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Abstract. The effect of water temperature and flow on the migration of fish was observed using weekly inspections of a fishpass on the lowland section of the River Elbe (Střekov, Czech Republic) from spring to fall 2003 and 2004. The effect was examined separately for immature (up to 2 years old) and adult fish and also the most abundant species (roach *Rutilus rutilus*, bleak *Alburnus alburnus*, chub *Squalius cephalus*, gudgeon *Gobio gobio*). More than 13 thousand fish from 23 species were recorded in the fishpass during both years. The highest levels of fish occurrence in the fishpass were observed during the spring spawning migrations of adults (April-May) as well as during the late summer and fall migrations of adult and immature fish (September-November). While the total number of both fish age categories was significantly related to the interaction of water temperature and flow, however, responses of individual species and age categories differed from each other. The numbers of adult bleak, chub and gudgeon increased with higher temperature. The maximum numbers of adult bleak migrated at medium values of temperature (15-20 °C) and flow (140-270 m^3 s^{-1}). The abundances of adult chub and adult plus immature gudgeon were higher with higher flow. The numbers of immature bleak and chub decreased with increasing flow. The numbers of adult and immature roach were influenced only by water flow with maximal numbers migrating under medium values of flow. Generally, we observed that immature fish and small- and middle-sized species required lower values of water flow than adult fish or large species to facilitate their movement. The exception was gudgeon, which required higher values of flow for its migration, a feature that could be related to its bottom dwelling nature or rheophily.

Key words: cyprinids, migration, general linear mixed models, adult fish, immature fish, discharge

Introduction

Considering all possible seasonal movements of fish in rivers, upstream spawning migrations are believed to be the most obvious (Lucas & Baras 2001). Feeding and refuge seeking represent other causes of intensive fish movements (Prignon et al. 1998, Travade et al. 1998). Besides internal mechanisms, fish migrations are controlled by a number of environmental factors, from which water temperature, water flow and photoperiod are listed as the most important (Northcote 1998).

We studied fish migration using catches in a fishpass that is located in the lowland section of the River Elbe, Central Europe. Due to such location, we expected mostly cyprinid species (family Cyprinidae) to occur in our samples. Recently, more attention has been focused especially on the spawning migrations of adult cyprinids in Europe (e.g. Geeraerts et al.

2007, Rakowitz et al. 2008, Slavík et al. 2009), but our knowledge about the effects of water temperature and flow on movements of these fish is still limited and occasionally even inconsistent. The number of cyprinids migrating to spawning areas increases with water temperature. A water temperature threshold that plays a role in initiating spring migrations of cyprinids has been described (6-13 °C, see review provided by Lucas & Baras 2001). Once this threshold is exceeded, further rises in temperature are not significant for the course of spawning migrations (Lucas 2000). Site-specific low and even extremely high water flow may disable the spawning migrations of cyprinids (Santos et al. 2002, Slavík et al. 2009). Besides these extreme values, water flow has not been found to directly influence spawning migrations of cyprinids (Lucas & Batley 1996, Slavík & Bartoš 2004). These conclusions are based mainly on observation of adult fish performing spring spawning migrations. But is there a general effect of water temperature and flow on fish migration, and is this effect the same for different sizes of fish?

The aim of this study was to describe a relationship between fish occurrence in the fishpass and the factors water temperature and flow. We expected to confirm a general temperature threshold is required for the onset of the migration in the spring. Above that threshold the number of fish was hypothesized to be defined by water flow. Furthermore, we separated the observed number of fish into two age categories, adult and immature fish, and we assumed that the effect of water temperature and flow observed would differ between them. Due to the lower kinetic energy of smaller fish, they require lower values of water flow to facilitate their movement (Slavík et al. 2009). For the same previously described reasons, we expected that the effect of water temperature and flow would vary between species. We therefore analyzed the four most abundant species occurring in the fishpass in addition to the total number of migrating fish.

Material and Methods

Study area

The pool fishpass is situated 321 km downstream from the River Elbe spring, Czech Republic (total catchment area 148268 km^2 in Germany, Czech Republic, Austria and Poland, Fig. 1). The fishpass is part of a lock (50°38′ N, 14°02′ E) in Střekov, close to Ústí nad Labem town.

The fishpass consists of 45 concrete pools – 38 standard and seven resting pools, which are extended in length (Fig. 1). The standard chambers are 3 m long, 2 m wide and 1.2 m deep. Dividing screens have two diagonally located orifices (0.3 × 0.3 m). The head between the chambers is 0.2 m. The total length of the fishpass is 250 m and the vertical difference between the downstream entrance and the upstream exit is 9 m. The average flow in the fishpass is 0.4 m^3 s^{-1}. The bottom is flat along the whole trail. The entrance is located approximately 150 m from the dam of a hydropower plant. The water outflow at the entrance forms an angle of ca 45 degrees with the main river flow. The location of the exit is not convenient for downstream fish migration as the exit angle and river flow is 90° and the exit area is negligible with respect to the river flow (Fig. 1).

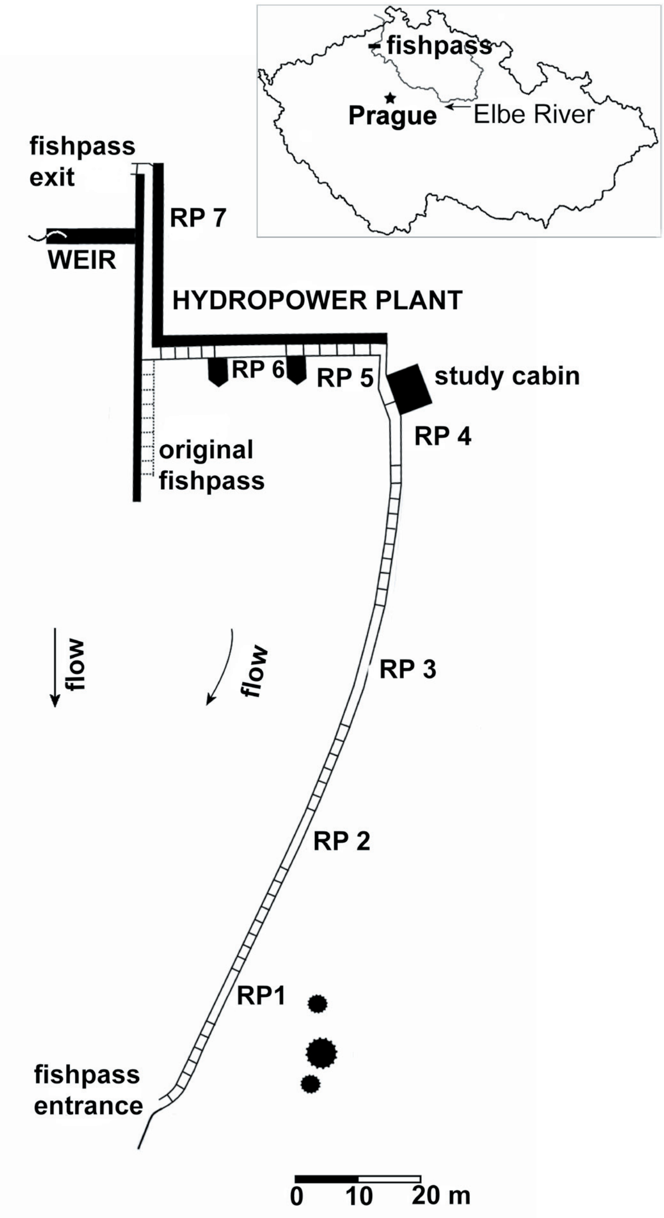

Fig. 1. Design of the studied fishpass and its location on the River Elbe in the Czech Republic. RP – resting pools.

Sampling procedures

Fish sampling in the fishpass was conducted weekly from 26 March to 6 November 2003, from 2 April to 1 July 2004 and from 9 August to 16 November 2004. Every sampling started around noon. To sample fish, the water inlet to the fishpass was closed. As the water drained, fish moved downstream to the last pool close to the entrance. Fish were captured using nets at this locality. All fish were identified and measured for standard lengths to the nearest mm and released. The age categories were separated according to species-specific standard lengths into immature and adult fish. The length thresholds were: 150 mm for roach, chub, barbel, perch, white bream, common bream and nase; 80 mm for bleak and gudgeon; 120 mm for dace.

During each sampling period, the water temperature was measured directly in the fishpass (the pool in front of the study cabin, Fig. 1) using the Oxi 340 microprocessor (WTW, Germany). Data on the water flow was provided by the Elbe River Authority, the responsible body for monitoring the water flow at the weir. The window of the upstream entrance (exit) of the fishpass is not regulated, and as such its flow is directly dependent on the flow at the weir. The course of the water flow and temperature over the sampling period is given in Fig. 2.

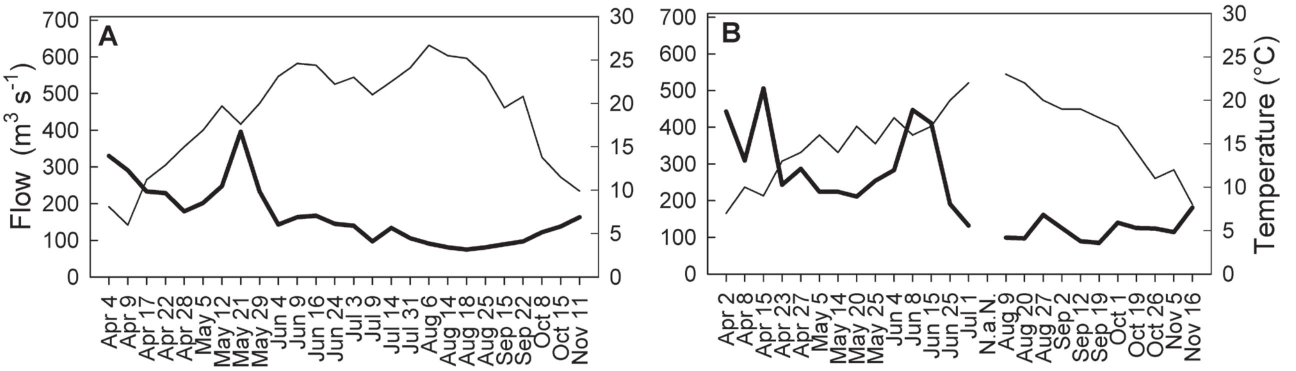

Fig. 2. *The course of water temperature (thin line) and water flow (thick line) during the study period in 2003 (A) and 2004 (B).*

Statistical analysis

Associations between the variables were tested using the General Linear Mixed Model (GLMM). The dependent variables were the numbers of fish recorded in the fishpass. Five separate models were applied for the dependent variables of the total number of fish (GLMM I) and numbers of four most abundant species, roach (GLMM II), bleak (GLMM III), chub (GLMM IV) and gudgeon (GLMM V). The data were $\log_{10}$ transformed for normality before GLMM analyses. The effect of the sampling year was tested first and was not found to be statistically significant in any model (GLMM I-V). Subsequently, to account for the repeated measures across different years, all analyses were performed using mixed model analysis with the year as a random factor using the PROC MIXED software (SAS, version 9.1). Fixed effects were the classes 'age category' – immature, adult and 'month' – April, May, June, July, August, September, October, November and the continuous variables 'temperature' (6-26.7 °C) and 'flow' (75-505 m^3 s^{-1}). The significance of each fixed effect, including interaction terms, in the mixed GLMM model was assessed by the F-test, with sequential dropping of the least significant effect, starting with a full model. Fixed effects that were not statistically significant are not discussed further. In the case of unbalanced data with more than one effect, the statistical mean for a group may not accurately reflect the response of that group, since it does not take other effects into account. Therefore we used the least-squares-means (LSM) instead. LSM (further referred to as 'adjusted means') are in effect, within-group means appropriately adjusted for the other effects in the model.

Associations between the dependent variable and other continuous variables were estimated by fitting a random coefficient model using the aforementioned PROC MIXED program as described by Tao et al. (2002). With this random coefficient model, we calculated the predicted values for the dependent variable and plotted them against the continuous variable with predicted regression lines. The degrees of freedom were calculated using the Kenward-Roger method (Kenward & Roger 1997).

Table 1. *List and numbers of fish caught in the fishpass in 2003 during each sampling period.*

Common name	Scientific name	Month	April					May				June				July				August				Sept.		Oct.		Nov.
		Date	4	9	17	22	28	5	12	21	29	4	9	16	24	3	9	14	31	6	14	18	25	15	22	8	15	5
Cyprinidae																												
Bleak	*Alburnus alburnus*		1	2	272	66	224	272	49	37	72		6	2	8		14	4	40		28	3	219	268	90		37	1
Roach	*Rutilus rutilus*		14		253	256	106	10	4	2	4			1		4		1				5	7	11	336	56	14	8
Barbel	*Barbus barbus*							2		3	1				1	3	2	2	11	11	13	35	31	7	4	41	327	1
Dace	*Leuciscus leuciscus*						1		1									1		2	37	80	18	3	13	85	178	2
Chub	*Squalius cephalus*		9	7	7	17	116	7	15	17	23	2	12	17	14	15	13	24	12	8	2	7	5		2	2	1	6
White bream	*Blicca bjoerkna*					24	42	21	125	9	63		7		1	3	3	1								4		
Gudgeon	*Gobio gobio*						2	21	51	43	4	4	7		2	7		3	2	1	8	3	15					
Common bream	*Abramis brama*						7	9	38	6	8	1	3		5	3	3	1	1							1		
Nase	*Chondrostoma nasus*						3	3	16																2	1	30	
Ide	*Leuciscus idus*				6	3	8		5	4	7				2	1		3			5	3	5				2	
Asp	*Aspius aspius*				1	2	3		7	2		2			1													
Crucian carp	*Carassius carassius*								4		3		3								1							
Tench	*Tinca tinca*									1																		
Percidae																												
Perch	*Perca fluviatilis*											1								2	2		41	4	2	1	5	
Pikeperch	*Sander lucioperca*															1					1	1		1				1
Brown trout (Salmonidae)	*Salmo trutta fario*							1		1	1																	
Grayling (Thymallidae)	*Thymallus thymallus*		1																									
Catfish (Ictaluridae)	*Ameiurus nebulosus*								2			7	19	12	1	2		2	1	1			1					
Eel (Anguillidae)	*Anguilla anguilla*											2	12	2	2	5	2											
Total number			25	9	539	368	512	346	317	125	186	19	69	34	37	44	37	42	67	25	97	137	342	294	449	191	594	19
Number of species			4	2	5	6	10	9	12	11	10	7	8	5	10	10	6	10	6	6	9	8	9	6	7	8	8	6
Water temperature (°C)			8.1	6	11.2	12.9	15	16.9	19.7	17.6	20	23.1	24.6	24.4	22.2	23	21	22.5	24.1	26.7	25.5	25.2	23.2	19.5	20.8	13.8	11.5	9.9
Water flow ($m^3 s^{-1}$)			330	291	233	229	179	202	248	396	233	143	163	167	145	140	97	134	106	91	81	75	81	89	97	122	138	163

Table 2. *List and numbers of fish caught in the fishpass in 2004 during each sampling period. Scientific names of species not previously mentioned: Prussian carp* Carassius gibelio*, rudd* Scardinius erythrophthalmus*, Northern whitefin gudgeon* Romanogobio belingi *and rainbow trout* Oncorhynchus mykiss.

Common name	Month	April					May				June				July	August			September			October			November	
	Date	2	8	15	23	27	4	14	20	25	4	8	15	25	1	9	20	27	2	12	19	1	19	26	5	16
Cyprinidae																										
Bleak			125	19	23	200	157	18	7	1	62		1	151	100	5 012	327	88	304	69	12	33	193	34	34	
Roach			51	3	182	167	58	8	1		5					9	8	8	3	18	5	6	12	8	31	5
Gudgeon					11	97	42	11			1			1				1								
Chub			1	1	1	4	10	3			34	1	6	33	24	6	7	4	1	6	3	2	5	4	2	
Dace		1	7	1			2															6	34	6	16	
Common bream					1	4	8	28	12		9	2		1	2		1	1							1	
Prussian carp							13	5	10		11	3	1	12	6	2	1									
White bream					1	8	9	18	7		7	1		1			1	1	1						1	
Barbel																	2	2		4	5	8	11	4	7	4
Ide					2	4	3	1	1		2	1		1			1	1							6	
Nase						2	5	1			8									2						
Asp							1							1		2	1	1		2	1					
Rudd						3	1		1		1															
Nothern whitefin gudgeon															1		1									
Percidae																										
Perch							2				4		2	3		3	4	10		12	7	4	3	14	2	
Pikeperch									1																	
Salmonidae																										
Brown trout						1								1				1								
Rainbow trout													1			1										
Catfish (Ictaluridae)														2	1	5	2									
Eel (Anguillidae)													3	1		3										
Total number		1	184	24	221	490	311	93	40	1	144	8	14	208	134	5043	368	129	313	122	39	65	264	76	109	9
Number of species		1	4	4	7	10	13	9	8	1	10	5	6	12	6	9	12	11	4	7	6	6	6	6	9	2
Water temperature (°C)		7	9.9	8.5	13.3	13.6	16.1	14.4	16.5	15.1	18.3	16	17.3	20.3	21.5	23.1	22.2	20.3	19.4	19.2	18.1	17.4	14.1	11.0	12.3	8.0
Water flow ($m^3 s^{-1}$)		443	309	506	243	287	224	224	211	254	283	447	411	191	132	99	97	161	125	89	85	140	125	124	114	181

Table 3. Type 3 tests of fixed effects for the final GLLM models.

Effect	Num DF	Den DF	F	P <
For GLMM I				
month*age category	15	83.9	8.16	0.0001
temperature*flow*age category	2	67.3	6.52	0.0026
For GLMM II				
month*age category	15	83.9	4.19	0.0001
flow*age category	2	46	5.28	0.0086
For GLMM III				
month*age category	15	82.4	4.38	0.0001
temperature*flow*age category	2	67.3	3.64	0.0315
For GLMM IV				
month*age category	15	82.5	2.31	0.0085
temperature*flow*age category	2	66.3	7.49	0.0012
For GLMM V				
month*age category	15	83.9	4.02	0.0001
temperature*flow*age category	2	67.3	10.72	0.0001

Results

A total of 13266 fishes representing 23 species were caught in the fishpass (Table 1, 2). Cyprinids (Cyprinidae) represented more than 96 % of the catch during both years. The most abundant and also the most frequent species recorded were bleak, roach and chub. Fish started to occur in the fishpass in significant numbers when the water temperature had reached 8 °C in the spring and fish stopped to utilize the fishpass when water temperature dropped below 10 °C in the autumn.

The final GLMM I, III, IV and V models included fixed factors expressed as interaction between 'month' and 'age category' and interaction between 'flow', 'temperature' and 'age category'. The final GLMM II model of roach occurrence in the fish pass included the fixed factor of interaction between 'month' and 'age category' identical to other models and the interaction between 'flow' and 'age category'. Details of the final GLMM models are shown in Table 3.

The total number of fish of both age categories caught in the fishpass varied according to the month (Fig. 3A). Two peaks were generally found: the first occurred during April and the second during October. The numbers of adult fish were significantly higher than those of immature fish in the April to July period. The numbers of both age categories were equal from August to November. The total number of adult fish increased with water temperature, with an optimum at medium temperatures (15-20 °C) and medium flow conditions (160-300 $m^3 s^{-1}$, Fig. 4A). The occurrence of immature fish decreased with increasing temperature and water flow. Their minimum numbers were recorded at the highest values of both temperature and flow (Fig. 4B).

The pattern of roach occurrence in the fishpass was similar to the general pattern described above, with more roach present in the fishpass during the spring than in the autumn (Fig. 3B). The numbers of adults and immature fish did not differ within individual month. Only flow had a significant influence on roach numbers with the highest numbers of both adult and immature fish recorded during medium values of flow (170-280 $m^3 s^{-1}$, Fig. 5).

The occurrence of bleak in the fishpass was similar to the general pattern described above, with more immature bleak present in the fishpass during the autumn than in the spring (Fig. 3C). The numbers of adult and immature bleak were similar in all monitored months with exception in April. The number of adult bleak peaked at medium values of temperature and flow as well (Fig. 6A). The number of immature bleak was stable across the temperature range and decreased with flow (Fig. 6B). The minimum numbers of immature bleak occurred in the fishpass at the minimum values of temperature and maximum values of flow.

The numbers of both age categories of chub did not differ throughout the season (Fig. 3D). Generally, the numbers of adults were higher than immature chub, which was significant in April, May and July. The number of adult chub increased with both temperature and flow, whereas the response of the immature fish was converse (Fig. 7).

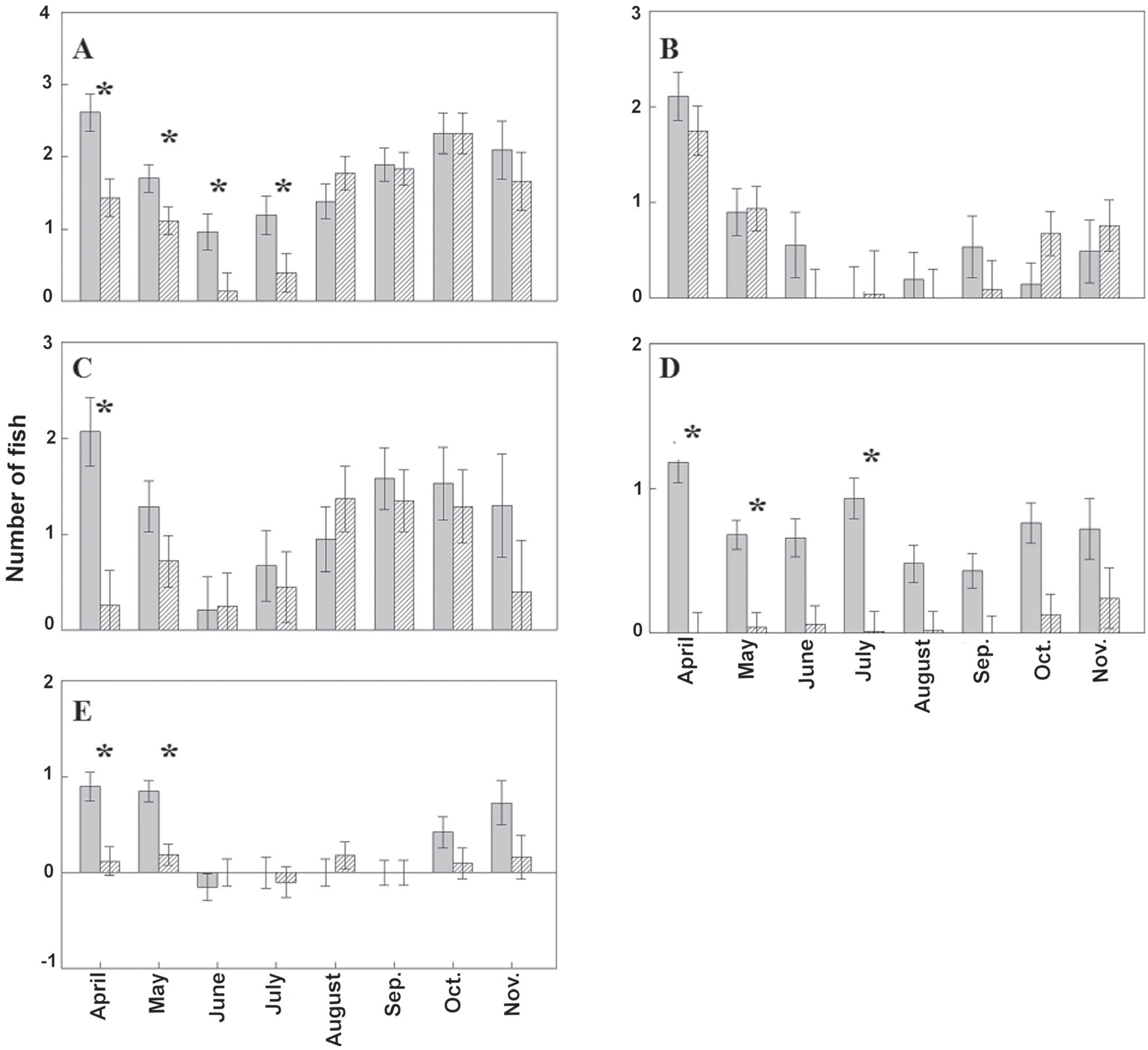

Fig. 3. *Numbers of (A) all fish, (B) roach, (C) bleak, (D) chub and (E) gudgeon caught in the fishpass throughout the months for both years studied. Grey columns refer to adults, striped columns to immature fish. A star above columns indicates a significant difference ($p < 0.05$) in numbers of adult and immature fish. Values are the adjusted means (+/– SE) of log_{10} transformed data.*

The number of adult gudgeon followed the general pattern of fish occurrence in the fishpass throughout the season. The number of immature gudgeon had no clear pattern, however (Fig. 3E). The number of adults was usually higher than that of immature gudgeon, which was significant especially in April and May. Both age categories of gudgeon responded to temperature and flow similarly, with numbers decreasing with both decreasing temperature and flow (Fig. 8).

Discussion

The movements of fish through the studied fishpass followed a clear seasonal pattern in both of the years 2003 and 2004. The numbers of adult and immature fish occurred in the fishpass were significantly influenced by the interaction of water temperature and flow.

The seasonal pattern of migration consisted of the spring spawning migrations of adults (April, May), the summer period of lower activity (June, July) and the late summer and fall refuge seeking migrations of both adults and immature fish (August-October). Fish started to occur in the fishpass in significant numbers when the water temperature had reached 8 °C, which agreed with the temperature threshold for the spring spawning migrations of lowland fish mentioned in other studies (Kotusz et al. 2006, Geeraerts et al.

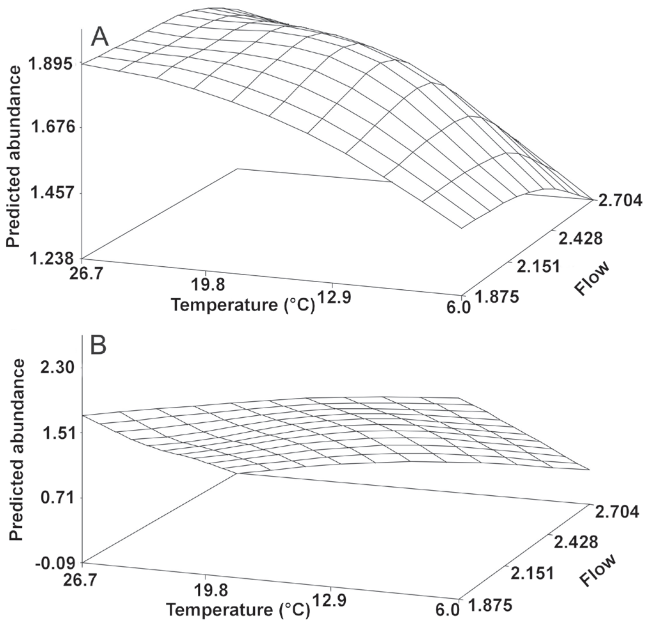

Fig. 4. *Predicted values (log_{10} transformed data) of the total number of adult (A) and immature (B) fish caught in the fishpass plotted against water flow (log_{10} transformed data in m^3 s^{-1}) according to water temperature (°C).*

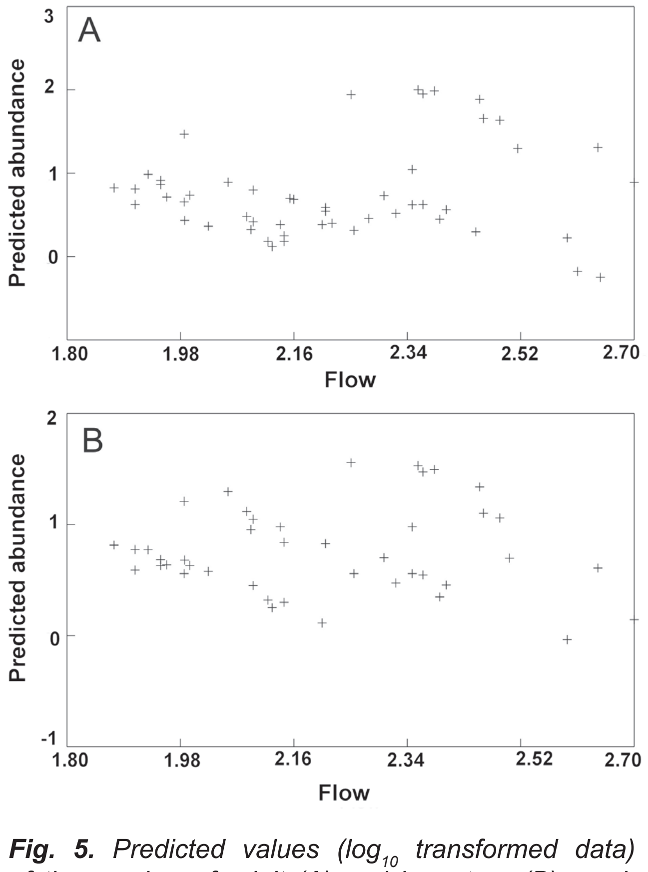

Fig. 5. *Predicted values (log_{10} transformed data) of the number of adult (A) and immature (B) roach caught in the fishpass plotted against water flow (log_{10} transformed data in m^3 s^{-1}).*

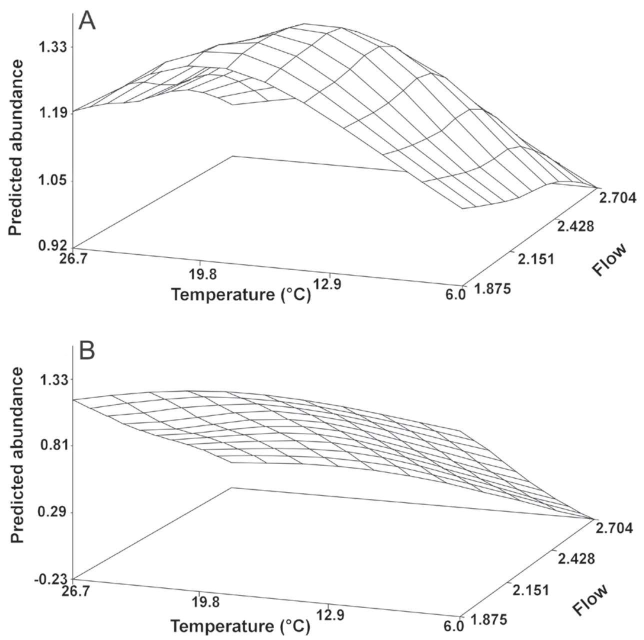

Fig. 6. *Predicted values (log_{10} transformed data) of the number of adult (A) and immature (B) bleak caught in the fishpass plotted against water flow (log_{10} transformed data in m^3 s^{-1}) according to water temperature (°C).*

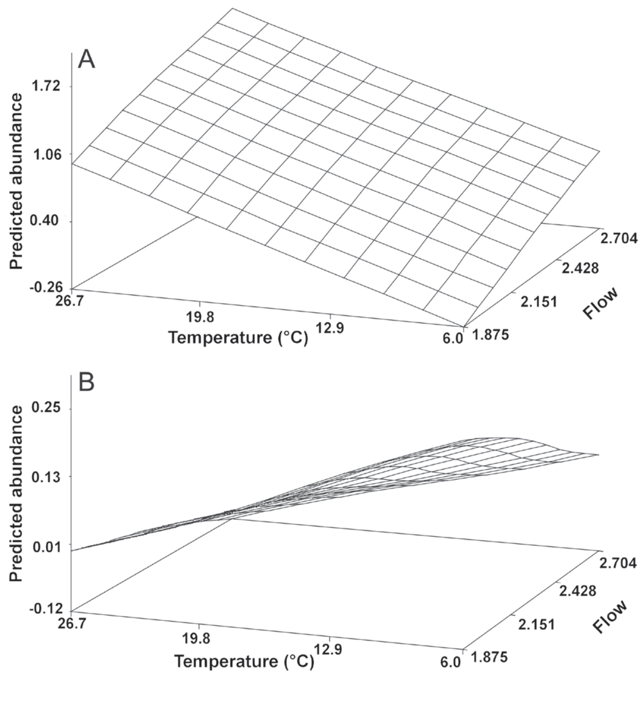

Fig. 7. *Predicted values (log_{10} transformed data) of the number of adult (A) and immature (B) chub caught in the fishpass plotted against water flow (log_{10} transformed data in m^3 s^{-1}) according to water temperature (°C).*

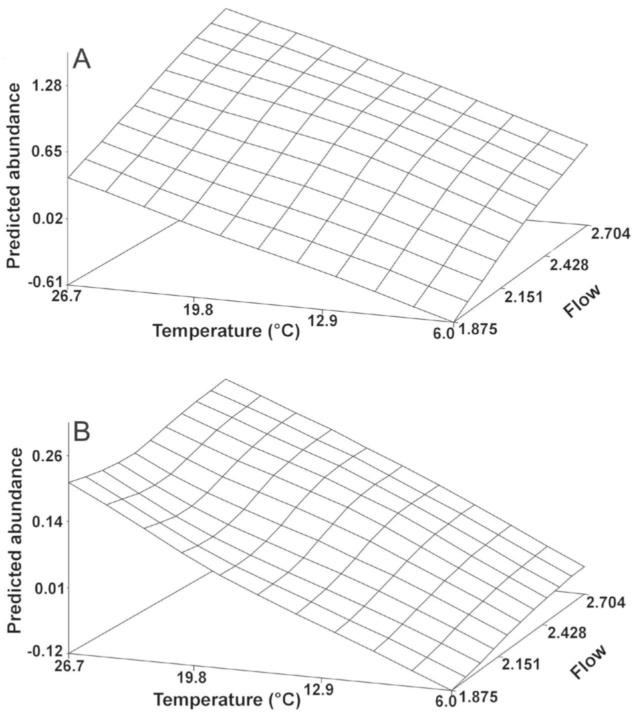

Fig. 8. *Predicted values (log_{10} transformed data) of the number of adult (A) and immature (B) gudgeon caught in the fishpass plotted against water flow (log_{10} transformed data in m^3 s^{-1}) according to water temperature (°C).*

2007, Ovidio & Philippart 2008). When the water temperature in the spring dropped below 8 °C, the migration activity decreased markedly (Table 1) as was previously described by Lucas (2000) and Hladík & Kubečka (2003). All 23 fish species registered in the fishpass were recognized as potential migrants (see Lucas & Baras 2001). June and July activities could be most probably considered as local movements (Slavík et al. 2009). Large numbers of immature cyprinids started to migrate in August and this phenomenon has been described in detail by Prchalová et al. (2006a). The number of fish decreased dramatically in the autumn when water temperature dropped below 10 °C. Both adult and immature fish were influenced significantly by water temperature. For adults, increasing temperature was more important, an element connected with the spring spawning migration. On the other hand, immature fish migrated at any temperature (bleak) or preferred lower (chub) or higher temperatures (gudgeon). These responses were the same in varying values of water flow.

During the spring spawning migration, bleak numbers peaked at 10-16 °C temperatures, roach at 11-13 °C, and chub at 15-16 °C. All these values are within the published ranges of temperature requirements for spawning migrations of these European species (e.g. Jurajda et al. 1998, Prignon et al. 1998, Travade et al. 1998, Kotusz et al. 2006). Common bream, white bream, gudgeon and nase exhibited a maximum occurrence in the fishpass during a steep temperature increase in 2003, which corresponds with observations by Lelek & Libosvárský (1960) and Rakowitz et al. (2008). In 2004, these species migrated with the highest intensity in a period of 13-16 °C water temperature, which is in agreement with the finding of Donnely et al. (1998) determining the minimal 13 °C temperature for the migration of common bream. However, it should be noted that reported temperature threshold and ranges optimal for migrations values could be site specific (Jonsson 1991, Jurajda et al. 1998). This stipulation could be valid for the reported values of water flow as well.

Eel occurred in the fishpass only during the summer (June-August) and all individuals were immature fish of similar size (200-400 mm SL). The presence of eel in the fishpass was most probably related to their upstream migration from the sea (Slavík 1996). The ascent of eel into fresh waters runs from April to September, with a peak in May to July (Porcher 2002), which corresponds with the summer occurrence of eel in the studied fishpass located approximately 770 km from the North Sea.

The previously published effects of water flow varied from no effect (Lucas 2000, Kotusz et al. 2006, Geeraerts et al. 2007) to recorded optimal values of water flow for the fish migration and its cessation in extremely high or low water flows (Horký et al. 2007, Slavík et al. 2009). Rakowitz et al. (2008) summed up that most studies on fish migration show the positive effect of decreasing water level on the number of migrating fish. In this study, the effect of water flow was species and size specific. Beach (1984) showed that non-leaping species (e.g. Cyprinidae, Percidae, Esocidae) must swim at least 30 % faster than the opposing flow to progress upstream. As the absolute swimming speed increases with fish size (see Wolter & Arlinghaus 2003), smaller fish are supposed to migrate in conditions of the lower water flow in comparison to adult fish (Slavík et al. 2009). This assumption was supported by our study: Adult bleak (small-sized species) and adult and immature roach (middle-sized species) migrated mostly during medium water flows (Slavík et al. 2009), whereas the number of adult chub (large-sized, rheophilous species) peaked during the highest flows. On the other hand, the number of immature bleak and chub decreased with increasing flow.

However, this pattern had an exception. The numbers of both adult and immature gudgeon (small-sized species) increased with temperature and flow almost linearly (Fig. 8). Gudgeon was the smallest species analyzed, and thus a negative correlation of occurrence with water flow would be expected. Nevertheless, as a benthic and reophilous species, gudgeon could react to increased water flow by increased migration activity, as is the case with the barbel (large-sized species; Baras et al. 1994, Slavík et al. 2009). Water velocity is represented by its relative minimum at the bottom and it is possible that benthic species need higher water flow to reach the same intensity of movements as species occupying the water column (i.e. bleak, roach and chub in this case).

The numbers of fish and the pattern of the spawning migration through the fishpass were unsatisfying for barbel, dace and asp. According to the fall catches in the fishpass and electrofishing in the adjacent river stretch (Prchalová et al. 2006b), these species were abundant in the river. However, nearly no adult specimens appeared in the fishpass during the spring, despite that these species are well known spawning migrants (Lelek & Libosvárský 1960, Lucas & Frear 1997, Jurajda et al. 1998, Lucas 1998). It seems that the fishpass, especially the location of its entrance (Bunt 2001), was unfavorable for the migration of these species, most probably because of their high degree of rheophily (Baras et al. 1994).

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