The reproductive potential of most of the

Table 2. Sampling schedule and nets used for sampling of fish assemblages at the six sites during 2001–2006. For each sampling, the table presents the number of sites sampled in individual year (2001–2006) and number hauls conducted by each type of seine net. Age – targeted age group of fish sampled.

		Sampling year					Seine net length			
Age	Month	2001	2002	2003	2004	2006	5 m	10 m	15 m	40 m
0+	June	6	6	6	6	6	8–12	0	0	0
0+	July	6	6	6	6	6	4–8	2–6	0	0
0+	August	6	6	6	6	6	4–8	0	2–6	0
0+	October	6	5†	6	6	6	4–8	0	2–6	0
Non-0+	October	6	4‡	6	6	0	0	0	0	2–12

†Missing site: Melanbon.
‡Missing sites: Melanbon, Štrosflek.

sampled 1+ fish was questionable. We therefore primarily considered 2+ and older fish (depending on the size and species, according to the literature sources; Baruš & Oliva 1995) as spawners in this study. Length–frequency distributions and literature comparisons (Pinder 2001) were also used to identify newly hatched fish, referring to individuals that are small (<15–20 mm SL, depending on the species) and that belong to the same or lower size group as did the smallest individuals of the species in the previous month.

Separate analyses were conducted for the most abundant cyprinid species: phytophilic rudd *Scardinius erythrophthalmus*, white bream *Abramis bjoerkna* and Prussian carp *Carassius gibelio*, and phyto-lithophilic roach *Rutilus rutilus* and bream *Abramis brama*. No 0+ species occurred regularly at all sites in all years, and therefore these five species were pooled together to strengthen the analyses, hereafter referred as the 'C-Phyt' group. Separate analyses were also conducted for ostracophilic bitterling *Rhodeus amarus* (Cyprinidae) and phyto-lithophilic perch *Perca fluviatilis* (Percidae). Dunn-Šidák corrections of significance levels were used to decrease the probability of committing a type I error (Sokal & Rohlf 1995) in multiple testing (critical *P*-value for eight repeats = 0.0064).

Varying flood regime, habitat conditions and fish assemblages created unique environment for fish reproduction in every year at each site. Therefore, we considered the samples from each site in each year as independent (see also Ondračková et al. 2004). The density of 0+ fish was log-transformed (ln[x + 1]) to reach normality and comply with requirements of the tests. Multiple linear regressions (MLR, forward stepwise model) were used to determine the influence of several predictors on the following fish assemblage parameters: density of 0+ fish (in June, July, August and October), number of 0+ fish species (in October), Shannon diversity index and evenness (H′ and E, respectively; Krebs 1989; both in October), number of fish species spawned during the season (calculated as number of 0+ fish species caught during the season) and density of 1+ fish in the following year (Table 3).

The following factors were considered as possible predictors: the density of spawners and spawner species richness, the density of predators and flood duration (Table 3, see further). Non-0+ perch, pikeperch *Stizostedion lucioperca*, pike *Esox lucius* and asp *Aspius aspius* were considered as possible fish predators (pooled together, hereafter referred as 'non-0+ predators'). Despite the small size, 0+ perch and 0+ pikeperch are also reported to be potential predators of 0+ fish (van Densen et al. 1996; Beeck et al. 2002). Therefore, the density of 0+ fish of these two species (pooled together, hereafter referred as '0+ predators') was considered to influence the density of 0+ fish in months following July. For each monthly sample, the flood duration was calculated as the number of days with flood and water temperature ≥16 °C from the first day when water temperature was 16 °C up to the day of sampling (e.g., up to the July sampling date when analysing July 0+ fish densities).

From the overall 30 samples, 22 samples had adequate information to be included as predictors based on non-0+ fish data (density of spawners, spawner species richness and density of non-0+ predators) because of the incompleteness of non-0+ fish sampling (Table 2). Multiple regressions were conducted on the 22 samples that were available for all predictors. However, when flood duration was the only significant predictor in the model (see Results), we conducted simple linear regression (LR) on all 30 samples using flood duration as the predictor. In that case, the model obtained by LR is presented in the Results. The predictor variables considered were not significantly correlated with one another (Pearson correlation, all $P > 0.05$).

The influence of the 'site' and the physical descriptors of the sites (maximal depth, site area and shore length) to fish assemblage parameters (listed in Table 3) were tested using mixed model analyses of variance and covariance. All statistical analyses were conducted using the Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA) and R 2.7.1. (R Foundation for Statistical Computing, Vienna, Austria) software.

Table 3. Variables entering the multiple regression analyses. Predictors assigned X were considered in the models explaining particular response variable. In analyses explaining fish densities (catch per unit effort [CPUE]), separate models were conducted for each of seven species and the C-Phyt group of species (results are shown in Table 5). Other response variables: number of 0+ species (0+ S), 0+ fish Shannon diversity index and evenness (0+ H′ and E, respectively) and number of 0+ species spawned during the season (spec. spawned).

Response variable	Date	Flood duration	Predators CPUE	0+ predators CPUE	Spawners CPUE	Spawners S
0+ CPUE	June	X	X		X	
0+ CPUE	July	X	X	X	X	
0+ CPUE	August	X	X	X	X	
0+ CPUE	October	X	X	X	X	
1+ CPUE	Following season	X	X	X	X	
0+ S	October	X	X	X		X
0+ H′	October	X	X	X		X
0+ E	October	X	X	X		X
Spec. spawned	June–October	X	X	X		X

The similarity between the spawner assemblage and 0+ fish assemblage at the start of the season in June was investigated using the Jaccard index of similarity (binary index) and Renkonen′s percentage similarity (PS, quantitative index, corresponding to Bray Curtis index calculated on percentages of individual species; Wolda 1981). Both coefficients range from 0 (no similarity) to 1 (identical samples). Similarly, these indices were calculated to investigate the similarity between the 0+ fish assemblage at the end of the season in October and the 1+ fish assemblage in the following year.

Results

None of the analysed fish assemblage parameters (listed in Table 3) differed among sites (mixed model analyse of variance, $P > 0.05$), and the fish assemblage parameters were not influenced by physical descriptors (maximal depth, site area, shore length; mixed model analyses of covariance, all $P > 0.05$). The density of spawners, spawner species richness, the density of non-0+ predators and the density of 0+ predators did not significantly influence any of the fish assemblage parameters (listed in Table 3; MLR, $P > 0.05$). Therefore, the final model always, if at all, consisted of simple LR describing the influence of flood duration on a particular dependent variable.

Assemblage composition

During the five sampling seasons, a total of 70,537 individual fish in the 0+ age class were caught, belonging to 24 species of five families (Table 4). The

Table 4. Relative abundances (in %) and frequencies (f; in %) of 0+ and non-0+ fish (in parenthesis) sampled on the six studied sites. Relative abundances are pooled for 5 and 4 sampling years (for 0+ and non-0+ fish, respectively). Frequencies were calculated as a number of year-site samples that included particular species, divided by the total number of year-site samples. Year-site sample is a sampling at a particular site in a particular year (total number of year-site samplings was 30 [six sites times 5 years] and 24 [six sites times 4 years] for 0+ and non-0+ fish, respectively). Overall column represents relative abundances pooled across all sites. CD, Čapí dolní; CS, Čapí střední; CH, Čapí horní; Mel, Melanbon; Spi, Špicmaus; Str, Štrosflek.

Common name	Scientific name	CD	CS	CH	Mel	Spi	Str	Overall	f (%)
Esocidae									
Pike	*Esox lucius* L.	<1 (1)	<1 (<1)	<1 (<1)	<1 (1)	<1 (<1)	<1 (1)	<1 (<1)	60 (79)
Cyprinidae									
Roach	*Rutilus rutilus* (L.)	3 (29)	18 (24)	27 (32)	16 (10)	33 (31)	10 (49)	16 (30)	83 (96)
Dace	*Leuciscus leuciscus* (L.)	(<1)			<1			<1 (<1)	7 (4)
Chub	*Leuciscus cephalus* (L.)		<1 (<1)					<1 (<1)	3 (4)
Ide	*Leuciscus idus* (L.)	<1 (1)	3 (<1)	6 (<1)	7 (<1)	1	15	4 (<1)	43 (33)
Rudd	*Scardinius erythrophthalmus* (L.)	10 (14)	25 (8)	29 (4)	29 (<1)	17 (6)	18 (2)	21 (8)	97 (88)
Grass carp	*Ctenopharyngodon idella* (Valenciennes)	<1 (<1)	(<1)					<1 (<1)	3 (8)
Asp	*Aspius aspius* (L.)	<1 (1)	<1 (1)	1 (<1)	<1	<1	<1 (1)	<1 (1)	33 (46)
Sunbleak	*Leucaspius delineatus* (Heckel)	1	<1	<1	4	<1	2	1	43
Tench	*Tinca tinca* (L.)	<1 (<1)	<1 (<1)	<1 (<1)			<1	<1 (<1)	23 (25)
Nase	*Chondrostoma nasus* (L.)		(<1)					(<1)	(4)
Stone moroko	*Pseudorasbora parva* (Schlegel)	<1 (<1)	<1	<1	<1	<1	<1	<1 (<1)	47 (8)
White-fin gudgeon	*Gobio albipinnatus* (Lukasch)		<1					<1	7
Bleak	*Alburnus alburnus* (L.)	1 (1)	2 (14)	1 (10)	3 (2)	7 (2)	8 (6)	3 (8)	87 (88)
White bream	*Abramis bjoerkna* (L.)	65 (23)	35 (22)	19 (37)	9 (11)	1 (22)	29 (3)	32 (26)	83 (92)
Bream	*Abramis brama* (L.)	6 (10)	6 (28)	8 (12)	11 (6)	2 (1)	7 (16)	7 (16)	83 (92)
Zope	*Abramis ballerus* (L.)	<1	<1 (<1)	<1 (<1)			2	<1 (<1)	13 (8)
Vimba	*Vimba vimba* (L.)		(<1)					(<1)	(4)
Bitterling	*Rhodeus amarus* (Bloch)	2 (2)	3 (<1)	2 (<1)	16 (<1)	<1 (<1)	4 (<1)	5 (<1)	73 (46)
Prussian carp	*Carassius gibelio* (Bloch)	11 (14)	3 (2)	1 (2)	<1 (2)	<1 (1)	<1 (<1)	4 (4)	70 (83)
Carp	*Cyprinus carpio* L.	<1 (1)	<1 (1)	(<1)	(<1)	(<1)		<1 (<1)	7 (42)
Cyprinid hybrid		<1 (<1)	<1 (<1)	<1 (1)	<1 (<1)	<1 (<1)	<1 (<1)	<1 (1)	50 (54)
Cobitidae									
Spined loach	*Cobitis taenia* L.		(<1)					(<1)	(4)
Weatherfish	*Misgurnus fossilis* (L.)		(<1)					(<1)	(4)
Siluridae									
Wels catfish	*Silurus glanis* L.		(<1)				<1 (<1)	<1 (<1)	3 (13)
Percidae									
Perch	*Perca fluviatilis* L.	<1 (2)	3 (<1)	4 (1)	2 (11)	30 (30)	3 (15)	5 (3)	93 (88)
Ruffe	*Gymnocephalus cernuus* (L.)	(<1)	<1 (<1)	<1 (<1)	<1 (9)	1 (5)	<1 (2)	<1 (1)	37 (63)
Pikeperch	*Stizostedion lucioperca* (L.)	<1 (1)	<1 (<1)	1 (<1)	1 (47)	6 (2)	<1 (<1)	1 (2)	53 (71)
Gobiidae									
Tubenose goby	*Proterorhinus marmoratus* (Pallas)	<1 (<1)	<1	<1	1 (1)		<1 (4)	<1 (<1)	70 (33)
Total number	of 0+ fish	17180	17351	9908	12915	6223	6960	70537	
	of non-0+ fish	5906	8010	6133	903	1105	1063	23120	
Number of species	[excluding hybrids]	19 (19)	21 (23)	18 (16)	17 (14)	15 (12)	19 (14)	24 (26)	

0+ fish assemblage composition often differed among years and even among particular months. During the four sampling seasons, a total of 23,120 individuals of non-0+ fish (1 year or older) were caught, belonging to 26 species of 6 families. We estimated that most of the non-0+ fish (88–99%, depending on species) were 1–3 years old, with 1+ fish forming 55–74% of non-0+ assemblage, according to the length–frequency distributions and literature comparisons. Cyprinidae and Percidae formed the majority of both 0+ and non-0+ fish assemblages (93% of cyprinids and 6% of percids identically in both assemblages). Similar species also dominated both assemblages (white bream, bream, roach and rudd in Cyprinidae; perch and pikeperch in Percidae). Despite the overall similarity between the non-0+ and 0+ fish assemblages (Table 4), the composition of spawner assemblage did not relate well with the composition of 0+ fish assemblage at the start of the season (mean Ja 0.38 ± 0.18 SD; mean Renkonen′s PS 0.24 ± 0.21 SD). Similar values of Ja and higher values of PS were calculated between the 0+ fish assemblage at the end of the season and the 1+ fish assemblage in the following season (mean Ja 0.38 ± 0.17 SD; mean Renkonen′s PS 0.52 ± 0.25 SD).

There was a positive relationship between the number of species spawned during the season and flood duration (LR, $P < 0.001$, $R^2 = 0.71$, $b = 2.2935$, d.f. = 1,27; flood duration was log-transformed to achieve linearity as the trend was asymptotic, reaching asymptote in approximately 90-day flood; Fig. 2). There was a positive relationship between number of 0+ fish species at the end of the season (October) and flood duration (LR, $P < 0.001$, $R^2 = 0.64$, $b = 0.0648$, d.f. = 1, 27; Fig. 2). Similarly, there was a positive relationship between Shannon diversity index of 0+ fish at the end of the season and flood duration (LR, $P < 0.001$, $R^2 = 0.35$, $b = 0.0059$, d.f. = 1, 27). On the other hand, Shannon evenness of 0+ fish at the end of the season was not significantly related to flood duration (LR, $P > 0.05$, d.f. = 1, 27; Fig. 2).

Cyprinid phytophilic and phyto-lithophilic (C-Phyt) fish

Flood duration influenced C-Phyt assemblage throughout the entire sampling season (Fig. 3). There was a positive relationship between the density of 0+ C-Phyt in all months studied and flood duration (LR, $P < 0.001$; Table 5; Fig. 4). Consequently, there was a positive relationship between the number of 1+ C-Phyt in the following year and flood duration (LR, $P < 0.001$; Table 5; Fig. 4). At the sites, where flood had receded, the density of 0+ C-Phyt decreased, resulting sometimes (eight cases) in no 0+ C-Phyt recorded at the site in October (Fig. 3).

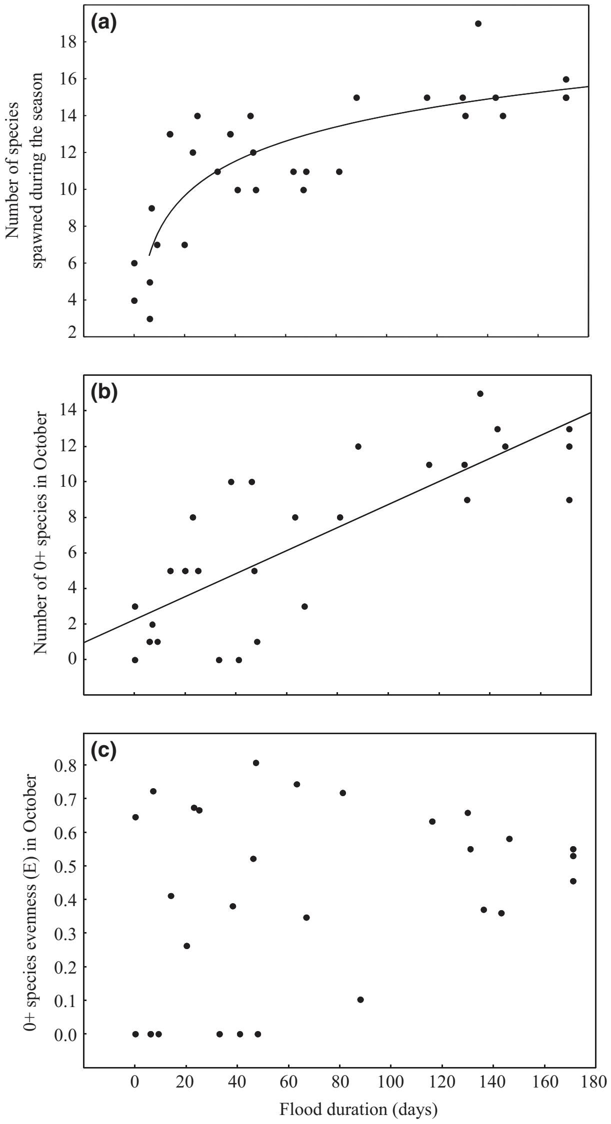

Fig. 2. Dependence of the (a) number of species spawned during the season, (b) number of 0+ fish species in October and (c) evenness of the 0+ fish assemblage in October on the flood duration. Plotted lines represent the best fitting curves. Fitted functions: (a) $y = 3.1732 + 2.2935[\ln(x + 1)]$; (b) $y = 2.2378 + 0.0648x$.

Individual species

There was a positive relationship between the density of 0+ rudd, white bream, roach and bream in all months studied and flood duration (LR, $P < 0.0064$, Table 5), except for rudd and white bream in June and bream in August (Table 5). In Prussian carp, there was a positive relationship only between the density in June and flood duration (LR, $P < 0.0064$, Table 5). There was a positive relationship between the density of 0+ bitterling in July, August and October and flood duration (LR, $P < 0.0064$, Table 5). There was no

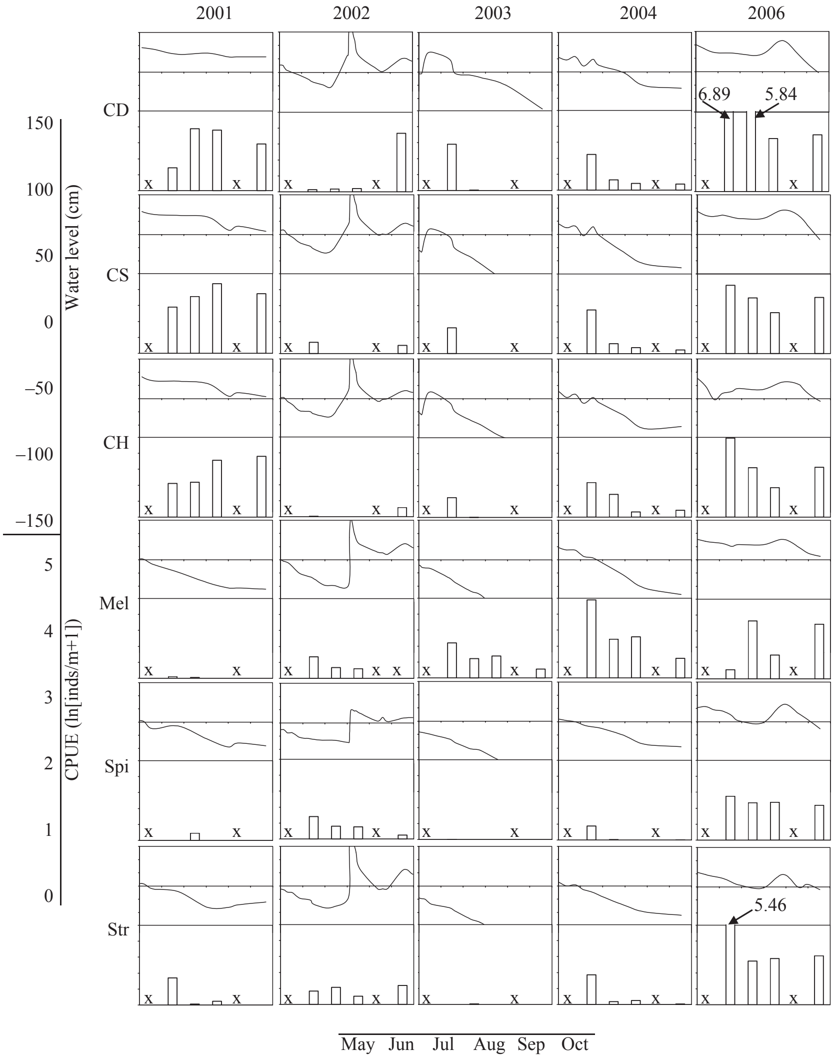

Fig. 3. Seasonal variation in water levels (cm; upper parts, solid line) and catch per unit effort of 0+ C-Phyt [ln (inds⁄m + 1); lower parts, columns] during five sampling seasons (2001–2004, 2006) at six studied borrow pits. Sites were flooded when water level ≥0 cm. Crosses stand for no sampling on the site. Site codes are provided in Table 4.

significant relationship between the density of 0+ perch and flood duration (LR, $P > 0.0064$, Table 5).

At the sites, where no flood occurred after June sampling, no newly hatched individuals were observed from July to October. At long-term flooded sites (eight sites), newly hatched individuals were found in July sampling in white bream at seven sites, rudd at three sites, roach, tench *Tinca tinca*, sunbleak *Leucaspius delineatus*, bitterling and bleak *Alburnus alburnus* in July at one site. However, in later months (August and October) no such individuals were found, with an exception of white bream and carp *Cyprinus carpio* in August at one site. After sudden late summer flood in August⁄September 2002 (five sites), we found newly hatched individuals of Prussian carp at five sites, bleak at two sites, white bream at two sites and stone moroko *Pseudorasbora parva* at one site. At the four sites in active floodplain, species richness of 0+ fish increased from August to October 2002 (3 and 8.2 species in average, respectively); though, most species lacked newly hatched individuals.

Discussion

Factors influencing the 0+ fish assemblage

Density of 0+ fish can be potentially influenced by various biotic and abiotic variables. However, flood duration was the only significant factor influencing density and diversity of 0+ fish in our study. The significance of flood duration was linked with almost a total absence of spawning and nursery areas in the water bodies themselves (bare steep banks and lack of aquatic vegetation). Instead, spawning and nursery areas were provided by flooded terrestrial vegetation. The suitability of the borrow pits as nursery habitats *per se* is therefore questioned (see Conclusions). Similarly to the main channel, the availability and quality of nurseries seem to be correlated with the morphology of the artificial borrow pits (Kurmayer et al. 1996); the function and quality of the inshore habitats seem to be essential. Thus, we assume that the suitability of studied borrow pits as nursery habitats

Table 5. Results of multiple regression analyses explaining catch per unit effort (CPUE) [ln (inds/m + 1) and inds per 100 m^2 for 0+ and 1+ fish, respectively] of seven most abundant species and the C-Phyt fish group. Significance of the model (*P* expressed by asterisks, see footnote), coefficients of determination (R^2) and raw regression coefficients (b, in parenthesis) are shown. Nonsignificant models are marked as 'n.s.', models nonsignificant after Dunn-Šidák correction are shown in italics.

Response variable	Significant predictor	d.f.	C-Phyt	Rudd	White bream	Roach	Bream	Prussian carp	Bitterling	Perch
June 0+ CPUE	Flood duration	1, 28	***0.41 (0.0544)	n.s.	n.s.	***0.36 (0.0358)	**0.24 (0.0391)	**0.32 (0.0194)	n.s.	n.s.
July 0+ CPUE	Flood duration	1, 28	***0.66 (0.0384)	***0.61 (0.0213)	***0.48 (0.0280)	***0.67 (0.0180)	***0.55 (0.0070)	_*0.23 (0.0028)_	***0.37 (0.0078)	n.s.
August 0+ CPUE	Flood duration	1, 28	***0.72 (0.0263)	***0.64 (0.0194)	***0.57 (0.0143)	***0.52 (0.0152)	n.s.	_*0.23 (0.0009)_	***0.50 (0.0059)	n.s.
October 0+ CPUE	Flood duration	1, 27	***0.83 (0.0236)	***0.81 (0.0140)	***0.66 (0.0167)	***0.52 (0.0104)	**0.28 (0.0032)	n.s.	***0.42 (0.0028)	n.s.
Following year 1+ CPUE	Flood duration	1, 14	***0.68 (1.2456)	_*0.37 (0.1204)_	***0.59 (0.4223)	**0.50 (0.4624)	_*0.27 (0.2083)_	n.s.	†	n.s.

*$P < 0.05$; **$P < 0.0064$ (critical *P*-value after Dunn-Šidák correction for multiple testing); ***$P < 0.001$.

†Analysis was not conducted because of the annual life span of bitterling in the area (Smith et al. 2000) and an unrepresentative sampling of bitterlings with 10-mm-mesh-sized net.

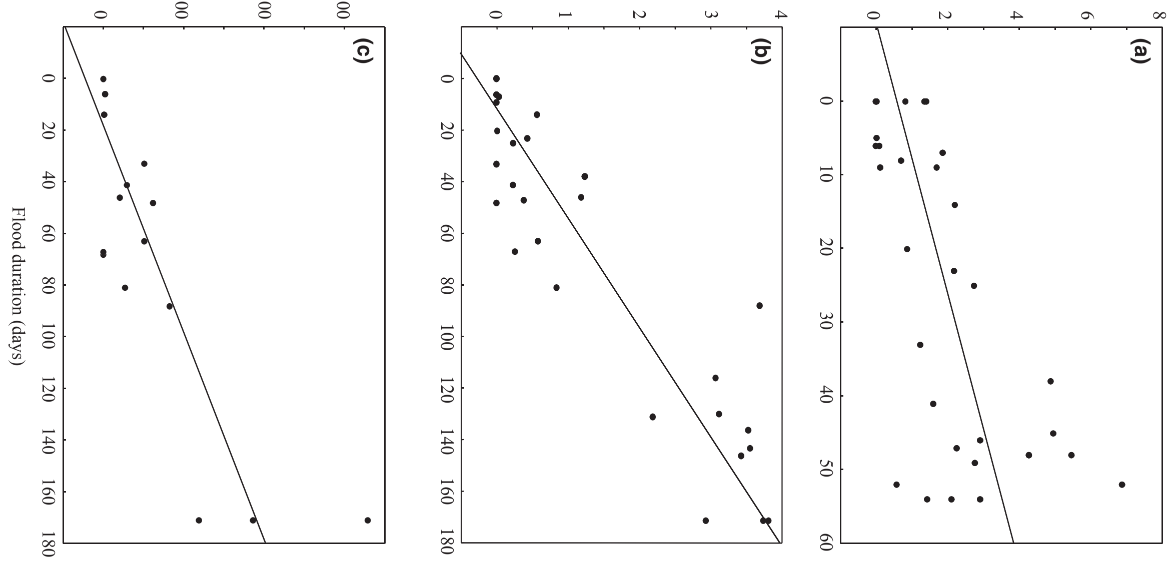

Fig. 4. Dependence of (a) the density of 0+ C-Phyt in June, (b) the density 0+ C-Phyt in October and (c) the density of 1+ C-Phyt in the following season on the flood duration. Plotted lines represent the best fitting curves. Fitted functions: (a) $y = 0.5761 + 0.0544x$; (b) $y = -0.2807 + 0.0236x$; (c) $y = -22.46 + 1.2456x$.

would be improved by modifying their morphology, for example increasing the heterogeneity of the shoreline (shallow areas, shelters; Sabo & Kelso 1991) and by building gentle bank slope that would allow vegetation to growth at the inshore areas.

The lack of statistical significance of other considered predictors (number of spawners and predators and physicochemical site characteristics) could be caused by high extent of variability explained by flood duration and/or small variance of the nonsignificant predictors. It should be pointed out that flood duration itself represented two primary factors that are reported to influence the density of 0+ fish: availability of spawning substrate and shelters (e.g., Grift et al. 2003; Bailly et al. 2008) and coupling of the thermal and flooding regimes (e.g., Schramm & Eggleton 2006). In addition, some factors not measured in our study could influence the density of 0+ fish, for example density of zooplankton (Nunn et al. 2007b), water bird predation or parasites (Ondračková et al. 2004; Cucherousset et al. 2007).

Spawners of the most abundant species were always present at the sites that diminished the influence of density of spawners to the density of 0+ fish. Moreover, the potential spawners assemblage composition did not fit well with the 0+ fish composition at the start of the season (mean Ja 38%, mean PS 24%). This disproportion could be caused by the lack of suitable spawning substrate on some sites (no spring flood for phytophilic species; lack of gravel substrate and flowing water for some rheophilic species that also rarely occurred in non-0+ assemblage), by occasional migration of non-0+ fish among the flooded borrow pits and probably also by the later spawning of some species (eggs of some species might not be hatched in June sampling yet).

Our analyses did not demonstrate a significant, direct relationship between the density of fish predators and the density of 0+ fish. However, predation by fish predators was the most probable cause of decreasing 0+ fish density on nonflooded (i.e., shelter-lacking) localities. Decreased water level has been documented to threaten fish by increasing the predation risk (Halyk & Balon 1983). The 0+ fish mortality caused by decreasing dissolved oxygen concentrations (Humphries et al. 1999; Lusk et al. 2004) was improbable in our study, as always at least 1 m of water remained at the sites, and we did not observe any dead fish.

The connection with the main channel in our study was quite rare and appeared mostly during late March, when the water was still cold for a massive spawning migrations (Hladík & Kubečka 2003; Cucherousset et al. 2007), and therefore most fish probably originated from the borrow pits. Only during the brief intensive overspill of the river in August 2002, several older 0+ individuals probably immigrated from the main channel to the four sites connected with the river, increasing 0+ species richness there (see Results). Drift phenomenon during this flood also participated on the overall higher number of 0+ species than non-0+ species at some sites (Table 4).

Flood provides spawning substrate

Flooded terrestrial vegetation provided suitable spawning substrate for phytophilic and phyto-lithophilic cyprinids in accordance with other studies (Grift et al. 2003; King et al. 2003; Bailly et al. 2008). Roach, bream and Prussian carp utilised mostly the May flood, and rudd and white bream utilised mostly the June flood. Only batch spawners (Prussian carp and partly white bream and bleak) were able to utilise a sudden late (August, 2002) flood for spawning, and only non-native Prussian carp increased its 0+ density comparably to spring floods (see also Ryšavá-Nováková et al. 2009). However, even in batch spawners, spawning in later months (August–October) was notably suppressed in years when the flood stayed at the site for entire growing season. Thus, the batch spawners took advantage of the spawning flexibility and ability to delay the spawning but did not use the possibility of increasing their numbers gradually during the long-term floods.

Ostracophilic bitterling did not use the flooded vegetation for spawning, and therefore its 0+ June density was not dependent on the spring flood duration. The dependence on the flood duration in later months (July–October) rather reflected the protective role of flooded vegetation, a finding that was also documented by Smith et al. (2000). Perch reproduction was not influenced by the flood duration at all. Perch lays egg strands on aquatic vegetation or branches, preferably in deeper areas (Gillet & Dubois 1995), and 0+ perch are reported to prefer deeper areas with submerged vegetation (Fischer & Eckmann 1997). At the studied sites, the 0+ perch was distributed evenly along the littoral zone with no preference for the flooded vegetation (Ryšavá-Nováková et al. 2009). The shallow zone of flooded emergent vegetation thus did not seem to be a convenient area for perch spawning and nursery.

Flood duration and flood regime strongly influenced 0+ species richness and the diversity of 0+ fish (H′), in accordance with Agostinho et al. (2001), but not the equitability (evenness) of 0+ fish assemblage, contrary to Agostinho et al. (2001). Long-term floods increased 0+ species richness and diversity mostly because of the protective function of flooding (see further) and also by allowing more species to spawn (asymptotically). An asymptotic trend was supported by the fact that phytophilic fishes in the study area are adapted to regular spring flooding events, and therefore a limited number of fishes were able to spawn in later months.

Flood influences 0+ fish survival

Flooded vegetation provides an efficient and extensive refuge against predators (Staas & Neumann 1994; Grift et al. 2003). Moreover, high food availability and higher temperature in flooded areas support the rapid growth of many juvenile fish (e.g., Balcombe et al. 2007) and henceforth increase their survival (Halyk & Balon 1983; Nunn et al. 2007a). The presence of shelter-providing flooded vegetation was crucial for the survival of 0+ cyprinids (mostly C-Phyt and bitterling) also in the studied borrow pits. Shortly after the flood had receded, the density of 0+ cyprinids decreased sharply, and a longer period without flood led to the complete disappearance of 0+ cyprinids, probably because of the predation. Such dramatic consequences of predation on 0+ cyprinids (bream) were detected also by Beeck et al. (2002).

Long-term floods increased the density of 0+ C-Phyt exponentially, with 90-day long flood as a threshold for highly extensive floodplain utilisation by C-Phyt fishes. Similarly, flood duration of 6 or more weeks is reported to be necessary for fish to successfully use the inundated floodplain for recruitment (Sparks et al. 1998; King et al. 2003). At the sites where floods occurred with longer duration, 0+ fish also seemed to survive the winter and strengthened the non-0+ assemblage in next year as 1+ fish. Compositions of 1+ fish assemblages in individual years were more similar to 0+ fish assemblages at the end of previous year than were spawner assemblages to their progeny. Overall, the non-0+ assemblage consisted mostly of young age classes (see also Jurajda et al. 2004), with 88–99% of C-Phyt estimated as 0+ fish from 1 and 2 years earlier. The connection with the river once per 2 or 3 years could serve as a liberation of fish to the river system (Nunn et al. 2007b), participating thus in the rejuvenation of the non-0+ assemblage.

Conclusions

Floodplain man-made water bodies are suggested to substitute natural backwaters and oxbows in providing suitable spawning substrate and shelter for 0+ fish (Sabo & Kelso 1991; Nunn et al. 2007b). However, flooded terrestrial vegetation carried out this function instead in the steep-banked, shelter-lacking borrow pits. We assume that artificial water bodies with similar features can act as useful nurseries only when long periods of raised water level inundate nearby terrestrial vegetation. Contrarily, water bodies that possess more aquatic vegetation and other natural shelters should act as suitable nurseries themselves. Generally, the density and diversity of 0+ fish in plesiopotamic water bodies is dependent on the number and permanence of shelters and spawning substrates (shallow littoral zone; aquatic, or flooded terrestrial, vegetation).

This study was conducted in a partly disrupted floodplain system, where the flooding of terrestrial vegetation (whether it is caused by an ephemeral connection with the channelised main channel or overbanking the borrow pits because of the rise in ground water level) shapes its production to the isolated borrow pits. Even in this disrupted system, fish reproduction was driven by the duration, timing and predictability of flood in a similar manner as natural floodplain rivers (Sparks et al. 1998; King et al. 2003; Bailly et al. 2008) – a finding that adheres to the flood pulse concept (Junk et al. 1989). The hydrological regime in the studied area still influences the phytophilic and phyto-lithophilic fish reproduction in the separated floodplain water bodies because of the ground water levels. Modification of the River Dyje is the probable cause of reduced reproduction of phytophilic species in the river stretch adjacent to the studied borrow pits (Valová et al. 2006). The borrow pits, together with the remaining backwaters, are potential sources of the older (≥2+) phytophilic fish that recruit into the main channel, a finding also observed in bream by Molls (1999). Thus, if the occasional connectivity provides a migration route for the fish to the river, the adverse affect of river channelisation on the non-0+ assemblage of phytophilic fish could be mitigated.

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