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

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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.

Key words: migration, distribution, reproduction, feeding ground

Introduction

When an artificial reservoir is built by damming a river, the original riverine fish have to cope with new ecosystem conditions, specifically in regards to feeding, overwintering and especially reproduction. Some species that colonize reservoirs are able to complete their entire life cycles in restricted parts of these water bodies (Vostradovský 1968, Vostradovská 1974, Kipling & Le Cren 1984). However, other fish species have to migrate to the extensive parts of reservoirs, including inflowing rivers, due to their different requirements for spawning and feeding grounds as well as winter refuges (Wilkonska 1967, Goldspink 1978, L´Abée-Lund & Vollestad 1985, Lucas & Baras 2001). The reservoir tributary is an ecotone situated on the boundary between a riverine and reservoir ecosystem and represents an important spawning ground for many fish species inhabiting Central European reservoirs (Lucas & Baras 2001, Hladík & Kubečka 2003). Many studies have described intensive migrations from the feeding grounds in the main body of a reservoir or lake to spawning grounds in the tributary for species such as potamodromous salmonids (Kipling & Le Cren 1984, Northcote 1997), pike (*Esox lucius*, Kubečka & Křivanec 1990), perch (*Perca fluviatilis*, Lilja et al. 2003), plus cyprinids such as asp (*Aspius aspius*, Vostradovská 1974), roach (*Rutilus rutilus*, Wilkonska 1967, L'Abée-Lund & Vollestad 1985, Lilja et al. 2003), white bream (*Blicca bjoerkna*, Lilja et al. 2003), bream (*Abramis brama*, Poddubny 1971, Hladík & Kubečka 2003), bleak (*Alburnus alburnus* and chub (*Squalius cephalus*, Hladík & Kubečka 2003).

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However, the importance of tributary spawning varies among species. In the Římov Reservoir, Hladík & Kubečka (2003) revealed the intensive spawning migrations of numerous species to the tributary and categorized them into obligatory tributary spawners and generalists. The obligatory spawners (bleak, asp, chub and white bream) require a riverine environment for spawning and do so predominantly in the inflowing river (Peterka et al. 2004). On the other hand, generalists (bream, roach and perch) spawn in the tributary as well as at different sites in the main body of the reservoir.

Soon after reproduction, the spawners abandon their spawning grounds and redistribute back to their feeding grounds (Lucas & Baras 2001). Each species has different feeding ground requirements and the heterogeneous nature of reservoirs provides many types of feeding grounds to support the requirements of a variety of species (Vašek et al. 2004, Prchalová et al. 2008, 2009). The lotic environment of the inflowing river changes substantially to a reservoir lentic environment. Inflowing nutrients from the river make the part adjacent to the tributary the most productive in the reservoir due to having the highest chlorophyll a and zooplankton concentrations. All these factors gradually decrease towards the dam (eg. Hejzlar & Vyhnálek 1998, Seďa & Devetter 2000, Mašín et al. 2003, Vašek et al. 2003). Prchalová et al. (2008, 2009) found that the distribution of fish species follows this gradient and distributes according to their specific habitat conditions and prey concentration requirements.

Species classified by Hladík & Kubečka (2003) as obligatory tributary spawners all possess different feeding ground requirements and thus should disperse accordingly after tributary spawning. Chub is considered to be an omnivorous species preferring running waters (Lammens & Hoogenboezen 1991) and they often occupy lentic waters as a winter refuge (Lucas & Baras 2001). White bream is a bentivorous species, prospering well in turbid and shallow eutrophic conditions (Olin et al. 2002, Mehner et al. 2005, Pekcan-Hekim & Horppila 2007). Bleak is a zooplanktivorus species (Bíro & Muskó 1995, Chappaz et al. 1999, Vašek et al. 2003) and asp is a predatory species (Lammens & Hoogenboezen 1991, Krpo-Cetkovic et al. 2010) that both prosper in eutrophic to mesotrophic conditions (Olin et al. 2002, Mehner et al. 2005). We hypothesized that these species should disperse according to their feeding ground preferences after tributary spawning.

Spawning generalists are not strictly bound to tributary spawning grounds as they are only one of many possible such sites in a given reservoir. Therefore, it could be expected that the tributary spawning grounds are important mainly for individuals with feeding grounds located nearby and thus low post-spawning dispersal can be expected. Roach was observed to disperse throughout the whole waterbody after spawning in the tributary of Lake Arungen, Norway (L'Abée-Lund & Vollestad 1985). Bream remained closed to the tributary of the Elektrėnai reservoir (Lithuania) after tributary spawning (Poddubny 1971). These findings suggest that the assumption of low post-spawning dispersal is valid for bream while roach distribution is driven differently. Post-spawning dispersal patterns have not been studied intensively in common European fish species and therefore it is not known whether these patterns are species- or reservoir/lake-specific.

A large experiment focusing on the migration of fish was carried out in the canyon-shaped Římov Reservoir, particularly focusing on the importance of the tributary in this phenomenon. Fish were captured during migration through the tributary zone of the

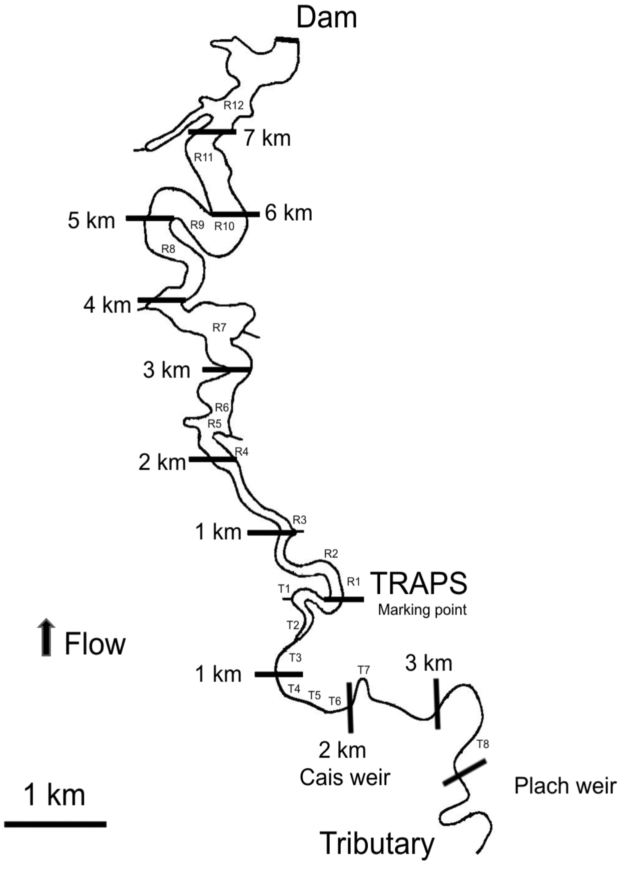

Fig. 1. Map of the Římov Reservoir, Czech Republic, and its only inflow, the River Malše. The locations of weirs, traps (marking point) and sampling sites (R1-R12 and T1-T8) with indications of their distances from the marking point are shown.

reservoir by two giant traps during four consecutive seasons in the years 2000-2004. All captured fish were marked and released. The partial results of this experiment were presented in Hladík & Kubečka (2003, 2004). These authors focused to the seasonal pattern of fish migration through the tributary and the effect of reservoir water level fluctuation on spawning migration to the tributary (discussed below in the "Study Area" section). The presented study builds upon these aforementioned studies and investigates the post-spawning dispersal of tributary spawners to the reservoir and inflowing river. Dispersal patterns were evaluated separately for each species during three successive periods – early after spawning (early summer), the late summer and next spawning season (spring).

Study Area

The Římov Reservoir (Fig. 1) was built in 1978 on the River Malše 20 km south of České Budějovice, Czech Republic (dam co-ordinates: 48°51′00″ N, 14°29′29″ E). It is a deep, elongated, steep-sided, drinking-water supply reservoir. The length of the reservoir is about 8 km measured along its middle axis. The mean flooded area is 210 ha, average depth is 16 m and average storage time is about 90 days. The reservoir is dimictic with well-developed thermal and oxygen stratification in summer. No current occurs in the reservoir main body. The littoral habitats offer areas with different slopes ranging 1-40 %. No true aquatic plants are present in the reservoir and the availability of flooded-terrestrial, near-shore vegetation depends on the water level (Hladík & Kubečka 2004). The reservoir serves mainly for supplying drinking water and the production of electric power. Thus its water level exhibits an annual cycle, with the highest level after snow melting, followed by a gradual decrease by several meters during summer. The main food source for dominant fish species is zooplankton (Vašek et al. 2003). According to the nutrient concentration, the reservoir can be classified as eutrophic to mesotrophic with phosphorus, phytoplankton and zooplankton concentrations decreasing downstream along its longitudional axis (Hejzlar & Vyhnálek 1998, Seďa & Devetter 2000, Vašek et al. 2003).

The River Malše is small with an average discharge of 4.1 $m^3.s^{-1}$ and is the only significant inflow into the reservoir. A description of the river section sampled in this study (see Material and Methods – Fish sampling) was given by Peterka et al. (2004). The river section can be characterized as typical grayling zone, with a 0.15-0.8 $m.s^{-1}$ current velocity and depths mostly under 0.5 m. Submerged macrophytes occur only occasionally, mostly *Batrachium* sp., which are used as a spawning substrate by roach and bream. Potamoplankton are very rare, and thus available food sources are bentos or terrestrial insects. The inflowing river is usually several degrees cooler than epilimnion or the reservoir during summer (Hejzlar et al. 1993).

The reservoir fish community is dominated by cyprinids such as bream, roach and bleak and the percids ruffe and perch. These species comprised approximately 90 % of the abundance (fish older than young-of-year) in gillnet catches in the years 1999-2007 (Prchalová et al. 2009). A study of the River Malše fish community revealed that species typical for the reservoir were very abundant in the river as well and the proportion of riverine species was relatively low. Roach dominated in whole river section sampled this study (see Material and Methods – Fish sampling, Hladík et al. 2008).

The importance of the tributary for fish from the Římov Reservoir was initially described by Hladík & Kubečka (2003, 2004). In the first study, they characterized fish migration through the tributary zone of the reservoir mainly by daily numbers and species composition. They followed six periods of fish migration into and out of the reservoir tributary and divided reservoir species into several groups according to their affinity for tributary spawning – obligatory tributary spawners and generalists (both mentioned in the Introduction of this paper), and species spawning out of the tributary (carp *Cyprinus carpio*, pikeperch *Sander lucioperca*, catfish *Silurus glanis* and ell *Anguilla anguilla*). In the following study, they examined the influence of flooded terrestrial macrophytes availability on tributary spawning migration. The authors found only higher numbers of white bream and bream migrating to the tributary in the year when no flooded macrophytes were available in the reservoir main body. The other investigated species (roach, bleak, perch, chub and roach × bream hybrid) did not react to the absence/occurrence of flooded macrophytes in the reservoir main body. Their numbers in tributary spawning run were similar in all investigated years or changed according to their proportions in the reservoir stock.

Material and Methods

The study was divided into two parts: 1) the capture and marking of migrating fish in the tributary, 2) sampling of fish in the whole area of the reservoir system, i.e. from the dam to the first impermeable Plach weir of the inflowing the River Malše (Fig. 1).

Fish marking

Fish migrating through the tributary area during the spring and summer of 2000-2003 were captured by two specially-constructed giant traps. Each trap was composed of three chambers (entrance frame 3 × 3 m, length of traps 15 m, wings 3 m high and 40 m long, mesh size 15 mm in all parts; for more details see to Hladík et al. 2002 and Hladík & Kubečka 2003). The depth of the installation was from 0.75-2.75 m. Each trap covered the whole cross-section of the river. One trap captured upstream migrants while the other downstream migrants. After extensive sampling during spring and summer 2000, this activity was concentrated to the main fish migration periods during the subsequent seasons (Table 1). These traps sampled the total river discharge for 88 % of the sampling periods; the remaining periods were unmonitored because of flooding (Hladík & Kubečka 2003). During periods of intensive fish migration, the traps were checked and the catches processed daily; during periods of less intense migratory activity, they were monitored three times a week. Fish were identified, measured and batch-marked using a combination of fin clipping and VIE fluorescent elastomer tags (Northwest Marine Technology, Shaw Island, Washington, USA). The VIE tags were injected under the transparent skin of the head and into spaces between the fin rays (Malone et al. 1999). Only adult individuals with running gonads, which represented the bulk of the catch, were taken into account for this study. Therefore, individuals larger than 150 mm were marked, with the exception of bleak in which only individuals larger than 120 mm body length were marked.

Table 1. Timetable of sampling and marking events in the River Malše and Římov Reservoir.

Year	Marking	Sampling	
		River	Reservoir
2000	April 7-August 23	June 26-30	June 26-30
		August 19-23	August 19-23
2001	March 29-July 16		May 3-5
		June 23-25	June 23-25
		August 18-19	August 18-20
2002	March 20-June 4		May 3-4
			July 1-4
2003	April 29-May 16		May 7-8
			August 28
2004			April 29-May 1

Table 2. Total sampling effort described by meters of examined shoreline of the river or reservoir by electrofishing, square meters of exposed gillnets or sampled littoral areas by seining carried out each year of the study.

Gear	2000	2001	2002	2003	2004
Electrofishing in river [m]		2900	1800		
Electrofishing in reservoir [m]		4100	4700	3700	8500
Gillneting [m^2]	10277	16014	13557	15152	-
Seining [m^2]	38200	41700	26100	31600	-

Fish sampling

Fish were sampled at 22 sites. Eight sites were distributed throughout the river zone (T1-T8, Fig. 1), two sites were at the marking points (each at the position of one tributary trap, MP1-2) and twelve sites in the main body of the reservoir (R1-R12, Fig. 1). Sampling was performed four times in the river: twice in early summer and two more times in the late summer of the years 2000 and 2001 (sampling in the river during spring was not performed and the data are not available for the river at spring). Sampling was done ten times at the marking points and in the main body of reservoir; four times during the spring spawning in the years 2001-2004 (only littoral habitats), three times during early summer in the years 2000-2002 and three times during late summer in the years 2000, 2001 and 2003 (littoral, bentic and pelagic habitats). A detailed time schedule of the study is given in Table 1.

At the river (sites T1-T8, Fig. 1), fish were sampled by electrofishing (BMA-Honda electroshocker, 230V, 50Hz, 2A, Bednář company, Czech Republic), with a single pass applied by wadding through the water. The tributary sampling sites were distributed from traps to the first impermeable Plach Weir: sites T1-T3 were located at the upper part of the reservoir impoundment and at an adjacent part of the river characterized by relatively large deep pools, sites T4-T6 were located below the former partially permeable Cais Weir built approximately 2 km above the traps, site T7 was just above the Cais Weir, site T8 was located below the Plach Weir built approximately 4 km above the traps (Fig. 1). Sampling sites located in the giant traps positions (in marking point) were sampled by giant traps themselves or by electrofishing during periods where traps were not operated (see Table 1).

In the main body of the reservoir, various fishing methods were used for fish sampling: electro-fishing (BMA-Honda electroshocker, 230V, 50Hz, 2A, Bednář company, Czech Republic) and seining (nets of lengths from 10 to 200 m, a width of 4 m and mesh size 10 mm) in the littoral parts and gillnetting (extended Nordic multimesh gillnets; length of nets 40 m; sixteen mesh sizes – 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55, 70, 90, 110, 135 mm) in benthic (width of the net 1.5 m) and pelagic (width of the net 4.5 m) habitats. Detailed descriptions of these methods are given in Vašek et al. (2004) for gillnetting, Hladík el al. (2008) for electrofishing, and Říha et al. (2008) for littoral seining. A summary of the sampling efforts using all the mentioned methods throughout the study period is given in Table 2.

All fish caught during the marking and sampling process were determined to species, standard length measured within 5 mm accuracy and checked for the presence of tributary marks (fin clipping and VIE mark).

Dispersal analyses

Post-spawning dispersal was tested in seven species: bream, roach, bleak, perch, asp, white bream and chub. These species were divided according to their representation in the fish stock of the reservoir: dominant species (more than 10 % abundance), such as bream, roach and bleak; subdominant species (1-10 %), perch and asp; and rare species (< 1 %), white bream and chub (Prchalová et al. 2009). The post-spawning dispersal of other species captured in the tributary during the experiment (see Hladík & Kubečka 2003) was not tested due to the very low numbers of recaptured individuals.

The post-spawning dispersals of these species were evaluated for three subsequent periods: 1) early summer – June/July – the period after the main spawning run of the tributary spawners, when only multiple spawners (bream, bleak and white bream) are found in the tributary (period 5 according to Hladík & Kubečka 2003), 2) late summer – August/September – the period with no spawning activity of the dominant species, and movement is guided by local feeding (period 6 according to Hladík & Kubečka 2003), 3) next spawning season – the period corresponding to the spring spawning runs of different species of the reservoir (periods 1-3 according to Hladík & Kubečka 2003).

Dispersal during a given twelve-month interval was studied only for fish marked at the beginning of this interval. The study covered four consecutive intervals during the years 2000-2004. At every interval, the whole population of each fish species in the reservoir-river system was considered a closed population because individuals from the newly recruited year classes in the spring were not counted. The mortality of marked and unmarked fish was considered as equal and no new recruits were allowed (Amstrup et al. 2005).

The dispersal of fish within the reservoir system was evaluated for each period separately by the logistic regression model. This model tested whether the probability (proportion of marked fish to all fish of an individual species in the appropriate size range per sampling site) of a captured marked fish is dependent on the distance from the marking point at the tributary. The model assumed that the capture probability of the marked fish decreases with distance from the marking point. The model description is as follows: the binomial distribution $Bi(n_r, p_r)$ was assumed for the number of recaptured marked fish within each sample. This distribution has one known parameter, n_r, the number of all fish examined for marks, and one unknown parameter, p_r, the probability that the fish had the mark. This binomial random variable was measured at different distances from the tributary traps (both in the River Malše and in the main body of the reservoir) and described the distribution of the probability on the distance from the tributary traps. This parameter was fitted by the logistic regression model for binomial distribution, whose equation is as follows:

$$p_r(x) = \frac{Exp(a+bx)}{1 + Exp\ (a+bx)}$$

where p_r is the capture probability of the marked fish, x the distance from the tributary marking point and a and b are parameters of this logistic model.

The resultant fitted function $p_r(x)$ has two parameters, just as a classical simple regression would: parameter a stands for an intercept and parameter b describes

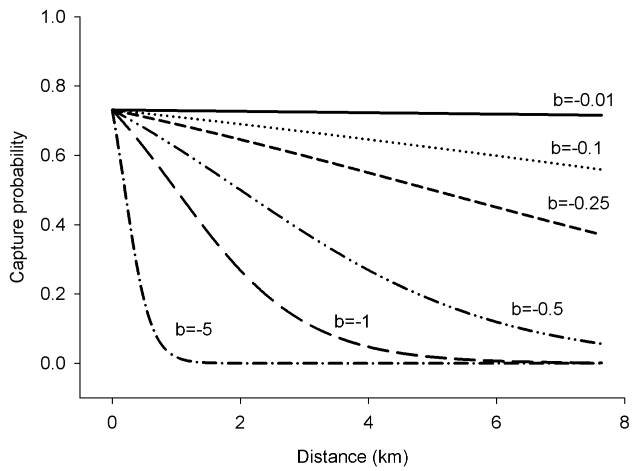

Fig. 2. Hypothetical examples of model outputs for six values of parameter b. For all examples, the a parameter has a value of 1.

the dependence of the capture probability of marked fish on the distance from the tributary marking point. The model assumes a decrease of capture probability and in this case parameter b has a negative value. The lower parameter b value implies a higher slope for the fitted function, which means that if parameter b

Table 3. Number of marked fish (column M). Number of recaptured fish and total number of captured fish (in brackets) during the study at various distances from the traps (row below site abbreviations and given in km) and at particular sites in the river (T), directly at the marking point (MP) and in the reservoir (R, see Fig. 1). Sampling sites within 1 km from the traps were combined into units for a better overview. The numbers are delineated according to the sampling period (SP; 1 – early summer, 2 – late summer and 3 – next spawning season). Sampling was not performed in the river during the third period and is indicated as ND (no data).

Species	M	SP	T8 3-4 km	T7 2-3 km	T4-T6 1-2 km	T1-T3 0-1 km	MP 1- 2 0 km	R1-R2 0-1 km	R3 1-2 km	R4-R5 2-3 km	R6 3-4 km	R7 4-5 km	R8-R10 5-6 km	R11 6-7 km	R12 7-8 km	Total
W. bream	363	1	0(0)	0(0)	0(0)	8(11)	8(21)	0(3)	0(0)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	16(36)
		2	0(0)	0(0)	0(0)	1(1)	6(11)	0(3)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	7(16)
		3	ND	ND	ND	ND	78(150)	0(1)	0(0)	0(0)	0(0)	0(1)	0(0)	0(0)	0(0)	78(152)
Chub	479	1	0(36)	0(23)	11(203)	21(128)	20(82)	0(1)	0(0)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	52(474)
		2	0(0)	0(0)	0(65)	8(44)	10(12)	0(16)	0(0)	1(1)	0(0)	0(0)	0(0)	0(0)	0(0)	19(138)
		3	ND	ND	ND	ND	74(362)	0(2)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	74(364)
Bleak	14088	1	3(13)	1(4)	38(84)	29(33)	748(1651)	5(29)	0(0)	15(141)	16(50)	23(36)	12(31)	0(0)	0(0)	940(2123)
		2	0(0)	0(0)	0(0)	0(0)	104(121)	9(72)	0(20)	20(54)	14(46)	16(85)	27(88)	0(52)	17(74)	207(612)
		3	ND	ND	ND	ND	510(952)	0(0)	0(0)	0(0)	1(1)	2(2)	0(0)	0(0)	0(0)	513(955)
Asp	348	1	0(0)	0(0)	0(0)	0(0)	6(14)	0(1)	0(0)	1(5)	1(4)	0(0)	0(6)	0(0)	0(0)	8(30)
		2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(1)	0(3)	0(1)	3(6)	0(0)	0(0)	4(11)
		3	ND	ND	ND	ND	119(240)	0(0)	0(0)	0(0)	0(1)	0(0)	0(0)	0(0)	0(0)	119(241)
Bream	6053	1	0(0)	0(4)	2(30)	98(203)	139(332)	1(34)	2(13)	1(188)	1(73)	2(76)	3(225)	0(0)	0(39)	249(1217)
		2	0(0)	0(0)	0(0)	0(18)	23(28)	10(126)	2(65)	4(354)	0(54)	1(96)	4(308)	0(3)	0(18)	44(1070)
		3	ND	ND	ND	ND	1062(4565)	17(486)	0(78)	0(260)	1(111)	1(90)	1(143)	0(8)	0(93)	1082(5834)
Perch	3991	1	0(4)	2(20)	10(495)	6(192)	85(292)	6(23)	0(0)	2(80)	0(17)	0(53)	0(72)	0(0)	0(45)	111(1293)
		2	0(0)	0(0)	0(48)	0(43)	85(118)	10(34)	0(5)	6(75)	0(19)	4(153)	2(114)	0(88)	4(84)	111(781)
		3	ND	ND	ND	ND	252(1203)	0(10)	0(2)	0(3)	0(8)	0(11)	0(3)	0(0)	0(16)	252(1256)
Roach	8664	1	3(220)	0(408)	25(1022)	9(400)	87(609)	4(25)	0(0)	4(32)	0(3)	0(37)	1(23)	0(0)	0(13)	133(2792)
		2	0(0)	0(0)	3(285)	1(157)	24(50)	4(121)	3(22)	15(345)	2(90)	9(188)	8(83)	0(54)	0(99)	69(1494)
		3	ND	ND	ND	ND	373(1680)	1(1)	0(0)	0(3)	0(4)	0(0)	0(0)	0(0)	0(1)	374(1689)

decreases, then the capture probability of a marked fish closer to the tributary marking point increases. The dependence of the capture probability of marked fish on the distance from the marking point was arbitrarily divided according to this *b* value into low dispersal ($b \geq -0.5$) and high dispersal ($b < -0.5$). In the case of low dispersal, fish were distributed close to the tributary marking point. In the case of wide dispersal, fish could be found across the whole reservoir or inflowing river. Model examples for several *b* values are given in Fig. 2. When the model was insignificant, then the capture probability did not depend on the distance from the tributary marking point. In many cases, we experienced a lack of data due to little or no fish caught and thus the model could not be calculated.

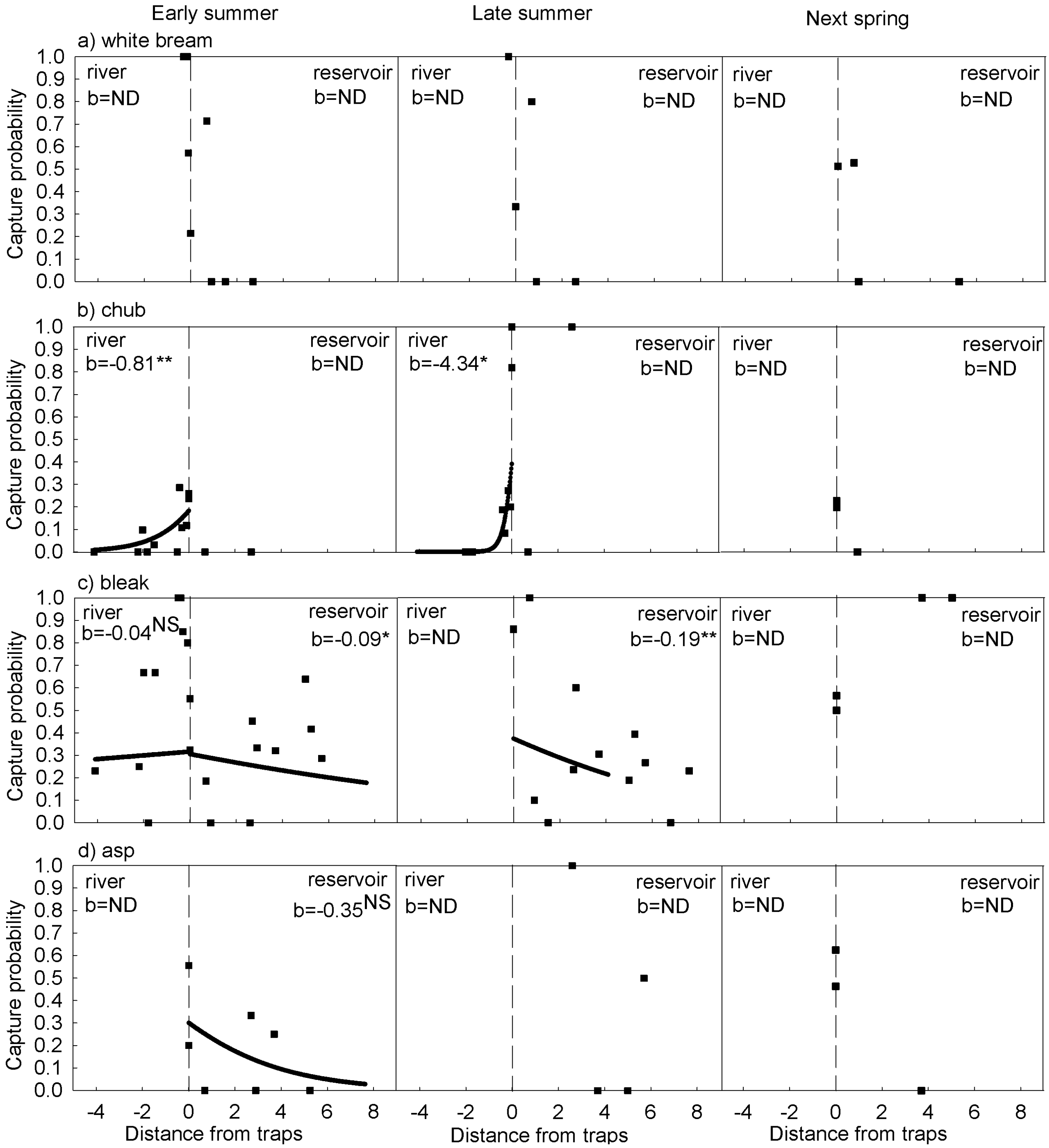

Fig. 3. Fitted functions of the post-spawning dispersal of obligatory tributary spawners during the three sampling periods. Distance from the tributary is on the X axis and the probability of capturing a marked individual on the Y axis. The values and significance of the parameter b for the dispersal model is given for each species as well as river and reservoir locales. Insufficient data for the model are indicated as ND (no data). $^{**}p \leq 0.001$, $^{*}p < 0.05$, NS = not significant.

Results

A total of 33986 fish were captured and marked at the tributary marking point during their migration to tributary spawning grounds in the years 2000-2003. Overall, 22578 fish were sampled in the reservoir and the inflowing river during the subsequent sampling, from which 4462 fish were marked (Table 3).

Dispersal of obligatory tributary spawners

White bream (all marked individuals as well as all individuals captured during sampling) was recorded exclusively near the tributary in all three sampling periods (only three individuals without tags were caught further than 1 km away from the tributary marking point in the main body of reservoir; Table 3). The dispersal model was thus not applicable due to the extremely low dispersal of the marked individuals (Fig. 3a).

Chub was almost exclusively recorded in the tributary during all three sampling periods, thereby also demonstrating a very low dispersal (only two individuals were caught further than 1 km from the tributary marking point in the main body of reservoir; Table 3, Fig. 3b). During next spawning season, marked fish were recorded only at the tributary marking point (Table 3).

Bleak was randomly distributed in the tributary in the early summer, while it left the tributary for the reservoir in the late summer. In the reservoir, bleak exhibited very high dispersal in the early and late summer (Fig. 3c). This species was captured only at the tributary marking point (except three individuals) during the next spawning season (Table 3).

The majority of asp vacated the riverine spawning grounds immediately after reproduction and returned

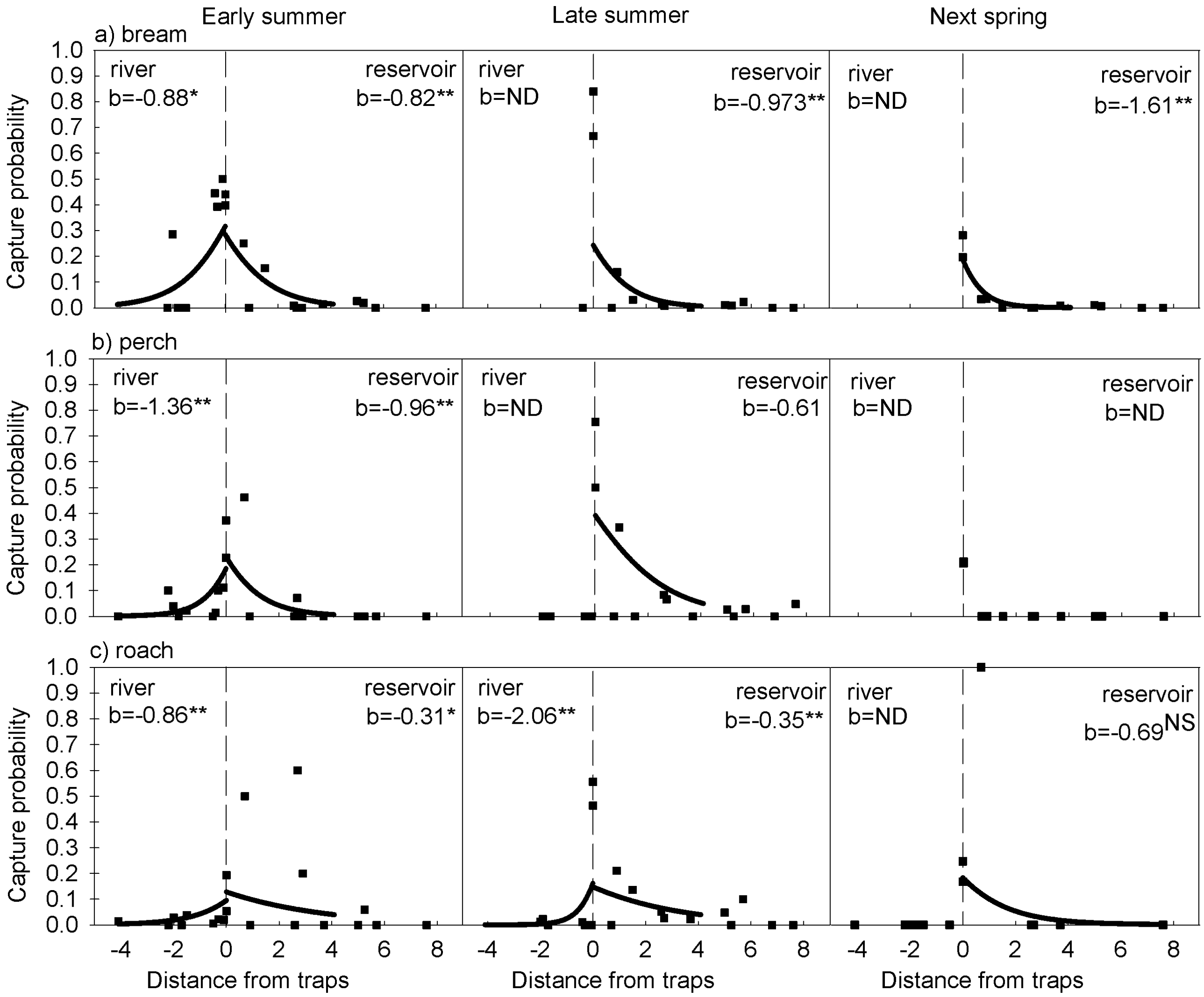

Fig. 4. Fitted function of tributary marked spawning generalist distribution during the three sampling periods. Distance from the tributary is on the X axis and the probability of capturing a marked individual on the Y axis. The values and significance of the parameter b for the dispersal model are given for each species as well as river and reservoir locales. Insufficient data for the model are indicated as ND (no data). $^{**}p \leq 0.001$, $^{*}p < 0.05$, NS = not significant.

to the reservoir. Some asp remained close to the tributary marking point until the early summer and were repeatedly caught in our traps (model insignificant; Table 3, Fig. 3d). In the late summer, only eleven individuals of asp were caught overall and the dispersal model was not applicable to such a low number. However, all individuals (marked and unmarked) were caught only in the main body of the reservoir and four such individuals were marked (Table 3). Such a high proportion of marked fish supported the high dispersal of this species after spawning. In the next spring, asp were recorded only at the tributary marking point (marked and unmarked individuals; Table 3, Fig. 3d).

Dispersal of generalists

During all three sampling periods, the marked bream and perch stayed close to the tributary, demonstrating a relatively low dispersal (Table 3, Fig. 4a, b). Low numbers of marked fish species were recorded further from the tributary marking point (maximum distance of 6 km and 8 km for bream and perch, respectively; Table 3). Proportions of marked fish of both species were highest in the tributary marking point during the next spawning season.

In the early and late summer, a high proportion of tributary marked roach remained close to the tributary marking point in the river (low dispersal; Fig. 4c). Some roach dispersed quickly to the main body of the reservoir, resulting in a high dispersal in the early and late summer. During the next spawning season, the marked roach were found almost exclusively at the tributary marking point (Table 3).

Discussion

The results of this study has revealed that bleak and asp exhibit high post-spawning dispersal, roach an erratic dispersal while other species from both the tributary spawners and generalists groups showed a relatively low dispersal from the tributary. However, some individuals of all species except white bream and chub were observed to wander far from the tributary spawning ground. All species exhibited a relatively high affinity for the tributary spawning ground.

Obligatory tributary spawners

Species classified in our study as obligatory tributary spawners are considered to be mostly eurytopic (except rheophilic chub) with preference for spawning on stony (lithophils – asp), macrophyte rich (phytophil – white bream) or both (polyphil – bleak) substrates (Balon 1975, Aaart & Nienhuis 2003). The possession of these attributes means that all these species should be able to also spawn in the main body of reservoir not only in the tributary. In the case of asp, spawning only in tributaries of reservoirs was supported by the observation of Vostradovský (1974) from the Želivka Reservoir, and thus can be considered as obligatory tributary spawners. On the other hand, while the tributary spawning grounds for bleak and white bream are of high importance, it seems that the location of this activity is not as strictly observed as was suggested by Hladík & Kubečka (2003). Our results showed that a high proportion of these species predominantly and repeatedly spawned in the tributary, as the proportion of marked individuals in the total catch was very high in the whole reservoir during summer sampling as well as in the tributary at spring (Table 3). However, both species were able to occasionally spawn also in the reservoir main body. Main body spawning was observed in bleak only during one year of the study when uncovered stony shores in the littoral areas of reservoir were available (Hladík & Kubečka 2004). The spawning activity of white bream was not detected in the main body of the reservoir but could be assumed from the higher intensity of tributary migration in the year when no submerged macrophytes were available in the reservoir main body (Hladík & Kubečka 2004). It could be concluded that bleak is not an obligatory spawner but most likely "a species with a preference for tributary spawning" because tributary marked fish dispersed throughout the whole reservoir body after spawning. On the other hand, white bream exhibited the lowest dispersal and was almost exclusively caught in the reservoir tributary during all sampling seasons. The predominant occurrence of white bream near the tributary is also in concordance with results obtained from long-term gillnet sampling in the reservoir (Prchalová et al. 2009). This observation suggests that white bream is rather a sedentary species with a high tendency for spawning and feeding in the eutrophic conditions near the tributary part of the reservoir. Therefore, it may utilize tributary spawning simply because of the proximity of this spawning ground to its normal area residence.

Chub was found to migrate to the tributary in the spring and occupy the inflowing river near the tributary marking point during the summer. The observation of spawning chub in the River Elbe (Germany) has shown that chub had migrated to the nearest spawning site a distance 1-13 km far from their feeding habitat (Fredrich et al. 2003). In the Římov reservoir, the tributary is the nearest suitable spawning site because part of the chub population use the main body of reservoir as a winter refuge (Hladík & Kubečka 2003). The observed low dispersal from the tributary spawning ground is in accord with results from another such fish-marking experiment carried out in the River Pilica (Poland), where low dispersal (0-200 m) of chub was found (Penczak 2006). Also Lucas & Baras (2001) suggested that this species often use the same area of the river for spawning and subsequent summer feeding.

A portion of the migrating bleak remained in the tributary until early summer and colonized the whole sampled river section from the tributary marking point up to the Plach Weir. The reason for their prolonged stay in the tributary was probably their multiple-spawning behavior (Kestemont et al. 2001). In the late summer, bleak redistributed to the whole reservoir to feed. Vašek et al. (2003) found that zooplankton is the main diet of bleak in the Římov Reservoir. Zooplankton prey is dispersed throughout the reservoir with the highest density near the tributary and upper part of the water body, and decreases towards the dam (Vašek et al. 2003). The trend of capture probability of a tributary-marked individual as well as the distribution of a whole reservoir population of bleak (Prchalová et al. 2009) followed this gradient of their prey concentration.

The results of our study showed that asp dispersed from the tributary to the upper and middle parts of the reservoir. In spite of the low numbers of captured and recaptured asp during the summer, their preference for the upper part of the reservoir is supported by the findings of Prchalová et al. (2009). Yet in contrary to these findings, it seems that asp is a highly mobile species in the riverine environment. Freidrich (2003) found a surprisingly high dispersal of asp in the River Elbe. The author tracked 34 individuals of asp for one year. The length of occupied river sections, as distance from the marking point, ranged from 10-40 km, with some individuals wandering even 100 km. Asp is a predatory species that mainly feeds on small sized individuals of dominant fish species (Krpo-Cetkovic et al. 2010). In the Římov Reservoir, the highest abundance of dominant fish species and their juveniles were found also in the upper and middle parts of the reservoir (Prchalová et al. 2009). Therefore, asp preference for the near tributary parts of the reservoir could be explained by the highest density of its prey in these parts.

Generalists

Generalists except roach exhibited low post-spawning dispersal during the early and late summer periods. In the early summer, many marked individuals were found at the tributary. Bream is a multiple-spawning cyprinid species (Poncin et al. 1996) and its high occurrence in the tributary was caused by repeated reproductive behaviour. Perch occurrence in the tributary was driven by its own spawning and consequently by predation on cyprinid eggs and juveniles during cyprinid spawning runs. In the late summer, they abandoned the tributary and occurred only in the main reservoir body. A major proportion of the recaptured tributary-marked bream and perch stayed close to the tributary marking point and only a minor proportion migrated a further distance from this area. It could be concluded that a high proportion of perch and bream individuals that spawned and were marked in the tributary used feeding grounds up to 1 km away from the marking point. This observed low post-spawning dispersal as well as division of the population into sedentary and mobile groups is consistent with the studies of Poddubny (1971) and Whelan (1983) in the case of bream and Collette et al. (1977) and Johnson (1978) for perch. The reason for these separate sedentary and mobile sub-populations remains elusive.

Roach dispersal was erratic as a portion of marked roach remained in the tributary during both summer periods while other simultaneously dispersed to the reservoir body soon after spawning. These results correspond to the studies of L'Abée-Lund & Vollestad (1985, 1987). These findings suggest a homing tendency for some individuals and a high mobility for others within the same roach population. Baade & Fredrich (1998) documented that roach in the River Spree had a stationary period when movement was within the range of tens of meters, but subsequently some fish moved a longer distance to find a new location or returned to their former place (the home ranges of observed individuals varied between 75 and 3820 m). It seems that roach is a rather mobile species and the prediction of their post-spawning dispersal is difficult.

Reproductive homing

Many marked individuals of all the observed species were recaptured in the tributary marking point during the next spawning season. This observation demonstrates the presence of reproductive homing of these species, which is the tendency to repetitively return to the same spawning ground. This behaviour can be expected for species with a strong affinity to spawning in the tributary (chub, asp, bleak and white bream) of the Římov Reservoir because of its single tributary. This expectation is supported by the results of our study because during the successive spawning season, these types of fish were almost exclusively caught in the tributary and a high proportion of caught individuals bore the markings from the previous season (52 % in white bream, 50 % in asp, 54 % in bleak and 20 % in chub; Table 3). However, this finding also suggests that 48-80 % of the sampled fish were not caught during the previous spawning migration. There are two reasons for these fish evading initial detection. The first reason pertains to bleak and white bream, which occasionally spawned in the main body. Therefore these species could change between spawning in the main body and in the tributary from year to year. The second reason pertains to all the aforementioned species. The source of error of the present study is that it was extremely difficult to keep giant traps operational during high water discharges. Despite considerable effort to clean the trap wings and additional weight of the lead line, the traps were still not functional for about one tenth of the total study time. Events during these periods may have been significant as these high discharges could have stimulated both active and passive migrations (Lucas & Baras 2001).

The repetitive return to the same spawning ground has already been documented for generalists such as bream (Poddubny 1971, Whelan 1983), roach (Wilkonska 1967, L'Abée-Lund & Vollestad 1985) and perch (Kipling & Le Cren 1984). The proportion of marked individuals of these species in the tributary catch was lower than for most species with a strong tributary spawning boundary, varying between 21-23 % (Table 3) during the next spawning period. In the main body of the reservoir, only spawned bream were detected because perch and roach have unique spawning behaviours that precluded their capture, such as spawning at night for short period for the latter and depth stratified spawning for the former. The proportion of tributary marked bream in the main body of the reservoir was only 1.6 %. Therefore, we can conclude that a relatively large proportion of bream used the tributary spawning grounds repeatedly. However, the finding of marked bream in the main body of the reservoir suggests some individuals that had used the tributary spawning site reproduced in the reservoir body during the next season.

Conclusions

This study is unique in describing the post-spawning dispersal of seven different species in a single water body. In the case of white bream and bleak, it is the first observation of any dispersal pattern at all. The findings of the study confirmed the importance of tributary spawning grounds for the whole reservoir populations of white bream, chub, bleak and asp. The post-spawning dispersal of species with high affinity to spawning in the tributary of the Římov Reservoir (white bream, chub, bleak and asp) presumably was shaped mainly by their feeding ground requirement. However, the influence of diet concentration to this dispersal pattern could not be directly proven by this study because diet availability and consumption of tributary spawners was not studied during our experiment. Also other unknown overlying environmental and physical conditions could shape distribution of these species. The post-spawning dispersal of generalists showed that the assumed 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, and confirmed that the post-spawning dispersals of these species are driven by species-specific behavioral patterns.

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