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Seasonal dynamics and age structure of drifting cyprinid fishes: an interspecific comparison

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Abstract – We investigated interspecific differences in the downstream drift of seven species of young-of-the-year cyprinids over a 2-year period in two central European rivers, using a comparison of drifting fish with fish collected from nurseries at the same time and the same site as the drift samples. Species varied in the utilisation of the drift; *Rutilus rutilus*, *Gobio* spp., *Abramis brama* and *Carassius auratus gibelio* drifted abundantly, while *Leuciscus cephalus* and *Alburnus alburnus* were abundant in nurseries, but drifted at low densities. *Abramis bjoerkna* was equally represented among drifting and resident fish. Generally, fish drifted at two major developmental intervals; L3 stage and the stage at transition between larval and juvenile periods (L6/Juv), with interspecific differences in the ontogenetic timing of drifting. The propensity to drifting of certain developmental stages was also reflected in body size comparisons between drifting and resident fish. The stage-dependent drifting may be attributed to major changes in fish morphology, behaviour and swimming ability.

Key words: dispersal; downstream drift; early life history; migration; young-of-the-year fish

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Introduction

Downstream drift is unidirectional movement facilitated by water current. There is increasing evidence that the downstream drift of young-of-the-year (YOY) stream and river fishes is widespread and may play an important role in the population and metapopulation dynamics of many species. It is well documented that drift occurs during the first few months of life, and is typically nocturnal and widespread among broad taxonomical and ecological range of species (reviewed in Pavlov 1994). However, there are many questions regarding the drift that remain largely unresolved.

Several explanations of why fish drift have been hypothesised and each of them may be applicable to a certain taxonomic or ecological group. Most studies relate downstream drift to a juvenile (Juv) migration (e.g., Salmonidae: Northcote 1962; Percidae: Mion et al. 1998; Cottidae: Goto & Arai 2003; Gobiidae: Iguchi & Mizuno 1990; Catostomidae: Clifford 1972; Cyprinidae: Pavlov 1994; de Graaf et al. 1999). Drifting can also serve as an effective dispersal strategy (Robinson et al. 1998) and Schmutz et al. (1997) showed that a constructed man-made channel was rapidly colonised by drifting fish. Fish may also use drifting to facilitate their migration from flooded meadows as flood waters recede (Savenkova & Asanov 1988) and for short migrations related to habitat shift within the river channel (Schmutz & Jungwirth 1999). Finally, many studies have interpreted drifting as a passive dislodgement related to visual disorientation (Pavlov 1966; Manteifel et al. 1978; Brown & Armstrong 1985) or inability to withstand high flow velocities (Harvey 1987; VanderKooy & Peterson 1998).

Here, we use a species-specific approach to investigate differences in the importance of drifting and its seasonal and developmental timing among seven cyprinid species in two rivers of the central Europe. Our previous study (Reichard et al. 2002a) showed that drift is an important component of the life history in most European cyprinids and indicated there may be differences in the propensity to drift among species, analysed by comparing the relative abundance

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(RA) of drifting YOY fish to the RA of Juv collected during autumnal electrofishing censuses. Similarly, Zitek et al. (2004a) found differences between the assemblage structure of drifting fish and the adult stock, while Sonny et al. (2006) showed that species dominant in adult stock also dominated the drift samples. Precise data on the developmental stages of drifting European cyprinid fishes are scarce, though some studies suggest size- and stage-specific drifting in European cyprinids (Reichard et al. 2004; Zitek et al. 2004b; Sonny et al. 2006). Other seasonal studies do not separate species for the analysis of size structure and developmental stages of drifting fish (Carter & Reader 2000) or comprise relatively few species (Jurajda 1998). Some data on size- and stage-specific drift come from short-term (maximum 1 week) studies (e.g., Copp & Cellot 1988; Peňáz et al. 1992; Schmutz et al. 1997) that cannot encompass all developmental stages. Notably, no previous study compared drifting cyprinid fish to resident fish both collected at the same time.

In the present study, we investigated interspecific differences in propensity to drift, seasonal dynamics of drift density, and size and developmental stages of drifting fish in two European lowland rivers over 2 years, using a comparison with nondrifting fish collected from nurseries during the day and night and the drifting fish collected at the same time and from the same site. We present data on seven abundant cyprinid species that dominated our samples; bream *Abramis brama* (L.), silver bream *Abramis bjoerkna* (L.), bleak *Alburnus alburnus* (L.), chub *Leuciscus cephalus* (L.), gudgeon *Gobio* spp., Prussian carp *Carassius auratus gibelio* (Bloch) and roach *Rutilus rutilus* (L.).

Materials and methods

Study area

The study was undertaken in two adjacent lowland rivers (Danube basin, Czech Republic). The River Morava (60 m wide, an average discharge of 65 $m^3 s^{-1}$, maximum depth of 1 m) has been channelised and regulated by weirs. In the study area, the shoreline was a boulder bank with a deposit of silt. Woody debris and overhanging emergent vegetation provided shelter for YOY fish at the river margins, but there were no nurseries available in mid-channel (Reichard 2002). The River Kyjovka, smaller than the R. Morava (5 m wide, average discharge of 1.1 $m^3 s^{-1}$, maximum depth 0.5 m) has also been channelised, but has no weirs. The shoreline comprised an eroded clay bank with overhanging emergent vegetation. For a detailed description of the study sites see Reichard et al. (2002a).

Sampling

Sampling was conducted at 7- to 11-day intervals from May to August (15 dates from 4 May to 26 August in 1999 and eight dates from 26 May to 26 July in 2000). Samples of drifting fish were taken using a net with an opening of 0.6 m^2 (1.01 m width by 0.59 m depth) and the mesh size 0.5 mm. The mesh size used was a typical size for drift studies (for a review see Schmutz et al. 1997) and has been proven to be efficient for capturing fish >5 mm (Copp & Cellot 1988; Schmutz et al. 1997; Robinson et al. 1998; Reichard 2002; Zitek et al. 2004a; Sonny et al. 2006). Consequently, we believe that the mesh size did not affect the observed size structure of the drifting fish. The net was set 1–2.5 m from the bank for a period of 10–20 min (to avoid any clogging from suspended material). The position of net was chosen according to a pilot study that revealed that >95% of all fish drifted nearshore, at a distance of <3 m from the riverbank (Reichard et al. 2004). Samples were taken three times during the day (09:00, 12:00 and 18:00 hours) and three times a night (22:00, 24:00 and 02:00 hours) in each river on each sampling date. Daily mean values of river discharge and water temperature were obtained from the nearest hydrometeorological station of the Czech Hydrometeorological Institute in Strážnice (Fig. 1). The hydrometeorological data from the River Kyjovka were not available; there is no hydrometeorological station in the study stretch.

Resident YOY fish were sampled along the river banks (referred to as nurseries hereafter) using a dipnet (2 m pole, ring diameter of 40 cm, mesh size 0.5 mm). One sample was taken during daytime (09:00–12:00 or 18:00–19:00; light level >500 lx) and one at night (22:30–01:00; light level <5 lx) on the same dates that drift sampling was conducted. Each sample consisted of 4–34 dipnet hauls. The samples were collected downstream from the drift net in all types of nurseries available (depositional pool, low flow areas along the boulder bank and overhanging vegetation, riffles near a bridge pier). Sampling effort was in proportion to the availability of the different types of nursery habitats. All YOY fish caught were fixed in 4% formaldehyde within 30 min to ensure high quality tissue preservation and transported to the laboratory for identification and staging.

Sample processing and data analyses

Fishes were identified using Koblickaya (1981) and our own reference collection derived from laboratory-reared specimens. Because *Gobio gobio* (L.) and *Gobio albipinnatus* Lukasch cannot be separated as larvae, they were treated as *Gobio* spp. throughout the analyses. The Standard Length (SL) of all fish was

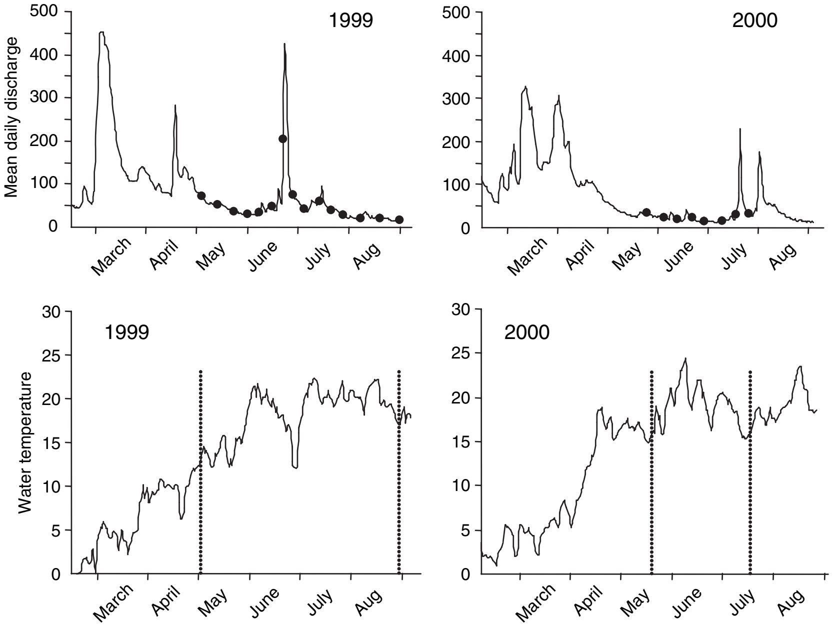

Fig. 1. Mean daily discharge (upper panels; in $m^3\ s^{-1}$) and mean water temperature (lower panels; in °C) of the River Morava recorded at Strážnice hydrometeorological station in 1999 and 2000. Black dots drawn on discharge data indicate individual sampling dates, vertical dotted lines on temperature data illustrate extent of the sampling period.

measured by digital calliper to the nearest 0.01 mm. Each fish was assigned to a developmental stage according to Peňáz (2001). Free embryos had a yolk sac and no external food in their gut. Larvae were characterised by exogenous feeding (*v.* free embryos), and by the presence of a finfold, instead of separate fins (*v.* Juv). Six distinct developmental intervals (referred to as L1–L6 hereafter) related to morphology, swimming ability and behaviour were recognised within the larval period. Juveniles had fully developed and differentiated fins and no remnants of the finfold. For a detailed description of the developmental intervals, including individual L1–L6 steps of larval period, see Peňáz (2001).

There were 18 and 14 species of cyprinids recorded to drift in the Rivers Morava and Kyjovka, respectively (Reichard et al. 2002a). In total, data for seven species were sufficient to be analysed in detail; five species from the R. Morava and three species from the R. Kyjovka. *Alburnus alburnus* was common in both rivers. Bitterling, *Rhodes amarus* (Bloch), the most abundant species in the drift, do not scatter the eggs over a spawning substrate, but lay them deep into the gill cavities of living unionid mussels where eggs and embryos develop for 4–6 weeks (Smith et al. 2004). This unique reproductive strategy has several important consequences for the life history of early developmental stages, including drifting (Reichard 2002), and therefore we have not included this species in the present study.

Drift density of each species was calculated as the number of individuals per 1000 m^3 of filtered water (the current velocity in the centre of the net opening multiplied by the area of an active net opening). Most fish in the study area drifted at night (Reichard et al. 2002b) and only night samples were used for the drift density estimates.

There was no difference found in the drift density and no temporal pattern among the three night-time samples for any species (Kruskall–Wallis tests, all $P > 0.05$). Consequently, the mean (±1 SE) drift density was calculated for each night. The abundance of resident fish was expressed as a catch per unit effort (number of fish per 10 dipnet hauls). Considering that the density estimates in nurseries were less accurate than the estimates of drift densities, we divided the density of the resident fish into three categories (0, 0–25 and >25 fish per 10 hauls) and used them only for a graphical representation. We calculated a drift index (Zitek et al. 2004a) to compare the RA of drifting fish to those in nurseries (for night samples), using a formula $E = [\text{RA in drift (\%)} - \text{RA in nurseries (\%)}]/[\text{RA in drift (\%)} + \text{RA in nurseries (\%)}]$.

The size structure of drifting fish was compared with the size structure of fish in nurseries using Kolgomorov–Smirnov two-sample tests. This procedure compares the shapes of distribution in the two samples and tests a hypothesis that the two samples were drawn from the same statistical population. All the data from the entire sampling season were pooled for analysis. Frequencies of the particular developmental stages collected from nurseries during day, collected from nurseries during night, and from the drift samples (collected at night) were compared to each other using the chi-squared tests. The frequencies of particular developmental stages in nurseries during day were used to calculate expected frequencies of the resident and drifting fish in the night samples. Data from the entire season were pooled for analysis. While the comparison between the resident fish from daytime samples and the drift samples measured propensity to drifting among particular stages, the comparison of the daytime and night-time samples from nurseries (collected using the same sampling gear) controlled for the sampling gear effect. Tests were corrected for multiple testing by a Bonferroni method whenever applicable. The analyses are based on 6789 individual fish (1625, 1645, and 3519 fish collected in nurseries during the day, at night, and drifting at night, respectively).

Results

Propensity to drift

There were clear differences in the propensity to drifting among species and these differences were consistent during the study years and among the populations. Relative abundance of *A. brama*, *Gobio* spp. and *C. a. gibelio* in the drift samples were higher than their RA in nurseries. *Alburnus alburnus* and *L. cephalus* were more frequent in samples from nurseries compared with drift samples. *Rutilus rutilus* and *A. bjoerkna* were equally represented in both the drift and nursery assemblages (Fig. 2). *Gobio* spp. (24% and 16% in 1999 and 2000, respectively) and *R. rutilus* (22% and 18%) dominated the drift samples in the R. Morava during both years, together with *R. amarus* (17% and 51%). In the R. Kyjovka, *R. amarus* (49%), *C. a. gibelio* (17%) and *A. alburnus* (13%) dominated the drift samples in 1999. In 2000, the drift densities in the R. Kyjovka were low (Fig. 3) and largely dominated by *R. amarus* (65%).

Seasonal patterns

The magnitude of the peak drift density and the start and duration of the drifting period varied among species (Fig. 3). The interannual variability in the drift densities and the seasonal dynamics within populations differed among species, being lowest for *A. brama* in the R. Morava (Fig. 3a) and highest for *R. rutilus* and *Gobio* spp. in the R. Morava (Fig. 3b). In the R. Kyjovka, there were large differences in drift densities between 1999 and 2000, though the seasonal patterns were similar (Fig. 3c). Only *A. alburnus* drifted abundantly in both rivers and the seasonal pattern was consistent between populations (bimodal, relatively late start of drifting compared with other species; Fig. 3a,c).

The maximum drift density for a single species was 535 ± 114.8 fish 1000 m^{-3} for *Gobio* spp. in the R. Morava in 1999, and 557 ± 147.6 fish 1000 m^{-3} for *R. rutilus* in the R. Morava in 2000 (Fig. 3b). In the River Kyjovka, *C. a. gibelio* reached a maximum density of 377 ± 49.9 fish 1000 m^{-3} in 1999 (Fig. 3c). *Abramis brama* was the first species that peaked in the drift in the R. Morava in the beginning of June 1999, followed by *R. rutilus* and *L. cephalus*. The drift of *A. alburnus* and *Gobio* spp. peaked in late-June. The first sampling in 2000 (26 May) probably coincided with a seasonal peak of the drift for *A. brama*, *R. rutilus* and *L. cephalus*, while *A. alburnus* and *Gobio* spp. peaked later (Fig. 3a,b). In the Kyjovka, the drift seasonal dynamics exhibited bimodal (*C. a. gibelio*, *A. alburnus*) or trimodal (*A. bjoerkna*) patterns (Fig. 3c).

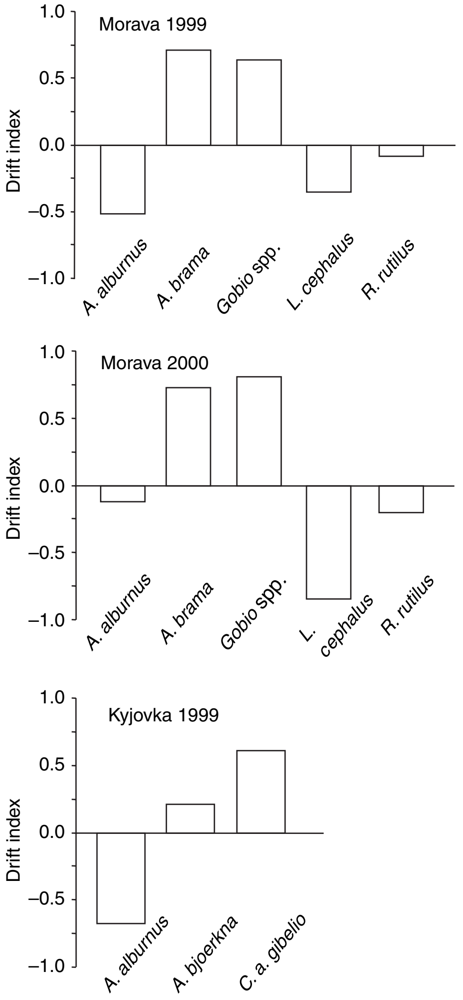

Fig. 2. Propensity of the seven abundant cyprinids to drift. The positive values of drift index (see text for its calculation) indicate propensity to drift, negative values indicate drift avoidance.

Size structure of drifting fish and its comparison to fish in nurseries

The size range of drifting fish varied among species; while 95% confidence interval for *L. cephalus* was 9.5–11.6 mm SL, it ranged from 18.4 to 27.1 mm SL for *A. alburnus* (Table 1). The length–frequency distribution of the drifting fish was different from fish

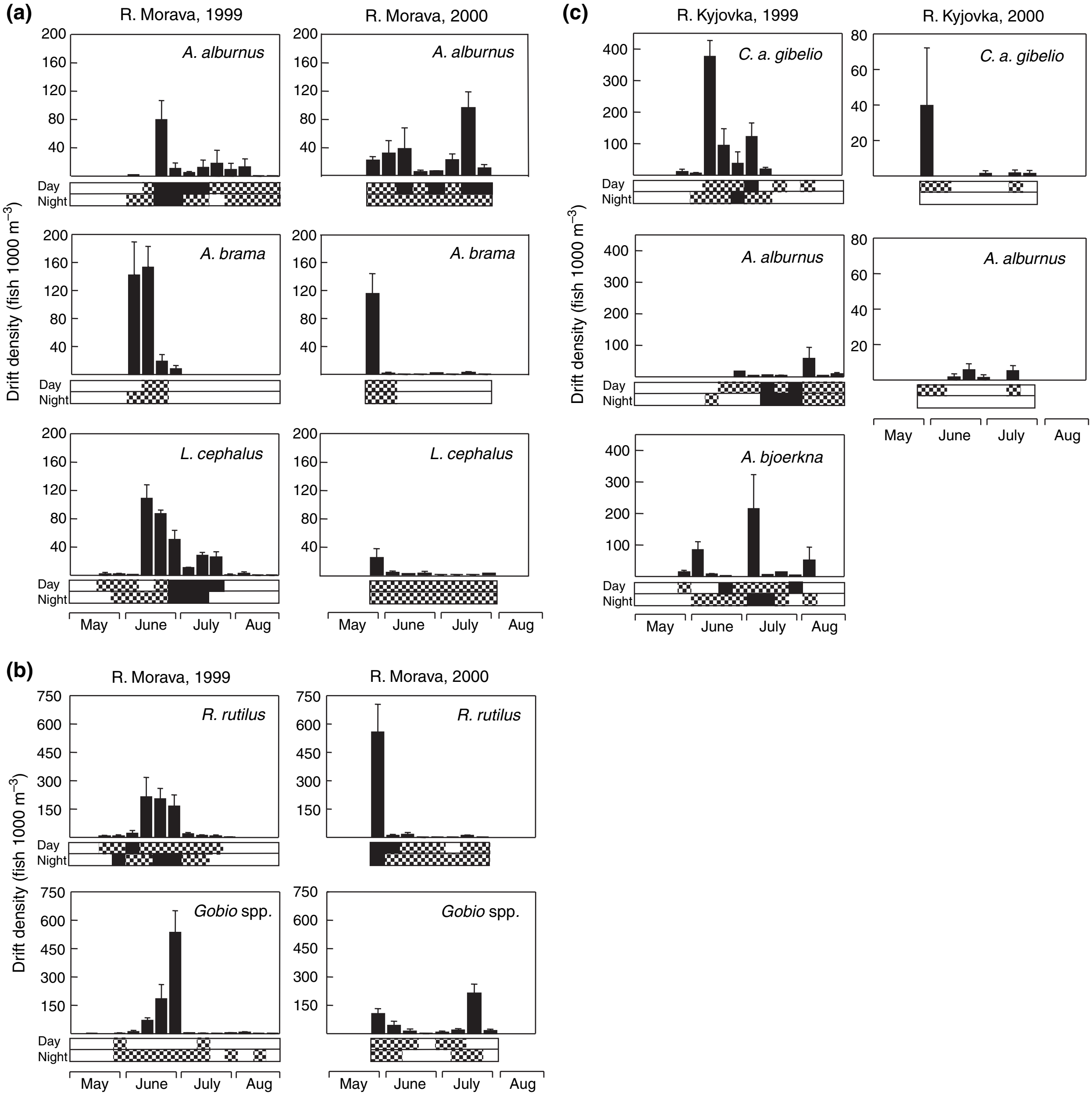

Fig. 3. Seasonal pattern in abundance of drifting and resident fish. Drift density (black bars, mean ± SE) was calculated from night samples. Fish abundance in nursery habitats (bars below the graph) was expressed as a number of fish per 10 dipnet hauls and scaled for daytime (upper bar) and night-time (lower bar) catches separately. White area: no fish present; checkerboard pattern: <25 fish per 10 hauls; black: >25 fish per 10 hauls.

that resided in nurseries (Kolgomorov–Smirnov tests, $P < 0.05$) in all species except for *A. brama* and *Gobio* spp. (Table 1). An example of the length–frequency distribution comparisons among the three categories (fish in nurseries during day, fish in nurseries at night and the drifting fish) is given in Fig. 4.

Developmental stages of drifting fish and fish in nurseries

Generally, there were two major developmental periods when YOY cyprinids drifted. Most drifting *A. brama* and *L. cephalus* were at stage L3, while most of *Gobio* spp., *R. rutilus* and *A. bjoerkna* were at L6 or Juv stage. For *A. alburnus*, both L3 and Juv stages were important components of the drift samples and for *C. a. gibelio*, L5 and L6 stages drifted along with Juv (Fig. 5). Comparisons of frequencies of the developmental stages that occurred in nurseries during day and the night samples of the resident and drifting fish often revealed significant differences (Table 2). Stages that were overrepresented in the drift were consistent among years and populations in *A. brama*,

Table 1. Body size (measured as Standard Length, in mm) of resident and drifting fish in the Rivers Morava and Kyjovka.

	Resident daytime			Resident night			Drifting at night			
	Mean	CI	*N*	Mean	CI	*N*	Mean	CI	*N*	K–S test
R. Morava 1999										
Alburnus alburnus	13.7	13.2–14.3	227	12.7	12.2–13.1	193	12.1	11.6–12.6	138	<0.001*
Abramis brama	10.0	9.7–10.3	25	10.7	10.3–11.2	23	10.5	10.4–10.6	298	>0.10
Gobio spp.	9.2	5.9–12.4	2	14.9	13.7–16.1	62	14.1	13.6–14.7	619	<0.025
Leuciscus cephalus	12.6	12.1–13.1	246	14.2	13.7–14.6	278	11.1	10.9–11.3	295	<0.001*
Rutilus rutilus	14.2	13.9–14.6	301	15.0	14.6–15.4	316	17.1	16.9–17.3	589	<0.001*
R. Morava 2000										
A. alburnus	17.8	16.7–18.9	201	17.1	15.3–18.9	79	14.3	13.4–15.1	144	<0.001*
A. brama	11.1	10.2–11.9	7	12.0	10.5–13.5	4	11.7	11.0–12.5	59	>0.10
Gobio spp.	11.6	9.0–14.2	6	12.6	8.6–16.6	12	16.5	15.3–17.6	265	<0.05
L. cephalus	18.3	15.2–21.5	52	25.0	22.6–27.4	83	10.6	9.5–11.6	16	<0.001*
R. rutilus	14.8	14.3–15.2	268	17.4	16.3–18.4	199	14.5	14.0–15.0	310	<0.001*
R. Kyjovka 1999										
A. alburnus	11.8	11.0–12.6	91	15.0	14.3–15.6	222	22.7	18.4–27.1	40	<0.001*
A. bjoerkna	12.4	11.7–13.2	61	16.1	15.1–17.1	90	13.6	13.1–14.1	212	<0.001*
C. a. gibelio	16.6	15.6–17.5	138	16.1	15.0–17.3	84	14.7	14.3–15.1	534	<0.001*

Mean, 95% confidence interval (CI) and sample size (*N*) are given for each category. Statistical significance of Kolgomorov–Smirnov tests between night samples of drifting and resident fish is also given. Asterisks denote statistical significance ($P < 0.0039$) after Bonferroni correction.

Gobio spp. and *L. cephalus*, unlike for *R. rutilus* (Juv stage in 1999 and L6 stage in 2000) and *A. alburnus* (L3, Juv, and L6 stages in the R. Morava 1999, R. Morava 2000, and R. Kyjovka 1999, respectively) where the stages varied.

Discussion

We showed that there are interspecific differences in the propensity to drifting, in the seasonal dynamics of the drift, and in the size and stage structure among seven species of cyprinids that drifted in two lowland rivers in central Europe. While for some species (*R. rutilus*, *Gobio* spp., *A. brama*) drifting appears to be an important part of their early life history, for other species drifting is less important (*A. alburnus*, *L. cephalus*). *Abramis brama* and *L. cephalus* drifted early in their development (stage L3, 9.5–12.5 mm SL), whereas *R. rutilus*, *Gobio* spp. and *C. a. gibelio* drifted mainly during the transition from larval to Juv period (stages L6/Juv, 14.0–17.6 mm SL). Drifting in *A. alburnus* and *A. bjoerkna* occurred in both developmental intervals.

The stage-dependence of the drift has previously been reported for other taxa, including sciaenids and clupeids (Muth & Schmulbach 1984), characids (Araujo-Lima & Oliveira 1998), percids (Mion et al. 1998), amphidromous gobiids (Iguchi & Mizuno 1990), ictalurids and centrarchids (Brown & Armstrong 1985), catostomids (Clifford 1972; Carter et al. 1986) and a North American cyprinid (Johnston 1997). Among these fishes, several strategies for using river current for a downstream transport have been proposed. For pelagophilous fishes, their downstream drift begins immediately after spawning and pelagic eggs develop in the water column while drifting (Balon 1975). Amphidromous gobies and potamodromous percids enter the drift after hatching to move from spawning to nursery habitats before the onset of feeding (Iguchi & Mizuno 1990; Mion et al. 1998), while other fishes drift during the distinct developmental interval within the larval period (Brown & Armstrong 1985; Carter et al. 1986; Jurajda 1998). Carter et al. (1986) reported that, in contrast to the riverine species drifting in well-defined developmental intervals, the introduced nonriverine species did not exhibit any body size pattern of drifting. This suggests that drifting by riverine fishes may be an adaptation to the riverine conditions rather than a passive dislodgement by river currents, and fish may enter the current actively as a result of stage- and species-specific behavioural responses to the light levels and a rheogradient (Manteifel et al. 1978).

Drifting may be attributed to swimming ability (Reichard et al. 2004). Most fish drifted at L3 or L6/Juv stage and these developmental intervals coincide with significant changes in their swimming ability (Copp & Kováč 1996; Garner 1999; Peňáz 2001). At stage L3, the anterior chamber of the swim bladder starts to fill with gas, which allows fish to swim actively. However, their manoeuvring ability remains poor because they still lack ventral fins and possess a large finfold area rather than discrete unpaired fins. At L6/Juv stage, their swimming ability is considerably improved, as both paired and unpaired fins are well developed (Peňáz & Gajdůšek 1979; Prokeš & Peňáz 1979). Drifting at L3 stage could be a density-dependent response to a competition. Cyprinids deposit a large number of eggs in clusters over the substrate. After the onset of exogenous feeding, larvae

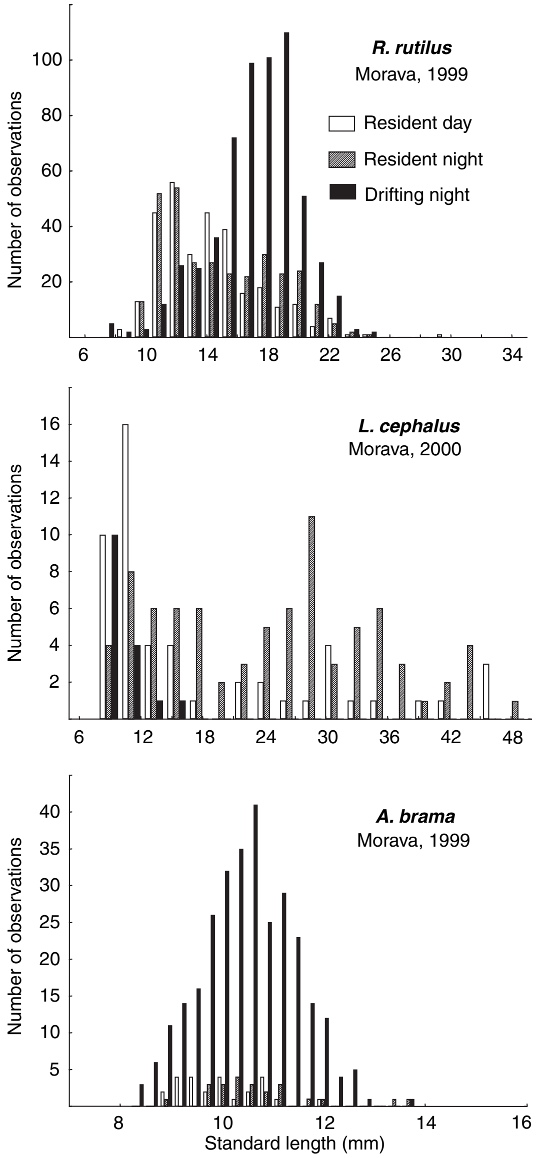

Fig. 4. Length–frequency distribution of drifting fish (black bars), fish resident in nurseries during day (white bars) and fish in nurseries during night (hatched bars) for *Rutilus rutilus*, *Leuciscus cephalus* and *Abramis brama*. Data from the entire study period within a given year were pooled. Note that the scale on the *Y*-axis differs among three species.

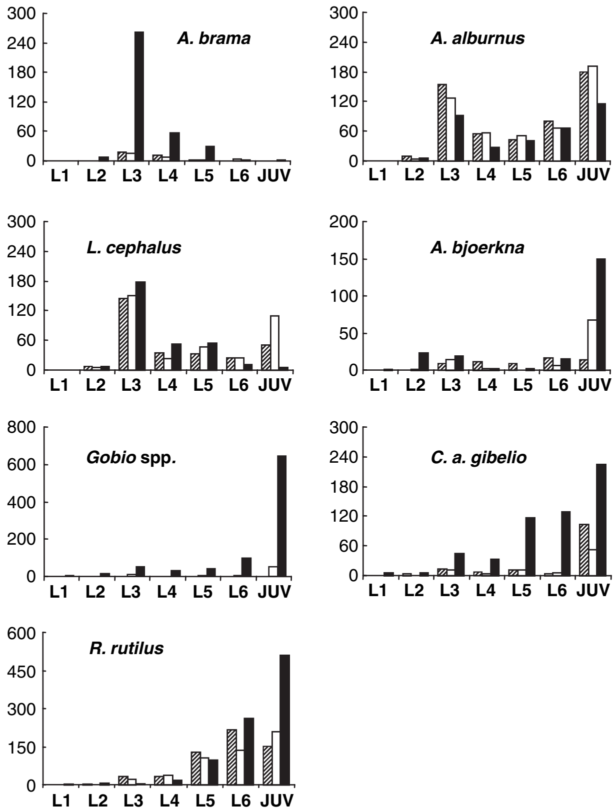

Fig. 5. Number of developmental stages in the samples of drifting fish (black bars), fish resident in nurseries during day (white bars) and fish in nurseries during night (hatched bars). Data were pooled within the species across years and rivers for the graphical representation.

have a limited swimming capacity and therefore dispersal ability (L1 and L2 stages). Fish at L3 stage have the capability to actively enter the river current and may use it as a means of transport (Pavlov 1994; Kováč 2000). Whether this movement is related to habitat shift from spawning to feeding areas (i.e., obligatory, performed by all fish) or is a density-dependent response to high competitor density or low food abundance (i.e., optional, only some fish drift) is unclear and requires an experimental study. A transition from larval to Juv period in cyprinid fishes (L6/Juv stages) coincides with a habitat and diet shift (Copp & Kováč 1996), and drifting is the most suitable means of transport between distinct habitats in riverine conditions (Schmutz & Jungwirth 1999). Notwithstanding these adaptive explanations of drifting, drift might also be largely accidental and its species- and stage-dependent structure may simply match the susceptibility of particular stages and species to be taken by the water current as a result of their behavioural responses to the light and the water current at certain stages. Only a general understanding of the YOY behaviour and ecology would allow linking ontogenetic changes to propensity to drift. Whilst habitat use of YOY European cyprinids has extensively been studied during the day (e.g., Copp 1992), sampling at twilight and night is deficient due to logistic constraints (Baras & Nindaba 1999a,b). This limits any final conclusion of why fish enter the river current to drift and what fitness consequences such decision can have.

Two long-term studies (Zitek et al. 2004a; Sonny et al. 2006) have previously investigated developmental stages of drifting fish, though none of them compared with YOY fish in nurseries. Notably, L1 and L2 stages dominated drift samples in both studies.

Table 2. Results of chi-squared tests on differences in frequencies of particular developmental stages in samples of resident and drifting fish from the Rivers Morava and Kyjovka.

	Resident fish			Drifting fish			
	χ^2	d.f.	*P*-value	χ^2	d.f.	*P*-value	Drifting stage
R. Morava 1999							
Alburnus alburnus	23.5	4	<0.0001*	20.1	4	0.0005*	L3
Abramis brama	5.3	3	0.149	65.1	3	<0.0001*	L3
Gobio spp.	Low sample size			Low sample size			Juv
Leuciscus cephalus	15.4	5	0.009	48.3	5	<0.0001*	L3
Rutilus rutilus	30.5	5	<0.0001*	626.1	5	<0.0001*	Juv
R. Morava 2000							
A. alburnus	13.6	5	0.019	234.2	5	<0.0001*	Juv
A. brama	Low sample size			Low sample size			L3
Gobio spp.	Low sample size			Low sample size			Juv
L. cephalus	67.7	5	<0.0001*	20.2	5	0.001*	L3, L4
R. rutilus	37.9	3	<0.0001*	26.3	3	<0.0001*	L6
R. Kyjovka 1999							
A. alburnus	272.1	4	<0.0001*	250.9	4	<0.0001*	L6
A. bjoerkna	180.1	4	<0.0001*	380.4	4	<0.0001*	L2, Juv
C. a. gibelio	14.8	5	0.011	1297	5	<0.0001*	L5, L6

Chi-squared value (χ^2), degrees of freedom (d.f.), statistical significance of the test (*P*-value) and developmental stages that were overrepresented in the drift samples are shown. Asterisks denote statistical significance ($P < 0.005$) after Bonferroni correction.

Comparison of the fish body sizes in the present study and studies by Zitek et al. (2004a) and Sonny et al. (2006) reveals that these differences cannot be attributed to a differential classification of developmental stages among studies, but rather reflect real differences in the ontogenetic timing of drifting among populations. We may also discount that the difference arose as an artefact of the sampling gear differences or methodology; all three studies used conical-shaped drift nets with mesh size of 0.5 mm. Zitek et al. (2004a) used nets with a 0.07 m^2 opening and positioned their nets at locations with the highest current velocities within a 2 m wide artificial side-channel connected to the R. Danube. Sonny et al. (2006) placed their nets with 0.09 m^2 opening 1 m from the bank, on the edge of the main current. The present study used nets with an opening of 0.6 m^2, but their placement on the edge of the main current is similar to Sonny et al. (2006). In our previous study from a different (but adjacent) river (Reichard et al. 2004), we have used smaller nets with an opening of 0.13 m^2 (all the other sampling gear specification being equal), but found the same developmental stages (L3 and older) in the drift. The size and developmental stage of drifting fish correlated positively with the distance from the bank and with the current velocity (Reichard et al. 2004). However, fish (mainly *A. brama*) at stage L3 dominated even those samples collected closest to the bank and L1 (<0.1%) and L2 (2.9% of 1666 drifting fish) stages were rarely encountered, rejecting the hypothesis that observed differences between the present data and the previous studies come from this correlation. Another possible explanation for the lack of L1 and L2 larvae in our samples might be that our sampling started later than the previous studies. However, our first sampling in 1999 (4 May) predated that of Zitek et al. (2004a) by 17 days, while temperature regime was very similar between the two studies (Zitek et al. 2004b). Similarly, Sonny et al. (2006) started their sampling in mid-May. This indicates that the lack of L1 and L2 stages in our drift samples is not likely to be accounted for a difference in methodology, but rather represents a characteristic of the study populations.

The abundance of *A. brama* in the drift samples from the R. Morava is notable, because *A. brama* is almost absent in the YOY fish assemblage of the lower Morava collected in September (Jurajda 1995, 1999). The drift data showed that bream spawned in the study stretch of the river and moved downstream at stage L3, i.e., about 8 days after hatching (Peňáz & Gajdůšek 1979). After the end of the drift period, no *A. brama* were caught in nursery areas. As *A. brama* drifted abundantly elsewhere (Pavlov et al. 1977; Carter & Reader 2000; Reichard et al. 2004; Zitek et al. 2004a), drifting could be an essential link in their complex migratory life cycle within a flood plain, with distinct spawning, nursery and adult habitats (Molls 1999; Grift et al. 2001; Lucas & Baras 2001).

Gobio spp. has also been overrepresented in the drift samples compared with samples collected in nurseries, in agreement with findings of Zitek et al. (2004a). We are aware that the low abundance of *Gobio* spp. from nurseries may be a consequence of the sampling bias, through underestimating the bottom-dwelling *Gobio* spp. in the dipnet samples. On the other hand, *Gobio* spp. drift densities were, along with densities of *R. rutilus*, highest of all species considered. *Gobio gobio* drifted at Juv stage in the R. Morava, though has been reported drifting at stage L3 in the River Rhône (Copp & Cellot 1988). However, the mean SL of 15.9 mm given by Copp & Cellot (1988) is the size at which gudgeon have already reached the Juv stage (present study; Peňáz et al. 1978; Prokeš & Peňáz 1979). Thus, the data on developmental stage are questionable, though the body size is within the range encountered in the present study. Zitek et al. (2004a) found that stage L1 largely dominated *Gobio* spp. drift.

Rutilus rutilus drifted frequently at the threshold between larval and Juv periods at SL of 14–17.5 mm. This species was shown to drift either at Juv stage (Peňáz et al. 1992), L3 and L6/Juv stages (Pavlov et al. 1990; Jurajda 1998), L1, L3 and Juv stages (Zitek et al. 2004a) or L1–L2 stages (Sonny et al. 2006). Notwithstanding the developmental stage, *R. rutilus* is a common species encountered in the drift (Pavlov 1994; Carter & Reader 2000; Reichard et al. 2001) and variability in the drift and migratory behaviour among and within roach populations is well described (Pavlov et al. 1990; Pavlov 1994).

Carassius a. gibelio is an exotic species from East Asia that became widespread in central Europe after the 1970s following its incidental release with a stock of Asian cyprinids for aquaculture in 1954 (Holčík 1978). *Carassius a. gibelio* is a common species in the R. Kyjovka and connected water bodies (Reichard 2002) and its drifting may serve as an effective dispersal strategy along and across the R. Kyjovka system. Zitek et al. (2004a) found *C. a. gibelio* almost absent in the drift samples, though they attribute this finding to a failure to spawn rather than to drift avoidance.

Abramis bjoerkna and *A. alburnus* exhibited multimodal seasonal patterns in the drift density. These two species drifted at two distinct developmental stages and are batch spawners. *Alburnus alburnus* is frequently encountered in the drift samples (Zitek et al. 2004a) and was the only species that drifted abundantly in both study rivers, while the drift of *A. bjoerkna* has rarely been reported (Pavlov 1966). *Leuciscus cephalus* were the dominant fish in the YOY fish assemblage in the R. Morava (Reichard et al. 2002a), but did not drift at high densities. *Leuciscus cephalus* is reported to drift infrequently (Copp & Cellot 1988; Jurajda 1998; Carter & Reader 2000; Reichard et al. 2001, 2004; Zitek et al. 2004a; Sonny et al. 2006), though is described to migrate upstream to spawn (reviewed by Lucas & Baras 2001).

In conclusion, we found interspecific differences in the utilisation of the drift, its seasonal patterns and size- and stage-dependency, and related them to life history patterns of the individual species. We hope that our study stimulate further research into the importance of drifting for stream and river fish populations. The future research should focus on the importance of drift behaviour at the population level. The next step should include an estimate of proportion of YOY individuals undergoing drift, the mortality risks of drifting and the distance travelled by an individual over a drifting period. While such questions pose a serious methodological challenge, answering these points will certainly confer significant insights into our understanding of drifting and its population consequences.

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