Journal of Fish Biology (2002) **60,** 87–101
doi:10.1006/jfbi.2001.1813, available online at http://www.idealibrary.com on IDEAL®

Interannual variability in seasonal dynamics and species composition of drifting young-of-the-year fishes in two European lowland rivers

M. Reichard*†‡, P. Jurajda* and M. Ondračková*†

**Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8, 603 65 Brno, Czech Republic and †Department of Zoology and Ecology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic*

(*Received 13 June 2001, Accepted 16 October 2001*)

Most young-of-the-year (YOY) fishes in two lowland rivers in the Czech Republic (Danube Basin) drifted from mid-May to mid-July and almost exclusively at night. The peak of drift density lasted *c.* 3 weeks and depended on water temperature (by its effect on fish spawning), but not on discharge. Peak drift densities varied between years and rivers from 80 to 1354 fish 1000 m^{-3}. More than 98% of drifting fish were cyprinids. *Rutilus rutilus*, *Rhodeus sericeus*, *Gobio* spp., *Alburnus alburnus* and *Abramis brama* were dominate in the 22 species encountered in the River Morava. *Carassius auratus gibelio* and *R. sericeus* were the most common of 17 species in the River Kyjovka. Species composition of drifting fishes was similar among years in the Morava but varied in the Kyjovka. The species composition of drifting fishes did not differ from those of the YOY fish assemblage in nursery areas during the drift season. Relative abundances in nursery areas decreased after the drift season in species that dominated in the drift, but increased in those that avoided drift. It is suggested that drift is a regular part of the life history of many cyprinid fishes and interannual variability in density and species composition of drifting YOY fish can be explained by variable spawning success among years. Differences in the relative abundances of the YOY fish assemblage in nurseries during and after the drift season suggests that drift may cause significant mortality.

Key words: larval drift; downstream movement; juvenile fish; dispersal; migration; early life history.

INTRODUCTION

The downstream drift of young-of-the-year (YOY, 0+ year) fishes has been found to play an important role in the life history of many riverine species. Fish drift is typically nocturnal and occurs during early developmental stages (Northcote, 1962; Brown & Armstrong, 1985; Pavlov, 1994). In contrast to many studies on downstream movement in YOY salmonids, an understanding of drift in other freshwater fishes is lacking and most questions of the functional significance of drift remain unanswered (Schmutz & Jungwirth, 1999; Bardonnet, 2001). For non-salmonid fishes, interannual variability in YOY drift parameters has been addressed in North American temperate rivers (Johnston *et al.*, 1995; Johnston, 1997; Mion *et al.*, 1998; Robinson *et al.*, 1998), in a Bangladesh monsoon river (de Graaf *et al.*, 1999) and in YOY fish migration from flooded meadows in Turkmenistan (Savenkova & Asanov, 1988). With the exception of

‡Author to whom correspondence should be addressed. Tel.: +420 5 4342 2521; fax: 420 5 4321 1346; email: reichard@brno.cas.cz

0022–1112/02/010087+15 $35.00/0

studies on coregonid fishes (Naesje *et al*., 1986), no study covering more than one year has been performed in a European river and even studies covering one entire drift season are scarce (Zambriborshch & Nguen Tan Chin, 1973; Carter & Reader, 2000) and often incomplete (Pavlov *et al*., 1977; Jurajda, 1998; Reichard *et al*., 2001).

In the present study interannual variability in seasonal dynamics and species composition of YOY fish drift was compared in two lowland rivers (Danube Basin, Czech Republic) over 3 years. The aim was to study the differences in the timing and magnitude of peak drift abundance, differences in species richness and relative abundance of drifting fishes among years. In addition the species composition and relative abundance of drifting fishes with that of YOY fish assemblages inhabiting nursery areas during and after the drift season were investigated.

MATERIALS AND METHODS

STUDY AREA

The River Morava, the larger of the two study rivers, was *c*. 60 m wide, with an average discharge of 65 $m^3 s^{-1}$ at the study site. The river has been regulated by a number of weirs and has a trapezoid channelized bed. The shoreline was a boulder bank with a deposit of silt. Woody debris and overhanging emergent vegetation were present and provided shelter for YOY fishes. Aquatic vegetation was rare. The maximum depth was *c*. 1 m during the lowest discharge. The river bed substratum was sand and gravel with a deposit of mud in lentic sections above weirs. The sampling site (48°41′ N, 17°00′ E) was located along the river bank 79 km upstream of the confluence with the River Danube and 750 m downstream of a weir. This section of the river bed consisted of cobbles (up to 10 cm in diameter) and gravel.

The River Kyjovka also has been channelized, although it has no weirs. The width of the river at the study site was *c*. 5 m with an average discharge of 1·1 $m^3 s^{-1}$. The Kyjovka sampling site (48°43′ N, 16°58′ E) was 6 km from the Morava sampling site and *c*. 10 km upstream of the confluence with the River Dyje. The river bed was predominantly gravel, which was silted in lentic areas. The maximum depth was 0·5 m during the lowest discharge. The shoreline comprised an eroded clay bank with emergent vegetation and overhanging willow *Salix* sp., which provided shelters for fishes.

DRIFT SAMPLING

Drift samples were collected at 7 to 11 day intervals from May to August (eight dates in 1997, 15 dates in 1999 and eight dates in 2000). In 1997, a drift net was set every 3 h over 24 h during each sampling date providing five daytime and three night-time samples. In 1999 and 2000, three daytime (1800, 0900, 1200 hours) and three night-time (2200, 2400, 0200 hours) samples were taken. The River Kyjovka was sampled *c*. 30 min later than the Morava on every sampling occasion.

The net used was 2 m long and comprised a conical shaped net (mesh size 0·5 mm) with an opening of 0·6 m^2 (1·01 m width by 0·59 m depth) leading to a 2 l plastic collection bottle at the cod-end. The net was set *c*. 1 to 2·5 m from the bank where most fishes drifted (unpubl. data) and was held in place with iron rods driven into the substratum. The net usually sampled the whole water column, though during high discharge water depth at the sampling site was greater than the height of the net. Under these conditions the net was positioned in the middle of the water column. After 10–20 min (according to the current velocity to avoid any clogging) the drift net was removed and all YOY fishes contained in the bottle were fixed in 4% formaldehyde within 30 min.

Water temperature, dissolved oxygen and light levels were measured using portable meters during each sampling event. Water velocity (current velocity meter positioned in the middle of the net opening) and water transparency (Secchi disc reading) were measured at the beginning (1800 hours) and at the end (0900–1200 hours) of each sampling period. Daily discharge and temperature data for the River Morava were obtained from the nearest hydrometeorological station of the Czech Hydrometeorological Institute in Strážnice, located 54 km upstream. A new hydrometeorological station began operation 150 m downstream of the sampling site in 2000. Using peaks in river discharges, a time delay between the two stations of 7 h was calculated. No major tributary influences the river discharge between the hydrometeorological station and the sampling site. The hydrometeorological data from the River Kyjovka were not available, as there is no hydrometeorological station on the stretch under study.

YOY FISH ASSEMBLAGES

YOY fish assemblages were surveyed in two ways. To compare the resident YOY fish assemblage with drifting fishes, samples were taken along the banks (referred to as nurseries hereafter) of both rivers. A total of 8–20 dipnet hauls were collected at all drift sampling dates. The dip net consisted of a 2 m long pole and a ring (diameter of 40 cm) with a fine net (mesh size 0·5 mm). Samples were taken in daylight downstream of the drift net and efforts were made to sample in all types of habitat available (in relation to their relative proportion). Dipnet surveys provided only an approximate estimate of the YOY fish assemblage and the catchability of bottom-dwelling species in particular may have been low.

Consequently, a second method was employed to ascertain the YOY fish assemblage using an electrofishing survey at the end of reproductive season (late August to early October). A Point Abundance Sampling strategy (Copp & Peňáz, 1988) was used with an electroshocker (pulsed DC, 220 V, 1·5–2 A, 50 Hz). Point samples (440) were taken in each year of the study in the Morava only. Water depth at sampling points ranged from 5 to 70 cm and water visibility was 21 to 53 cm during electrofishing.

SAMPLE PROCESSING AND DATA ANALYSES

Fishes were identified using Koblickaya (1981) and a reference collection derived from laboratory-reared specimens. *Gobio gobio* (L.) and *Gobio albipinnatus* Lukasch cannot be readily separated as larvae (Wanzenböck & Wanzenböck, 1993) and *Gobio* spp. were treated as one species throughout the analyses.

Drift density was used as a measure of drift abundance and was calculated as the number of individuals 1000 m^{-3} of filtered water (current velocity multiplied by the area of the active net opening). Current velocity in the centre of the net opening was higher in the Kyjovka than in the Morava and varied both among years (Kruskal-Wallis, $H_{2,26}=14{\cdot}6$; $P=0{\cdot}001$ for the Morava; and $H_{2,62}=23{\cdot}0$; $P<0{\cdot}001$ for the Kyjovka) and within years (Table I). As most fish in the study area drifted at night (Jurajda, 1998; Reichard *et al*., 2001), only night samples were used for drift density estimates. Means ± S.E. are given in the text.

The relationship between river discharge and discharge trend, and drift density was estimated using non-parametric Spearman correlation. Discharge trend was calculated as the difference between daily river discharge and daily river discharge on the preceding day. The rarefaction method was used to compare species richness because sampling effort varied among years. Rarefaction estimates the number of species expected in a sub-sample of individuals selected at random from a larger census and thus, standardizes samples to treat them as if they are the same size. Kendall coefficient of rank correlation (Kendall τ) was used to compare the similarity in the assemblage structure of drifting fishes among years, and drifting fishes with fishes in nursery areas during (May to August) and after (late August to early October) the drift season. Only species that drifted in two or three seasons in each river were used for comparison of drift among years (e.g. no null-null comparison was performed in that data set). Species present in one or both samples compared were entered in the comparison between drift and nursery assemblages.

TABLE I. Current velocity in the centre of drift net opening. Mean ± S.E. values and the test of intra-annual variability among sampling dates are given for the particular year and river. $P<0·05$ indicates significant intra-annual variability

	Current velocity ($m^3\ s^{-1}$)	Test	d.f.	*P*
River Morava				
1997	0·386 ± 0·0445	$H=15·0$	7,16	0·036
1999	0·371 ± 0·0106	$F=1·3$	14,15	0·306
2000	0·299 ± 0·0193	$H=11·0$	7,16	0·139
River Kyjovka				
1997	0·458 ± 0·0191	$H=15·0$	7,16	0·036
1999	0·556 ± 0·0158	$F=7·8$	14,15	<0·001
2000	0·615 ± 0·0175	$H=7·5$	7,16	0·378

H, Kruskal-Wallis; *F*, ANOVA.

For drifting fishes and fishes in nurseries during the drift season, multiple samples each day and year were pooled and relative abundance was calculated from the pooled data.

ANALYSIS OF SHORT TERM VARIABILITY

To ensure that the seasonal pattern corresponded with real seasonality rather than random changes in drift density and species composition, a test of short term variability was performed. No differences in drift density were found between five consecutive nights (8–12 June 2000) (Kruskal-Wallis, $H_{4,15}=6·3$; $P=0·18$). Similarly, assemblage structure based on the eight most abundant species (those for which at least two specimens were caught during the trial) was equal among the five nights (Kendall τ for night to night comparisons; all $n=8$; all $P<0·05$).

RESULTS

SEASONAL PATTERN

The seasonal pattern of drift in the River Morava showed a considerable increase in abundance in mid June in 1997 and 1999. The peak drift density lasted for 2–3 weeks [Fig. 1(a)]. In 2000, the first sampling in late May probably coincided with a seasonal peak. Daily mean temperatures in the 2 months preceding the first drift sampling were significantly higher in 2000 (mean 16·6 ± 0·17° C) compared with 1997 and 1999 (14·1 ± 0·65 and 13·5 ± 0·25° C, respectively) (ANOVA; $F_{2,93}=16·5$; $P<0·001$; Scheffé tests for *post-hoc* comparisons). Peak drift density was significantly lower in 1997 (310 ± 109·4 fish 1000 m^{-3}) than in 1999 and 2000 (904 ± 206·8 and 1354 ± 128·9 fish 1000 m^{-3}) (Kruskal-Wallis, $H_{2,9}=6·5$; $P=0·039$). Drift densities were not correlated with river discharge or discharge trend (Spearman rank correlation; $r_S=-0·02$; $n=31$; $P=0·93$; and $r_S=-0·28$; $n=31$; $P=0·14$).

In the River Kyjovka, seasonal changes in drift density followed a bimodal pattern. The first peak appeared in mid June, followed by a partial decrease and then a second peak in early July. In 2000, both peaks appeared earlier [Fig. 1(b)], similar to the situation in the River Morava. Peak drift density significantly differed among years but not between the first and second peak within years (ANOVA; $F_{2,12}=10·1$; $P<0·003$ for year effect, $F_{2,12}=0·04$; $P>0·50$ for peak rank

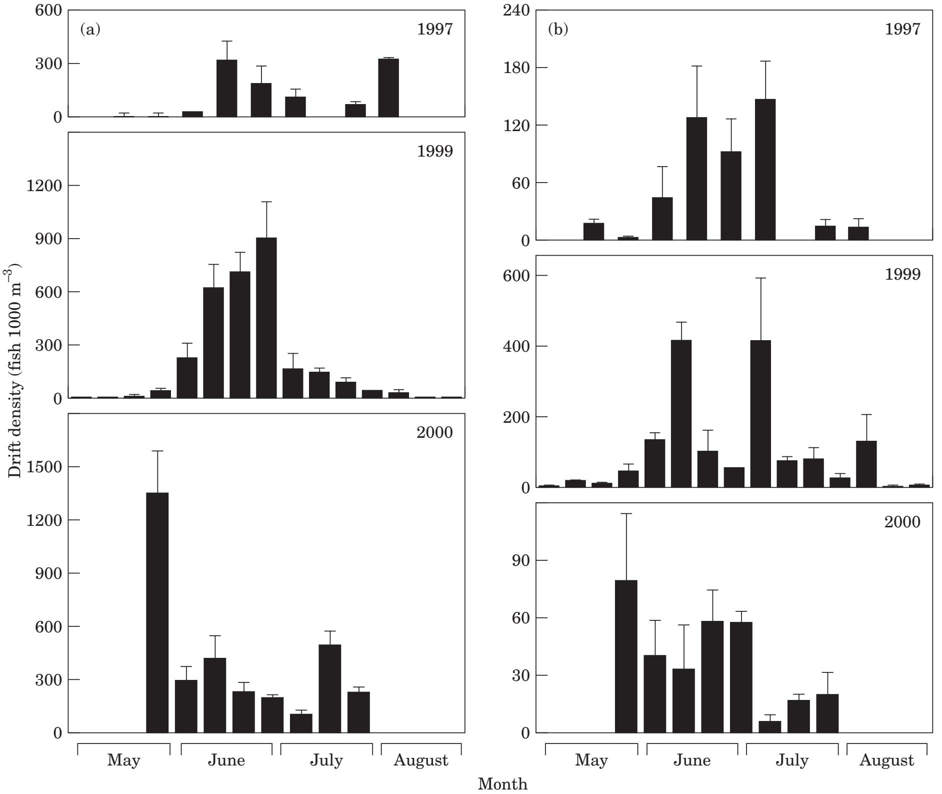

FIG. 1. Seasonal patterns of YOY fish drift in the Rivers Morava (a) and Kyjovka (b) in 1997, 1999 and 2000. Drift density (mean ± S.E.) was calculated from night samples.

effect and $F_{2,12}=0{\cdot}01$; $P>0{\cdot}50$ for the interaction). Peak drift densities were significantly higher in 1999 (417 ± 177·8 fish 1000 m^{-3}) than 1997 and 2000 (145 ± 39·4 fish 1000 m^{-3} and 80 ± 34·5 fish 1000 m^{-3}) (Scheffé test for *post-hoc* comparisons; $P<0{\cdot}05$).

Overall, drift density in the River Morava was twofold that in the Kyjovka in 1997 and 1999. However, an order of magnitude more fishes drifted in the Morava than in the Kyjovka in 2000 (Fig. 1).

SPECIES COMPOSITION

Over three seasons, 5133 drifting YOY fishes in the River Morava (600, 2766 and 1767 in the years 1997, 1999 and 2000, respectively) were captured. They belonged to 22 species from five families, although >99% of the fishes were cyprinids. Eight species drifted in all study years (Table II).

Species composition and relative abundance of drifting fishes in the River Morava did not differ among years (Kendall τ; Table III). The 11 most abundant fish species used in this analysis accounted for 95–99% of total fish abundance in each of the study years. The dominant species were roach *Rutilus rutilus* (L.), bitterling *Rhodeus sericeus* (Pallas), *Gobio* spp. and bleak *Alburnus alburnus* (L). Common bream *Abramis brama* (L.) were abundant in 1999 and 2000, though none were found in drift samples in 1997. Eight to 11 species were

TABLE II. List of species drifting in the River Morava in 1997, 1999 and 2000. Relative abundance (%) of species recorded in drift samples and in nursery habitats during and after the drift season are shown. Multiple samples per day and year were pooled and relative abundance was calculated from the pooled data. Species richness and total number of individuals are indicated

	1997			1999			2000		
	Drift	Nursery		Drift	Nursery		Drift	Nursery	
		During	After		During	After		During	After
Cyprinidae									
Abramis brama (L.)				11·4	2·2		3·6	0·8	0·1
Abramis sapa (Pallas)				0·2					
Alburnoides bipunctatus (Bloch)				0·1		0·1			
Alburnus alburnus (L.)	14·8	3·1	8·4	6·0	20·1	25·5	8·4	23·1	19·9
Aspius aspius (L.)	0·3	0·4	1·2			0·1			0·1
Barbus barbus (L.)	1·0		2·4	1·9	1·1	5·9	0·7		1·9
Blicca bjoerkna (L.)	0·7			4·0	0·9		0·3	0·5	0·1
Carassius auratus gibelio (Bloch)	0·5			0·2					
Chondrostoma nasus (L.)	0·2	0·2	1·2			0·3			1·7
Gobio spp.	3·8		2·4	23·6	0·2	3·9	16·3	0·7	11·8
Leucaspius delineatus (Heckel)	0·2	0·2							
Leuciscus cephalus (L.)	2·3	19·7	38·6	10·7	24·7	31·0	0·9	6·0	19·6
Leuciscus idus (L.)	0·2								0·9
Leuciscus leuciscus (L.)	0·7	5·2	4·8			0·2	0·1		1·1

TABLE II. Continued

	1997			1999			2000		
	Drift	Nursery		Drift	Nursery		Drift	Nursery	
		During	After		During	After		During	After
Pseudorasbora parva (Temminck & Schlegel)	2·0		3·6	0·4			0·1		0·4
Rhodeus sericeus (Pallas)	16·0	1·1	2·4	17·6	23·9	24·2	51·2	38·1	27·0
Rutilus rutilus (L.)	53·3	69·8	7·2	22·3	26·6	2·1	17·7	30·8	11·5
Scardinius erythrophthalmus (L.)			3·6	0·1	0·3				
Unidentified Cyprinidae	1·5	0·4		1·2	0·1		0·3	0·1	
Cobitidae									
Cobitis elongatoides Bacescu & Maier	0·2					0·2			0·1
Siluridae									
Silurus glanis L.			1·2	0·1		0·3			0·4
Percidae									
Perca fluviatilis L.	0·3		16·9			2·9			
Stizostedion lucioperca (L.)	0·5		4·8	<0·1		0·1			0·1
									0·6
Unidentified	1·0			<0·1			0·5		
Other species						3·2*			2·6**
Species richness	17	8	14	15	9	16	10	7	20
Number of individuals	600	557	83	2766	1135	997	1767	871	1692

**Lota lota* (L.) (Gadidae); ***L. lota*, *Proterorhinus marmoratus* (Pallas) (Gobiidae) and vimba *Vimba vimba* (L.) (Cyprinidae).

TABLE III. Similarity analysis of assemblage structure using Kendall coefficient of rank correlation (τ) on species relative abundance. Multiple samples each day and year were pooled and relative abundance was calculated from the pooled samples. Statistical significance refers to significant similarity

Morava	n	τ	P	Kyjovka	n	τ	P
Drift among years				Drift among years			
1997 *v.* 1999	12	0·46	0·037	1997 *v.* 1999	11	0·41	0·078
1997 *v.* 2000	12	0·64	0·003	1997 *v.* 2000	11	0·25	0·284
1999 *v.* 2000	12	0·74	0·001	1999 *v.* 2000	11	0·15	0·514
Drift *v.* nurseries during the drift season				Drift *v.* nurseries during the drift season			
1997	17	0·31	0·080	1997	11	0·44	0·059
1999	15	0·63	0·001	1999	15	0·48	0·014
2000	10	0·74	0·003	2000	11	0·33	0·162
Drift *v.* nurseries after the drift season							
1997	19	0·34	0·040				
1999	20	0·10	0·527				
2000	18	0·48	0·012				

caught at times of peak drift density when species richness of drift samples were highest [Fig. 2(a)]. Species richness was highest in 1997 (17 species) and lowest in 2000 (10 species) (Table II). This pattern remained consistent after correction for the number of individuals captured (Rarefaction method; Fig. 3).

A comparison of ranks of relative abundance between drifting fishes and the YOY assemblage in nursery areas during the drift season in the River Morava revealed a close similarity. This similarity was found also between drifting fishes and the YOY fish assemblage at the end of the drift season with the exception of 1999 (Kendall τ; Table III). However, a direct numerical comparison of the relative abundances of individual species showed that those species drifting frequently (*R. rutilus*, *R. sericeus* and *A. brama*) decreased, while species drifting infrequently (*B. barbus,* nase *Chondrostoma nasus* (L.), chub *Leuciscus cephalus* (L.)) increased their relative abundance in the YOY fish assemblage after the drift season (Fig. 4).

In the River Kyjovka 1821 fishes (548, 1084, and 189 in the years 1997, 1999 and 2000, respectively) from 17 species and four families with six species drifting in all study years (Table IV) were caught. Most, >98%, belonged to the cyprinid family.

The species composition and relative abundance of drifting fishes in the Kyjovka were not similar among years (Kendall τ, Table III). The 10 most abundant species used in the analysis accounted for 98–99% of total drift density. Prussian carp *Carassius auratus gibelio* (Bloch) and *R. sericeus* were common in all years, although their relative abundances varied considerably (Table IV). Silver bream *Blicca bjoerkna* (L.) and *Gobio* spp. contributed considerably to drift abundance in 1999 when drift density in the Kyjovka was highest. *Pseudorasbora parva* (Temminck & Schlegal) drifted abundantly in 1997. Four to eight species were captured at times of peak drift density [Fig. 2(b)]. A total of 14 species were caught in 1999 while only 10 species drifted in 1997 and 2000

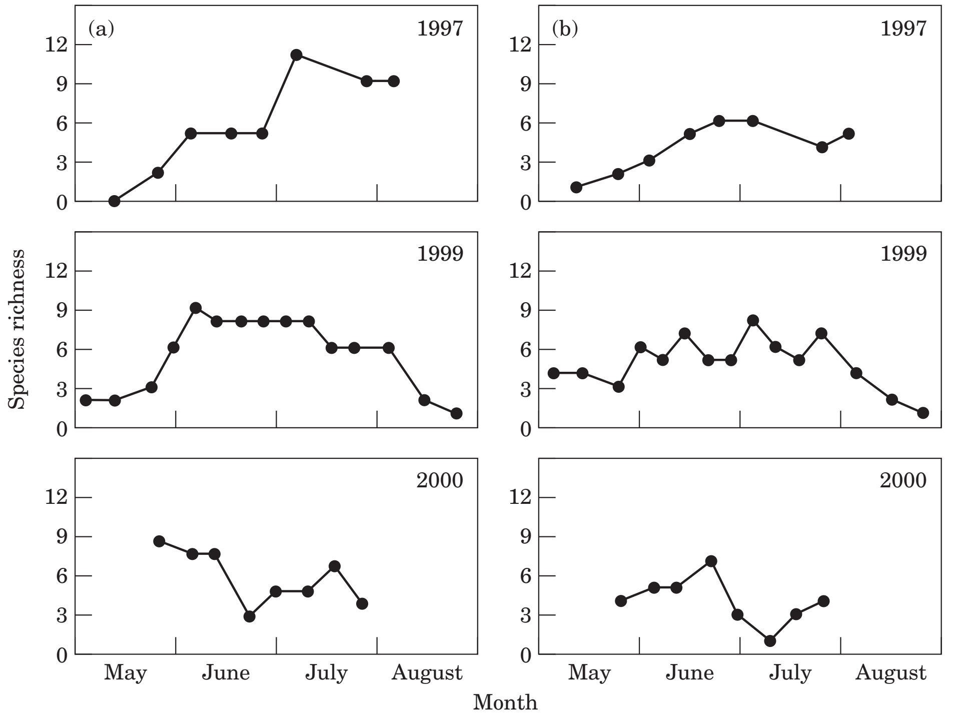

FIG. 2. Seasonal changes in species richness of drift samples (the sum of day and night samples combined) in the Rivers Morava (a) and Kyjovka (b).

(Table IV). However, species richness did not vary among years after correction for number of individuals captured (Rarefaction method; Fig. 3).

The similarity in the species composition and relative abundance of drifting fishes and fishes in nursery habitats in the Kyjovka was lower than in the Morava (Kendall τ; Table III).

DISCUSSION

Most YOY fishes in both rivers drifted within 1 month. The timing of the seasonal pattern of drift abundance showed interannual variation and was correlated with water temperature. In 1997 and 1999 the drift peaked during the second half of June, whilst higher water temperatures in 2000 were associated with earlier fish spawning and earlier peak drift abundance. However, the drift season in 2000 did not end sooner (Fig. 1) than in previous years as a second spawning occurred in some fishes as indicated by the presence of early developmental stages along the river banks (M. Reichard & P. Jurajda, unpubl. data). A seasonal pattern of night drift density was not correlated with the river discharge regime, which is contrary to other studies (Naesje *et al.*, 1986; Harvey, 1987; Pavlov, 1994; Johnston *et al.*, 1995; Johnston, 1997; Mion *et al.*, 1998; de Graaf *et al.*, 1999).

A rapid change in discharge can disrupt regular seasonal drift patterns. Habitat desiccation (Savenkova & Asanov, 1988) or flood events (Harvey, 1987)

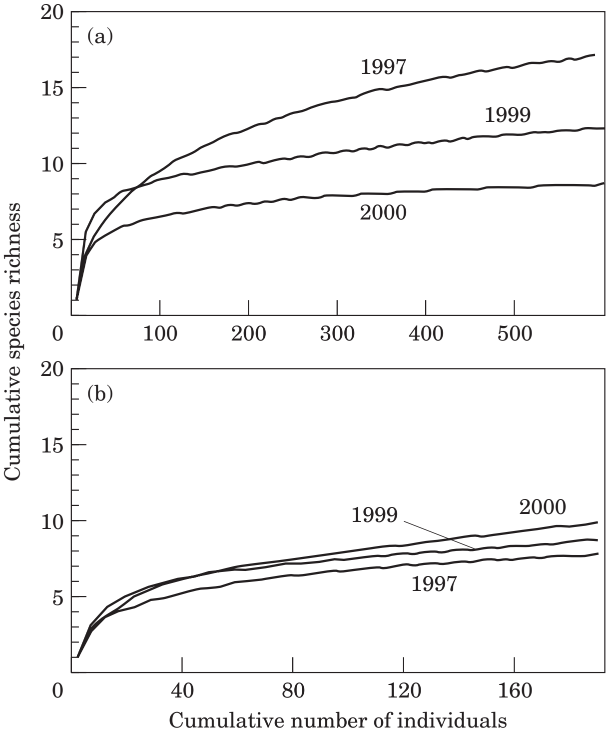

FIG. 3. Comparison of species richness in the drift among years in the Rivers Morava (a) and Kyjovka (b). The curve indicates the expected number of species for a given subsample of individuals selected at random from the pooled sample of the respective year.

can induce either active avoidance of unfavourable conditions or passive drift. The River Morava basin (including both study rivers) was affected by an extensive flood in July 1997. The effect of the flood on the drift was manifested in the cessation of diel periodicity. Water turbidity rather than increased discharge caused fishes to drift abundantly during daylight (Reichard *et al*., 2001). In the present study, seasonal patterns were expressed only in night samples and, thus, the effect of the flood on seasonal dynamics was not observed.

The powerful effect of water temperature (through its effect on the seasonality of reproduction) on the timing of drift in cyprinid fishes is evident from the comparison with drift in other rivers. For example, in an area of the Danube Delta with a higher mean water temperature than the study area, drift peaked in late May (Zambriborshch & Nguen Tan Chin, 1973) similar to the situation in 2000 when water temperature was highest. In contrast, drift culminated later than during the present study in the Russian rivers Volga and Kuban (Pavlov *et al*., 1977) which have a lower average water temperature.

A bi- or multi-modal seasonal pattern of the drift was found in rivers inhabited by a diverse fish community in which different taxa varied in their peak drift (Zambriborshch & Nguen Tan Chin, 1973; Carter *et al*., 1986; Corbett & Powles, 1986; Johnston, 1997; Robinson *et al*., 1998; de Graaf *et al*., 1999). The unimodal pattern observed in the River Morava is usually encountered when

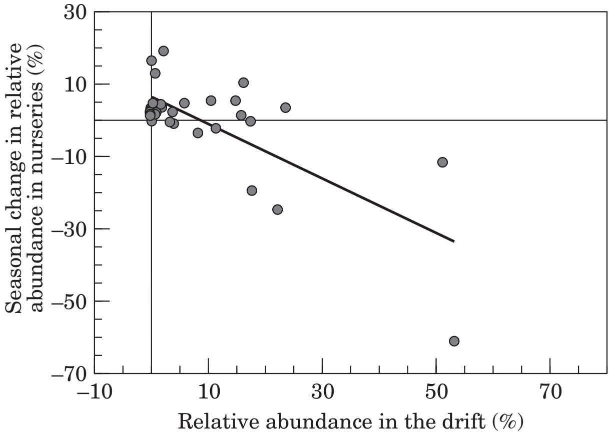

FIG. 4. Relationship between relative abundance in drift samples and a seasonal change in relative abundance in nursery areas during and after the drift season in the River Morava in 1997, 1999 and 2000. ◍, One species in one year and only species with relative abundance >1% in a given year were included in the analysis. Line was fitted by $y = -0{\cdot}742x + 6{\cdot}585$, $r^2 = 0{\cdot}514$.

individual species dominate in drift samples (Clifford, 1972; Jurajda, 1998). However, in the relatively species rich assemblage of drifting fishes in the Morava, several species overlapped in their peak drift density giving rise to a single, broad, unimodal peak composed of several species (unpubl. data). In the River Kyjovka, which was relatively species poor, the succession of species showed incomplete overlap of peak drift density (unpubl. data), giving rise to a multi-modal rather than unimodal pattern.

Variation in drift abundance has been previously documented, both among years (Johnston *et al*., 1995; Johnston, 1997; de Graaf *et al.*, 1999), and between adjacent rivers (Johnston, 1997) and has been attributed to spawning success. Although it is possible that seasonal peaks of drift abundance were missed during the present study in both rivers in 2000, YOY fish abundance in nurseries of the Kyjovka confirmed that low drift density reflected low spawning success, as documented by the low number of fishes present in nurseries that year (Table IV). In contrast, drift density as well as reproductive success in the Morava was highest that year (Table II and Fig. 1).

Cyprinid fishes formed a major part of the fish assemblage in the study rivers (Jurajda & Peňáz, 1994; Jurajda, 1995) and also dominated drift samples. Interannual variation in the species composition of drifting fishes was low in the Morava but significant in the Kyjovka. YOY fishes in the Morava originated from local reproduction (Jurajda, 1995). Local reproduction is also a major source of the YOY fishes in the Kyjovka. However, management of a pond system located 10 km upstream of the sampling site influenced YOY fish assemblage in this river. This influence was confirmed by the presence of an exotic species, grass carp *Ctenopharyngodon idella* (Valenciennes), in samples. Spawning success of some species (*B. bjoerkna*, *C. a. gibelio*, *P. parva*) varied considerably among years as revealed by the abundance of YOY fishes in nursery areas (Table IV). Thus, interannual variation in drift

Table IV. List of species drifting in the River Kyjovka in 1997, 1999 and 2000. Relative abundances (%) of species recorded in drift samples and in nursery habitats during the drift season are shown. Multiple samples per day and year were pooled and relative abundance was calculated from the pooled data. Species richness and total number of individuals are indicated

	1997		1999		2000	
	Drift	Nursery	Drift	Nursery	Drift	Nursery
Esocidae						
Esox lucius L.			0·5			
Cyprinidae						
Alburnus alburnus (L.)	1·1	1·7	6·1	13·0	4·8	0·2
Aspius aspius (L.)						
Barbus barbus (L.)			0·2			
Blicca bjoerkna (L.)		0·3	19·7	8·7	0·5	0·2
Carassius auratus gibelio (Bloch)	23·4	1·0	49·4	16·6	12·2	0·6
Ctenopharyngodon idella (Valenciennes)	0·2	0·1			0·5	
Gobio spp.	3·1	0·1	12·5	0·3	3·3	
Leucaspius delineatus (L.)				0·1		
Leuciscus cephalus (L.)	0·7		0·3	0·6	0·5	0·2
Leuciscus idus (L.)					0·5	
Pseudorasbora parva (Temminck & Schlegel)	43·6	7·4	6·2	6·7		0·2
Rhodeus sericeus (Pallas)	23·5	87·2	3·9	49·2	65·1	96·5
Rutilus rutilus (L.)	2·6		0·3	1·1	3·2	0·4
Scardinius erythrophthalmus (L.)			0·1	0·6		
Unidentified Cyprinidae	1·5		0·5			
Cobitidae						
Misgurnus fossilis (L.)			0·2			
Siluridae						
Silurus glanis (L.)			0·1		9·5	
Percidae						
Stizostedion lucioperca (L.)	0·2					
Perca fluviatilis L.	0·2		0·2			
Species richness	10	7	14	10	10	7
Number of individuals	548	701	1084	701	189	509

species composition and drift abundance is well explained by interannual variation in spawning success, as reported also by Savenkova & Asanov (1988) and Johnston *et al.* (1995).

Species composition of the drift closely resembled the structure of the YOY fish assemblage in nursery areas during the drift season, with the exception of the Kyjovka in 2000 when reproductive success of all species but *R. sericeus* was extremely low and fishes other than *R. sericeus* were caught rarely in nursery areas. The fact that most fishes present at the locality also drifted was reported from the River Volga basin (Pavlov, 1994) but, typically, few fish species dominated drift samples (Brown & Armstrong, 1985; Carter *et al.*, 1986; Jurajda, 1998). Some YOY fishes are known to avoid drift (Starnes & Hackney, 1983;

Kennedy & Vinyard, 1997). For example chub, *Leuciscus cephalus* (L.), was one of the most common species in adult and YOY fish assemblages in the River Morava (Jurajda & Peňáz, 1994; Jurajda, 1995), but was rare in drift samples. This species actively searched for low flow patches in an artificial channel to avoid drifting (Garner, 1999). Some benthic species (*B. barbus, C. nasus,* dace *Leuciscus leuciscus* (L.)) and perch *Perca fluviatilis* L. probably also avoided downstream movement (Table I). As benthic *Gobio* spp. drifted abundantly, the idea that drift avoidance is typical for benthic species (Pavlov, 1994) and for *Gobio* spp. in particular (Bardonnet, 2001) is discounted.

Drifting is risky (Huhta *et al*., 2000) and can lead to substantial mortality in fishes (Mion *et al.*, 1998; Robinson *et al*., 1998; Iguchi & Mizuno, 1999). The relative abundance of the YOY fish assemblage at the end of the drift season (late August to September) differed from the relative abundance of the assemblage of drifting fishes, although, using a rank test, this was statistically significant only in 1999. Mortality during or after downstream dispersal still affected reproductive success and the relative abundance of YOY fish assemblage. *Leuciscus cephalus* did not drift and its relative abundance in nursery areas was higher after than during the drift season (Table II). Similar results were obtained for benthic *B. barbus* and *C. nasus*. However, the lower relative abundances of these two species in nursery areas during the drift season could be attributed to a sampling bias (lower efficiency of dipnetting than electrofishing for catching benthic fishes). On the other hand, *R. rutilus*, *R. sericeus* and *A. brama* drifted abundantly and their relative proportion in the YOY fish assemblage after the drift season decreased (Table II). Alternative explanations could be that these species: (1) moved offshore in autumn and were not captured during electrofishing along the bank or (2) drifted out of the study area, which was not compensated by imigration of conspecifics from upstream reaches. However, the comparison of YOY fish assemblages between the studied stretch and a stretch of the River Morava 10–70 km downstream did not confirm such a pattern (Jurajda *et al*., 2001).

Nothing is known about the proportion of cyprinid fish populations performing downstream transport nor the effects on fish population dynamics. In migratory potamodromous [walleye *Stizostedion vitreum* (Mitchill)] and amphidromous (freshwater goby *Rhinogobius brunneus* Temminck & Schlegel) species, drift is an obligatory part of the life cycle and successful occupancy of suitable nursery habitats has a major effect on population density (Mion *et al.*, 1998; Iguchi & Mizuno, 1999). Although many species represented in drift samples of the present study are known to perform upstream spawning migrations (Schmutz & Jungwirth, 1999), they often fail to pass man-made barriers (Jurajda *et al*., 1998). *Rhodeus sericeus* did not perform upstream migrations (Jurajda *et al*., 1998) but did drift downstream. Although drift seems to be a convenient form of transport from spawning sites, the present results suggest that drift may cause significant mortality. However, a quantitative approach is needed to test this assumption.

We thank our many friends for help with fieldwork, two anonymous referees for their constructive comments and C. Smith for his assistance with English corrections. We also thank the Czech Hydrometeorological Institute in Brno for providing discharge and temperature data. Financial support came from Grant Agency of Academy of Sciences of the Czech Republic, Grant No. IAB6093106. MR was partly funded by Ministry of Education, Grant No. FRVS 600/2001.

References

Bardonnet, A. (2001). Spawning in swift water currents: Implications for eggs and larvae. *Archiv für Hydrobiologie Supplementband* **135**, 271–291.

Brown, A. V. & Armstrong, M. L. (1985). Propensity to drift downstream among various species of fish. *Journal of Freshwater Ecology* **3,** 3–17.

Carter, J. G., Lamarra, V. A. & Ryel, R. J. (1986). Drift of larval fishes in the upper Colorado River. *Journal of Freshwater Ecology* **3,** 567–577.

Carter, K. L. & Reader, J. P. (2000). Patterns of drift and power station entrainment of 0+ fish in the River Trent, England. *Fisheries Management and Ecology* **7,** 447–464.

Clifford, H. F. (1972). Downstream movements of white sucker, *Catostomus commersoni*, fry in a brown-water stream of Alberta. *Journal of the Fisheries Research Board of Canada* **29,** 1091–1093.

Copp, G. H. & Peňáz, M. (1988). Ecology of fish spawning and nursery zones in the flood plain, using a new sampling approach. *Hydrobiologia* **169,** 209–224.

Corbett, B. W. & Powles, P. M. (1986). Spawning and larva drift of sympatric walleyes and white suckers in an Ontario stream. *Transactions of the American Fisheries Society* **115,** 41–46.

Garner, P. (1999). Swimming ability and differential use of velocity patches by 0+ cyprinids. *Ecology of Freshwater Fish* **8,** 55–58.

de Graaf, G. J., Born, A. F., Uddin, A. M. K. & Huda, S. (1999). Larval fish movement in the River Lohajang, Tangail, Bangladesh. *Fisheries Management and Ecology* **6,** 109–120.

Harvey, B. C. (1987). Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* **116,** 851–855.

Huhta, A., Muotka, T. & Tikkanen, P. (2000). Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biology* **45,** 33–42.

Iguchi, K. & Mizuno, N. (1999). Early starvation limits survival in amphidromous fishes. *Journal of Fish Biology* **54,** 705–712. doi:10.1006/jfbi.1998.0909.

Johnston, T. A. (1997). Downstream movements of young-of-the-year fishes in Catamaran Brook and the Little Southwest Miramichi River, New Brunswick. *Journal of Fish Biology* **51,** 1047–1062.

Johnston, T. A., Gaboury, M. N., Janusz, R. A. & Janusz, L. R. (1995). Larval fish drift in the Valley River, Manitoba: influence of abiotic and biotic factors, and relationships with future year class strengths. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 2423–2431.

Jurajda, P. (1995). Effect of channelization and regulation on fish recruitment in a floodplain river. *Regulated Rivers: Research & Management* **10,** 207–215.

Jurajda, P. (1998). Drift of larval and juvenile fishes, especially *Rhodeus sericeus* and *Rutilus rutilus*, in the River Morava (Danube basin). *Archiv für Hydrobiologie* **141,** 231–241.

Jurajda, P. & Peňáz, M. (1994). Fish community of the lower regulated stretch of the River Morava, Czech Republic. *Folia Zoologica* **43,** 57–64.

Jurajda, P., Hohausová, E. & Gelnar, M. (1998). Seasonal dynamics of fish abundance below a migration barrier in the lower regulated River Morava. *Folia Zoologica* **47,** 215–223.

Jurajda, P., Reichard, M., Hohausová, E. & Černý, J. (2001). Comparison of 0+ fish communities between regulated-channelized and floodplain stretches of the River Morava. *Archiv für Hydrobiologie Supplementband* **135**, 187–202.

Kennedy, T. B. & Vinyard, G. L. (1997). Drift ecology of western catostomid larvae with emphasis on Warner suckers, *Catostomus warnerensis* (Teleostei). *Environmental Biology of Fishes* **49,** 187–195.

Koblickaya, A. F. (1981). *Key For Identifying Young Freshwater Fishes*. Moscow: Food Industry Publishing House (in Russian).

Mion, J. B., Stein, R. A. & Marschall, E. A. (1998). River discharge drives survival of larval walleye. *Ecological Applications* **8,** 88–103.

Naesje, T. F., Jonsson, B. & Sandlund, O. T. (1986). Drift of cisco and whitefish larvae in a Norwegian river. *Transactions of the American Fisheries Society* **115,** 89–93.

Northcote, T. (1962). Migratory behavior of juvenile rainbow trout, *Salmo gairdneri*, in outlet streams of Loon Lake, British Colombia. *Journal of the Fisheries Research Board of Canada* **19,** 201–270.

Pavlov, D. S. (1994). The downstream migration of young fishes in rivers: mechanisms and distribution. *Folia Zoologica* **43,** 193–208.

Pavlov, D. S., Pakhorukov, A. M., Kuragina, G. I., Nezdoliy, V. K., Nekrasova, I. P., Brodskiy, D. A. & Ersler, A. L. (1977). Some pecularities of downstream migrations of young fishes in the Volga and Kuban rivers. *Voprosy Ikhtyologii* **17,** 415–428 (in Russian).

Reichard, M., Jurajda, P. & Václavík, R. (2001). Drift of larval and juvenile fishes: a comparison between small and large lowland rivers. *Archiv für Hydrobiologie Supplementband* **135**, 373–389.

Robinson, A. T., Clarkson, R. W. & Forrest, R. E. (1998). Dispersal of larval fishes in a regulated river tributary. *Transactions of the American Fisheries Society* **127,** 772–786.

Savenkova, T. P. & Asanov, A. Yu. (1988). Observations of downstream migration of juvenile fish in the lower part of the Atrek. *Voprosy Ikhtyologii* **28,** 649–656 (in Russian).

Schmutz, S. & Jungwirth, M. (1999). Fish as indicators of large river connectivity: the Danube and its tributaries. *Archiv für Hydrobiologie Supplementband* **115**, 329–348.

Starnes, L. B. & Hackney, P. A. (1983). Larval fish transport: a case study of white bass. *Transactions of the American Fisheries Society* **112,** 390–397.

Wanzenböck, J. & Wanzenböck, S. (1993). Temperature effects on incubation time and growth of juvenile whitefin gudgeon, *Gobio albipinnatus* Lukasch. *Journal of Fish Biology* **42,** 35–46.

Zambriborshch, F. S. & Nguen, Tan Chin. (1973). The descent of fish larvae into the sea through the Kiliya arm of the Danube. *Voprosy Ichtyologii* **13,** 103–108 (in Russian).