Arch. Hydrobiol. 159 3 395–407 Stuttgart, March 2004

Spatial distribution of drifting cyprinid fishes in a shallow lowland river

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With 3 figures and 4 tables

Abstract: We investigated downstream drift of the early developmental stages of cyprinid fishes in a shallow lowland river to ascertain the spatial dynamics of this mode of transport. Drift density and mean body size were compared among four sampling stations positioned at different distances from the riverbank through a series of diel sampling periods. Common bream (*Abramis brama*) was the dominant species (76 %), followed by silver bream (*Abramis bjoerkna*) and roach (*Rutilus rutilus*). Ninety-five percent of drifting fish were larvae. Most fish drifted 1 to 3 m from the shore, at a maximum density of 131 fish 100 m^{-3}. Relatively few fish drifted in midchannel and most fish drifted at night. Body size of drifting fishes was positively correlated with distance from the bank. Consistent results were obtained from analysis of developmental stages, with younger larvae drifting near to the bank and older larvae and early juveniles drifting in midchannel. We propose that the spatial distribution of drifting fish is linked to their swimming ability and fish larvae may enter the river current as a means of active transport.

Key words: downstream drift, early life history, larval dispersal, fish migration, young-of-the-year fish, 0+ juvenile fish.

Introduction

Drift, the downstream movement of aquatic organisms, has been the focus of research by freshwater ecologists over the last three decades. Though a substantial body of knowledge to explain invertebrate drift has accumulated (Müller 1974, Brittain & Eikeland 1988, Anholt 1995, Kopp et al.

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DOI: 10.1127/0003-9136/2004/0159-0395 0003-9136/04/0159-0395 $ 3.25

2001), an understanding of downstream movements in fishes remains largely incomplete (SCHMUTZ & JUNGWIRTH 1999). Drift in fishes typically occurs during the early developmental stages (free embryos, larvae and juveniles) (BROWN & ARMSTRONG 1985, PAVLOV 1994) and a seasonal peak of drift abundance in the first weeks after hatching is typical. In temperate lowland rivers in the Northern Hemisphere this peak usually occurs in June and July (GALE & MOHR 1978, MUTH & SCHMULBACH 1984, PAVLOV 1994, REICHARD et al. 2002 a). Downstream movements of the early developmental stages of fishes encapsulate several ecologically distinct phenomena, juvenile migration of diadromous fishes (NORTHCOTE 1962, JOHNSTON 1997, MORIYAMA et al. 1998), short migrations linked to habitat shift (SAVENKOVA & ASANOV 1988, SCHMUTZ & JUNGWIRTH 1999), juvenile dispersal (SCHMUTZ et al. 1997, ROBINSON et al. 1998) and passive wash-out by strong river discharges (HARVEY 1987).

The spatial distribution of drifting fish within a river channel varies among taxa and with the physical features of the river (PAVLOV 1994). Except for large Russian rivers (ZAMBRIBORSHCH & NGUEN TAN CHIN 1973, PAVLOV et al. 1977 a, PAVLOV et al. 1977 b), few studies have been completed in Europe. In the studies that have been undertaken, sampling has been directed at either the midchannel (COPP & CELLOT 1988, SCHMUTZ et al. 1997) or nearshore (JURAJDA 1998, REICHARD et al. 2001). Only PEŇÁZ et al. (1992) directed sampling to both nearshore and midchannel habitats.

In this study we present quantitative comparisons of the spatial distribution of drifting fishes across a temperate lowland river. We studied differences in total drift abundance, in taxonomic composition, developmental stage and body size of fishes among four sampling stations differing in distance from the bank and water velocity.

Material and methods

Study site

Sampling was conducted in the River Dyje (Danube basin, Czech Republic) in 1999. The Dyje is a shallow lowland river with a daily discharge varying between 28 and $32\,m^3s^{-1}$ during the present study, controlled from a reservoir located 40 km upstream. The width of the river at the sampling site was 46 m, and riffles and pools were absent from the main channel except near weirs. The sampling site represented a typical stretch of the river and was not influenced by weirs. The closest weir was 3.5 km upstream from the sampling site, and there are no weirs downstream.

The maximum depth of the river in the study area was approximately 1 m, and the river bottom was mainly gravel with some sand and pebbles. The riverbank was reinforced with cobbles of 10–20 cm and was overgrown with grasses. There were some

Table 1. Habitat characteristics of sampling stations in the River Dyje for three sampling periods, showing distance from the bank to midpoint of the net, mean depth of water column, and mean current velocity. Means are given with 1 standard error.

	Distance (m)			Depth (m)			Water velocity (m s^{-1})		
	17 June	24 June	1 July	17 June	24 June	1 July	17 June	24 June	1 July
Station 1	0.4	0.4	0.5	0.40±0.062	0.40±0.056	0.26±0.048	0.28±0.011	0.20±0.000	0.20±0.008
Station 2	1.1	1.0	1.3	0.47±0.021	0.47±0.020	0.29±0.031	0.33±0.000	0.27±0.000	0.25±0.032
Station 3	2.7	–	2.8	0.58±0.028	–	0.45±0.036	0.42±0.000	–	0.42±0.000
Station 4	–	13.3	12.8	–	1.10±0.000	1.01±0.042	–	0.61±0.000	0.54±0.020

gravel bars and exposed beaches in shallow areas during the lowest river discharges in summer.

Sampling regime

Samples were collected three times during the period of peak drift (Reichard et al. 2002 a) on 17–18 June, 24–25 June and 1–2 July 1999. Samples were collected from three (17–18 and 24–25 June) or four (1–2 July) sampling stations, at increasing distances from the riverbank. The depths at which samples were taken, distance from the bank, and current velocity are presented in Table 1.

A passive drift net was used at each station. The net was 2 m long and comprised a conical shaped net (mesh size 0.5 mm) with an opening of 0.13 m^2 (0.49 m width by 0.27 m depth) leading to a plastic collection bottle at the cod-end. Sampling started in the late afternoon (17:00–18:00) and continued hourly until morning (06:00–08:00). Samples were taken more frequently (approximately every 20 minutes) at sunset (21:00–22:00). All stations were sampled simultaneously. This sampling design provided 13 to 19 samples for each station on each sampling occasion, giving a total of 143 samples collected during the study. Nets were placed in the river for 15–30 minutes depending on the time of day, a longer interval was used during the day when low abundances of drifting fishes were observed. A maximum period of 30 minutes for each sample ensured that the net did not become clogged during sampling.

Environmental data

Mean water temperatures (± standard error) were 20.5 ± 0.12 °C, 17.7 ± 0.15 °C and 22.7 ± 0.20 °C for 17 June, 24 June and 1 July, respectively. Mean dissolved oxygen in the study area was 7.4 ± 0.25 mg l^{-1}. Mean water transparency, determined using a Secchi disc during daylight, was 60 ± 3.2 cm over the study period. Water velocity for each sample was measured with a mechanical current velocity meter positioned at the centre of the net opening (Table 1). Discharge data were obtained from the nearest gauging station of the Czech Hydrometeorological Institute, located 7 km upstream. Illumination was measured using a portable light meter once during a sampling occasion, but twice (at the start and end) during sunrise and sunset samplings, when illumination levels changed. Twilight refers to a civil twilight, defined as a period after sunset (and before sunrise) when illumination is sufficient for terrestrial objects to be clearly distinguished (Reichard et al. 2002 b). This corresponded with the light levels between 3 and 5 lx in our study. Night samples were defined as those after (or before, respectively) civil twilight.

Sample processing and estimates of drift abundance

Drift samples were sorted in a white plastic tray within 30 minutes of collection. All fishes in the samples were preserved in 4 % formaldehyde. Fishes were identified using Koblickaya (1981) and our own reference collection. Gudgeon, *Gobio gobio* (L.), and whitefinned gudgeon, *Gobio albipinnatus* Lukasch, cannot be readily separated as larvae and were pooled for analysis as *Gobio* spp. Fish developmental intervals (six steps within larva period and a juvenile period) were determined in accordance with Balon (1975) and Peňáz (2001). The standard length (SL, length from tip of the snout to the end of the notochord) of all fishes was measured to the nearest 0.01 mm, using a digital calliper. No changes in standard length as a result of preservation in formaldehyde were considered.

Drift density was used as a measure of abundance throughout the study. It was calculated as the number of individuals per 100 m^3 of filtered water (current velocity multiplied by the area of the net opening). An alternative measure, the number of fish drifting through the sampled section per time unit (drift rate), was not necessarily correlated with drift density, because water velocity varied among sampling stations. Thus, high drift density close to the bank (where water velocity was low) need not have been reflected in estimates of drift rate. Despite this, we found a strong correlation between these two measures (Pearson correlation: $r = 0.970$, $p < 0.001$) and the same results were obtained using either measure of drift abundance.

Statistical analysis

Differences in drift density and standard length across sampling stations were tested using General Linear Model ANOVAs. The factor “Station” described both distance from the bank and water velocity, since they correlated strongly and were consistent among dates (Table 1). Initially, a two-way ANOVA was used to estimate an effect of the sampling date. When the date effect was significant, one-way ANOVAs for each date were used to test differences among stations within a given date. We included power analyses for two-factor tests with relatively lower replicate combinations to show the probability of committing a type II error. Individual samples (drift density data) and mean SL of night-time samples (body size data) were treated as replicates for among stations comparisons. We used the mean SL rather than SL values of all fish in the individual sample to avoid pseudoreplication. Drift density data were $\ln(x + 1)$ transformed to equalise variances. Although drift densities tend to peak at a particular time of the night (Pavlov 1994, Jurajda 1998), the exact timing of the peaks differs among nights (Reichard et al. 2001) and the variation in drift densities in samples collected within a single night is usually considerable lower than among dates (Reichard et al. 2001, 2002 a, also see Results for the date effect). The Scheffé method was used for *post hoc* comparisons among means. For day-night ratio analysis, twilight abundance data were excluded and day and night abundances were compared using the

Mann-Whitney U test for each station separately. A χ^2 analysis of contingency tables was performed to test differences in relative abundances of developmental intervals among sampling stations.

Results

Species composition

A total of 1587 fish belonging to 15 species was caught. Common bream (*Abramis brama*) were dominant on all sampling dates and at all stations, constituting over three-quarters of all drifting fishes. Silver bream (*Abramis bjoerkna*) and roach (*Rutilus rutilus*) were the only other species representing more than 3 % of the catch at every sample date. All species caught, except the tubenose goby (*Proterorhinus marmoratus*), were cyprinids (Table 2).

Drift density

The drift density differed among dates (Two-way GLM ANOVA; $F_{(2,59)} = 5.22$, $p = 0.008$, power = 0.81) and stations ($F_{(3,59)} = 8.01$, $p < 0.001$, power = 0.97). The interaction was not significant $F_{(4,61)} = 0.33$, NS), though the power to detect a significant difference was low (power = 0.14). Similar results were

Table 2. Taxonomic composition of fish drift samples from the River Dyje in summer 1999. Number of fishes caught (N) for all stations pooled and their relative abundance (%) is shown for all dates combined (Total) and for three individual sampling dates.

		Total		17 June		24 June		1 July	
Common name	Scientific name & Authority	N	%	N	%	N	%	N	%
common bream	*Abramis brama* (L.)	1201	75.7	767	81.6	157	68.3	282	64.1
silver bream	*Abramis bjoerkna* (L.)	121	7.6	31	3.3	8	3.5	82	18.6
roach	*Rutilus rutilus* (L.)	112	7.1	80	8.5	32	13.9	16	3.6
bitterling	*Rhodeus sericeus* (Pallas)	45	2.8	18	1.9	18	7.8	10	2.3
barbel	*Barbus barbus* (L.)	38	2.4	16	1.7	3	1.3	20	4.5
gudgeon	*Gobio* spp.* (Cuvier)	22	1.4	9	1.0	4	1.7	9	2.0
tubenose goby	*Proterorhinus marmoratus* (Pallas)	4	0.3	0	2		0.9	2	0.5
asp	*Aspius aspius* (L.)	3	0.2	1	0.1	0		2	0.5
bleak	*Alburnus alburnus* (L.)	3	0.2	3	0.3	0		0	
rudd	*Scardinius erythrophthalmus* (L.)	2	0.1	2	0.2	0		0	
goldfish	*Carassius gibelio* (Bloch)	2	0.1	2	0.2	0		0	
ide	*Leuciscus idus* (L.)	2	0.1	0		2	0.9	0	
chub	*Leuciscus cephalus* (L.)	1	0.1	0		0		1	0.2
dace	*Leuciscus leuciscus* (L.)	1	0.1	1	0.1	0		0	
Japanese minnow	*Pseudorasbora parva* (Schl. et Tem.)	1	0.1	1	0.1	0		0	
unidentified		29	1.8	9	1.0	4	1.8	16	3.6

* Includes gudgeon *Gobio gobio* (L.) and whitefin gudgeon *Gobio albipinnatus* (Lukasch).

obtained for common bream only, and for all other species pooled (excluding common bream) data. No significant differences were found when only three nearshore stations were sampled on 17–18 June, but drift density was significantly lower in midchannel on the other two dates (Table 3). Generally, most fish were caught at Stations 2 and 3 (Table 3). The highest drift density recorded was at Station 2 (Table 4) with a maximum of 131 fish 100 m^{-3} on the night of 17 June. For midchannel samples (Station 4) the highest drift density was 4 fish 100 m^{-3} (24 June, sunset). Drift density was lower at twilight and fish drifted only occasionally during the day (Table 4).

Table 3. Estimates of mean night drift densities (± 1 standard error) among sampling dates and stations (Stn.) for, (a) common bream, *Abramis brama*, and (b) for other species pooled excluding common bream. Data were analysed using a one-way GLM ANOVA for each date. Ln (x + 1) transformed data were used for analyses, but untransformed data are shown. Distinct letters denotes statistically different subsets (Scheffé tests, $p < 0.05$).

		(a) common bream				(b) other species			
Date	Stn.	Estimate	F	p	Subset	Estimate	F	p	Subset
17 June	1	72 ± 14.3	2.6	NS	A	14 ± 2.4	2.3	NS	A
	2	108 ± 20.0			A	23 ± 4.7			A
	3	56 ± 10.6			A	12 ± 3.9			A
24 June	1	8 ± 1.4	31.5	<0.001	A	5 ± 1.3	9.7	0.001	A
	2	22 ± 4.3			B	8 ± 1.8			A
	4	2 ± 0.6			C	0 ± 0.2			B
1 July	1	17 ± 7.4	23.3	<0.001	A	18 ± 4.4	14.1	<0.001	A
	2	47 ± 13.0			A	30 ± 9.0			A
	3	29 ± 3.4			A	10 ± 2.2			A B
	4	3 ± 0.9			B	1 ± 0.6			B

Table 4. Mean estimates (± 1 standard error) of drift densities at different dates, stations and periods of the diel cycle for all species pooled. All sunrise and one sunset estimate are based on only one sample and no estimate of the SE has been calculated.

Date	Station	Night	Sunrise	Day	Sunset
17–18 June	1	85.4 ± 15.08	35.5	2.4 ± 1.61	7.6 ± 2.92
	2	130.7 ± 21.26	9.5	0.7 ± 0.54	29.0 ± 17.51
	3	68.3 ± 9.69	31.9	3.0 ± 1.29	12.2 ± 4.59
24–25 June	1	13.5 ± 1.51	10.5	0.5 ± 0.53	0.0
	2	30.4 ± 4.63	9.3	0.4 ± 0.39	9.3
	4	1.5 ± 0.56	0.7	0.3 ± 0.26	4.1
1–2 July	1	34.4 ± 8.78	30.0	0.8 ± 0.45	7.9 ± 0.37
	2	76.9 ± 19.92	12.8	0.4 ± 0.27	2.9 ± 2.91
	3	38.9 ± 4.25	0.0	0.3 ± 0.17	1.5 ± 1.52
	4	3.7 ± 1.37	0.0	0.5 ± 0.20	0.0 ± 0.00

Day-night ratio

At all stations and dates fish drifted significantly more at night than during daylight (Mann-Whitney *U* test; all $p < 0.01$). The most pronounced diel pattern was found at Station 2 (day/night ratio 1:78 to 1:190), followed by Station 3 (1:23 to 1:153) and Station 1 (1:23 to 1:41). At Station 4 the day/night ratio varied from 1:6 to 1:8. An intermediate number of fish drifted during twilight (day/twilight ratio 1:4 to 1:31).

Variation in body size and developmental stages

The standard length of drifting common bream was significantly different among stations (Main Effect GLM ANOVA; $F_{(3,58)} = 114.8$, $p < 0.001$, power > 0.99), though the effect of date was not significant ($F_{(2,58)} = 1.9$, NS, power = 0.29). Across dates, mean SL was 9.4 ± 0.20 mm at Station 1, 10.8 ± 0.20 mm at Station 2, 12.6 ± 0.27 mm at Station 3, and 15.5 ± 0.29 mm at Station 4. Despite the relatively low power of the date effect analysis, the same trend was found for all dates (One-way ANOVAs, all $p < 0.05$) with three or four independent subsets identified at each date (Scheffé tests; $p < 0.05$; Fig. 1). Fish size was significantly positively correlated with distance from the bank (Spearman correlation; $r_s = 0.894$, $N = 64$, $p < 0.001$).

For all species pooled excluding common bream, no correlation between standard length and distance from the bank was detected (Spearman correlation; $r_s = 0.162$, $N = 55$, NS), but there was a positive correlation for silver bream (Spearman correlation; $r_s = 0.450$, $N = 31$, $p = 0.011$) and roach (Spearman correlation; $r_s = 0.491$, $N = 17$, $p = 0.045$) analysed separately.

The relative abundance of each developmental interval of common bream varied with distance from the riverbank (Contigency tables, $p < 0.001$; Fig. 2).

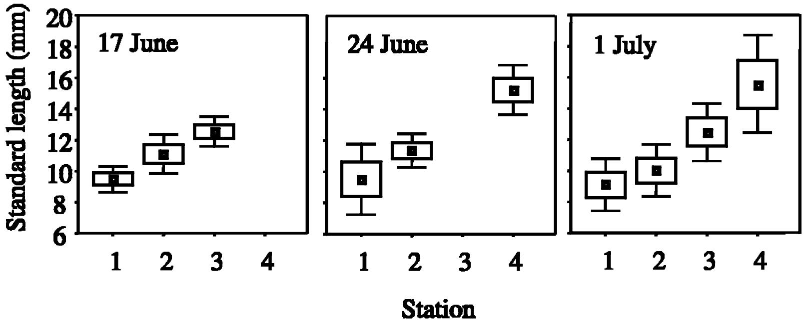

Fig. 1. Mean standard length of drifting common bream, *Abramis brama* at four sampling stations during three sampling dates. Error bars are one standard error. All means are significantly different from each other (One-way ANOVAs followed by Scheffé tests, $p < 0.05$).

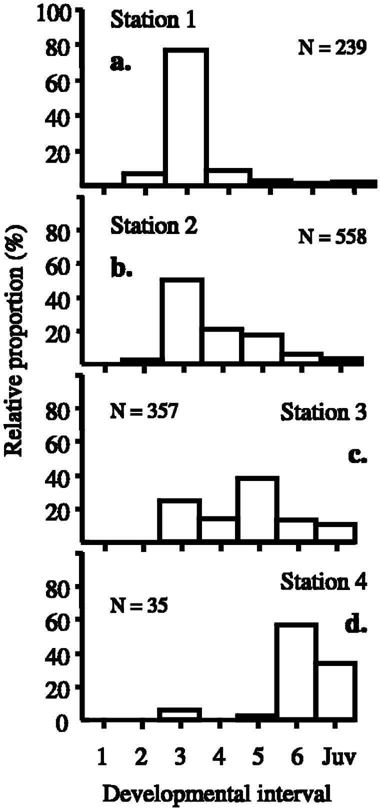

Fig. 2. Relative proportion of developmental stages of drifting common bream, *Abramis brama*, at four sampling stations for all dates combined. Figures refer to numbers of fish (N) at each station. Developmental interval (1 to 6) refers to larval steps, Juv denotes juvenile period.

At Station 1, 77 % of individuals were L_3 larvae (Fig. 2 a). In contrast, 91 % of common bream were L_6 larvae or early juveniles at Station 4 (Fig. 2 d). Stations 2 and 3 were intermediate between these extremes (Fig. 2 b, c). Larger fish drifted during the day at Station 1 (Mann-Whitney *U* test; $Z_{(10,327)} = 3.23$, $p = 0.001$), but we detected no differences between standard length in this species at day and night/twilight at other stations (Mann-Whitney *U* test; $p > 0.05$).

Discussion

We found that the greatest number of larval and juvenile fishes drifted nearshore, predominantly at a distance of 0.7–3.0 m from the riverbank (Fig. 3). At this distance water velocity varied between 0.20 and 0.45 m s^{-1} and the depth

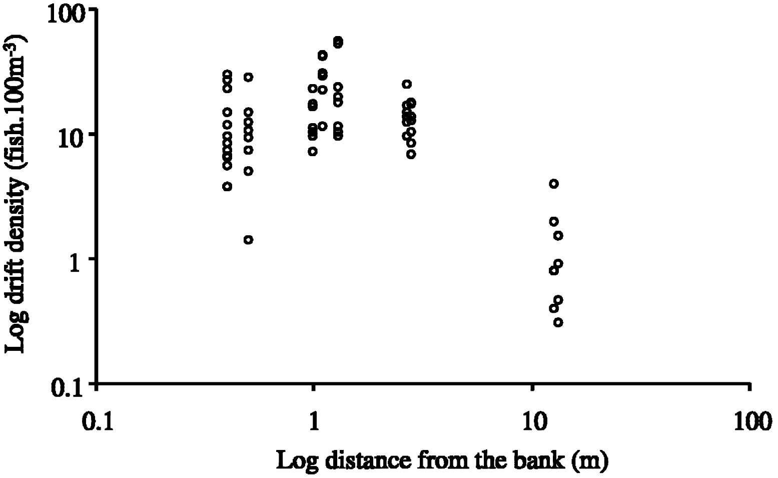

Fig. 3. Relationship between drift density (for all species pooled) and distance from the bank. Each data point represents an individual sample.

of the water column was < 0.5 m. In contrast, relatively few fish drifted in midchannel where water velocity was > 0.50 m s^{-1}. A similar propensity of fishes to drift near the bank has often been reported elsewhere (e. g. PAVLOV et al. 1977 b, BROWN & ARMSTRONG 1985, HARVEY 1991, PEŇÁZ et al. 1992), though GALE & MOHR (1978) described a random spatial distribution of drifting fish and CORBETT & POWLES (1986) found that walleye, *Stizostedion vitreum* (MITCHILL), drifted mainly in midchannel.

Fish body size was positively correlated with distance from the bank for all fishes pooled and separate species alone (Fig. 1). Also PAVLOV et al. (1977 a) noted that smaller cyprinid larvae tended to drift near the bank while juveniles drifted further from the bank, though they did not test this observation directly. We believe that this correlation may be linked to swimming ability. In common bream, L_3 larvae formed the major proportion of drifting fish closest to the bank (Fig. 2). At this developmental interval the anterior chamber of the swim bladder starts to fill with gas and the locomotory powers of the fish are greatly enhanced. However, although fish start to swim actively, their swimming ability remains relatively poor because they still possess a large finfold area rather than discrete fins (PEŇÁZ & GAJDŮŠEK 1979). Larger and older larvae were found to drift further from the shore (Fig. 2), which parallels their increased swimming ability. L_6 larvae and early juveniles constituted more than 90 % of common bream drifting in midchannel. Their swimming ability at this stage is greater, with both paired and unpaired fins well developed (PEŇÁZ & GAJDŮŠEK 1979). Thus, larger individuals may be more susceptible to drifting because they are more active. However, as more able swimmers they might also be expected to be better able to return to the river bank and avoid drifting. Indeed, we observed that significantly fewer larger fishes drifted and there is evidence that drifting fish of all sizes are readily able to settle near the bank should they choose to (CARTER et al. 1986, IGUCHI & MIZUNO 1990, PAVLOV 1994, GADOMSKI & BARFOOT 1998).

Drift in fishes may be a passive process, whereby individuals are washed downstream by strong currents (ZAMBRIBORSHCH & NGUEN TAN CHIN 1974, BROWN & ARMSTRONG 1985), with individuals in poor condition most at risk of being swept away (BODENSTEINER & LEWIS 1994). Alternatively or additionally, it may be an active process, whereby individuals use water currents to assist their movement to locations where they can maximise their energy gain and/or avoid predators (SAVENKOVA & ASANOV 1988, ROBINSON et al. 1998).

Some of our results may be interpreted as evidence that drift in cyprinid fishes is a passive process. Nearshore areas serve as nurseries for European riverine cyprinids (e. g. WINKLER et al. 1997). Thus, regardless of the extent to which drift is active or passive, fishes may be expected to drift near the river bank in a straight flowing river, like the Dyje. We observed that most drifting fishes were near the bank, and this finding is common to many studies (e. g. BROWN & ARMSTRONG 1985, HARVEY 1991, PEŇÁZ et al. 1992). We also observed that drift was significantly more common at night. Cyprinid larvae use visual cues for orientating themselves (PAVLOV 1979), and may lose orientation when visibility decreases at twilight (PAVLOV 1994). Thus, larvae may be more at risk of being swept away by strong currents at night. The highly significant positive correlation of size/age of drifting fishes with distance from the bank in this study may be also explained on the basis of passive drift. This explanation might be that larger individuals possess greater locomotory powers and thus, move further from the shore. As more able swimmers they might also be expected to be better able to return to the river bank should they choose to (CARTER et al. 1986, PAVLOV 1994, GADOMSKI & BARFOOT 1998) and avoid drifting. This accords with their lower abundance in drift samples in general.

However, there are also adaptive explanations for the observed drift patterns. The factor that may influence the distribution of passively drifting fishes is river morphology and flow turbulence. Both may have the effect of distributing passively drifting fishes throughout the whole river channel, irrespective of body size or time of day. However, this pattern of distribution of drifting fishes was not observed in the present study, and has been observed in other studies only rarely (e. g. GALE & MOHR 1978). Drifting at night could reduce the risk of being detected by visual predators (CORBETT & POWLES 1986, HARVEY 1991). Experimental evidence showed that larval and juvenile cyprinid fishes actively entered flowing water at night (PAVLOV & SHTAF 1981, PAVLOV 1994) which contrasts with their daytime behaviour (GARNER 1999).

Larger and more mobile juveniles may drift at greater distances from the bank to take advantage of higher flow velocities, thereby minimising the period for which they are more vulnerable.

Thus, we propose that drift in cyprinid fishes may involve individuals actively entering and leaving the water current as a means of transport. We discount drifting by cyprinid larvae as a feeding strategy, because even a typically rheophilic cyprinid larvae and early juveniles are not able to forage at water velocities exceeding five body lengths per second (e. g. FLORE & KECKEIS 1998). Instead, drifting may be related to habitat shifts or could be a density-dependent response to high competitor densities or low food abundance.

Further research is needed to determine what cues larval and juvenile cyprinid fishes might use for entering and settling from the drift, how they distribute themselves in rivers in relation to competitor density, food availability, and predator abundance, and what implications drift behaviour has for their population dynamics. To understand the mechanisms of drifting, an experimental approach is needed to test hypotheses based on field studies. Specifically, experimental manipulations with abiotic (structural and environmental variables) and biotic (local fish density, predator presence, food availability) factors will help to determine what cues larval and juvenile cyprinid fishes use for entering and settling from the drift, and how they distribute themselves in rivers in relation to these factors.

Acknowledgements

We thank EDITA MAZUROVÁ, EVA VYSLOUŽILOVÁ, MONIKA ŠUGERKOVÁ and RADIM D. BLAŽEK for help with fieldwork. Financial support for the project came from Grant Agency of the Czech Academy of Sciences, Grant No. IAB 6093106 and MARTIN REICHARD was partly supported by Czech Ministry of Education, Grant No. FRVS 600/2001. River discharge data were obtained from the Czech Hydrometeorological Institute in Brno.

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Submitted: 12 June 2002; accepted: 24 November 2003.