Inter-annual and diel patterns of the drift of cyprinid fishes in a small tributary of the Meuse River, Belgium

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Abstract. The biological processes underlying larval cyprinid drift are still unclear, in particular the distinction between the active and passive components. The present study examined fish drift, water temperature and light intensity in the River Mehaigne (Belgium) over a two-year period using a two-fold method that combines punctual 24 h samples with 3 weekly 1 h dusk samples over the drift season. Inter-annual comparisons revealed variations in the relative abundance of roach *Rutilus rutilus* and chub *Leuciscus cephalus*, explained by a reduced spawning success of chub due to a lower mean water temperature in 2004. Cyprinid larval drift peaked under increasing temperatures, whereas river discharge and turbidity had no apparent effect. A nocturnal repartition of the diel drift distribution was observed, with the highest drift density during late dusk (< 1 Lux) suggesting a loss of rheotaxis in dark conditions. Moreover, the mean body size of roach and chub varied significantly between different times of the day, roach TL increasing from dusk to dawn while chub TL was smallest at night. Biological significance of the drift is discussed with respect to specific larval ecology and morphology.

Key words: roach *Rutilus rutilus*, chub *Leuciscus cephalus*, downstream displacement, drift strategy, rheotaxis, visual acuity

Introduction

Downstream movements of fishes in rivers are, at least partially, mediated by water current (Pavlov 1994). In order to understand better the processes underlying space use and population distributions, it is essential to distinguish the proportions of passive (current-mediated) and active (behaviourally-determined) displacements (Mauritzen et al. 2003). Drift of riverine young-of-the-year fishes is considered to be an important biological mechanism that ensures larval dispersal and relocation to nursery grounds. The seasonal pattern of larval drift is mainly dependent on a species' reproductive timing and on hydrological conditions during larval life (Brown & Armstrong 1985, Reichard et al. 2001). Drift of young-of the-year fishes has been studied in many geographical areas and in a large variety of taxa (Gale & Mohr 1978, Copp & Cellot 1988, Bardonnet & Gaudin 1990, Flecker et al. 1991, Bardonnet et al. 1993, Johnston et al. 1995, Johnston 1997, Araujo-Lima & Oliveira 1998, Robinson et al. 1998, de Graaf et al. 1999), with studies of non-salmonid species more commonly from Eastern and Central European rivers (Pavlov et al. 1978, Jurajda 1998, Reichard et al. 2001, 2002a,b, Oesmann 2003, Zitek et al. 2004a,b) than those of Western Europe, (Peňáz et al. 1992, Hofer & Kirchhofer 1996, Copp et al. 2002).

The diel pattern of cyprinid drift is mainly described as nocturnal (Pavlov et al. 1978, Peňáz et al. 1992, Jurajda 1998, Reichard et al. 2001, 2002b, Copp et al. 2002, Zitek et al. 2004b), except under low water transparency, when this diel pattern disappears

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(Reichard et al. 2001). Underwater visibility appears to be an important factor affecting both seasonal and diel patterns of cyprinid larval drift. However, it is still unclear whether low underwater visibility induces a passive disorientation associated with a loss of visual references (Bardonnet 1993, Pavlov 1994), or with a preferential choice by the fish to drift under low light conditions to avoid predation risks (Bardonnet 2001). Moreover, it is probable that larval drift has different dynamics and significance among species according to larval morphology and ecological interactions.

These differing hypotheses reveal that the biological processes underlying larval cyprinid drift are still not well understood. Most studies have focused on punctual or time spaced (weekly or longer-spaced) investigations of 24 h samples (Peňáz et al. 1992, Hofer & Kirchhofer 1996, Jurajda 1998, Reichard et al. 2001, 2002a, Oesmann 2003). Only a few more frequent investigations of 24 h have been carried out (Zitek et al. 2004a,b) over extended periods (Reichard et al. 2002b, Copp et al. 2002).

In our study in the River Mehaigne (Belgium), we used a two-fold approach in an attempt to characterize better the patterns of larval cyprinid drift over two successive years. Firstly, we conducted a classical method of punctual 24 h diel samples during the drift seasons. In addition, we conducted 1 h dusk samples more frequently over the whole drift season in an attempt to characterise the influence of environmental factors on daily drift variations. Using both a general and a specific approach, we tried to understand the distinction between the active and the passive proportions of drift with respect to specific larval morphology and ecology.

Study Site, Material and Methods

Mehaigne Stream is 65.6 km in length and drains a basin of 360 km^2, entering the River Meuse 4 km upstream of the city of Huy. Over the last five years, the stream had a mean annual river discharge of 2.96 m^3 s^{-1} and contained a fish assemblage (in the downstream 4 km; Table 1) that has had a relatively constant species composition for many years (J.-C. Philippart, unpublished data). Fish drift was estimated 2 km upstream of the confluence with the River Meuse, in order to sample a maximum number of larvae coming from upstream. The drift net was made of 0.5 mm nylon mesh and had an opening of 0.3 m x 0.3 m (area of 0.09 m^2) and a 1 m long conical shape. The net was placed 1 m from the left bank, on the edge of a main current where the net covered the entire water depth. The width of the river at the sampling site was 10 m. After each sampling, the net was emptied and all the filtrate was placed in 5% formaldehyde for examination the day after, as identification of larvae was difficult at night in the field. In our seasonal protocol, we sampled 3 d a week, with intervals of two or three days from 15 May to 31 July in 2003 (31 dates). As fish larvae were caught already on the first sampling day in 2003, the study period was extended from 21 April to 31 July in 2004 (39 dates). Because drift is known to be more intense during twilight and night periods (Bardonnet et al. 1993, Pavlov 1994, Reichard et al. 2001), samples were collected during three consecutive periods of 20 min in the first hour after sunset. As such, the use of three time replicates within one hour period was used instead of lateral, vertical or longitudinal repetition during the same time interval, as usually performed in other studies. Moreover, each year on five occasions, we collected 14 samples over a 24 h period, with 20 minute samples taken every 2 h during day and night periods, and every hour during dawn and dusk (Fig. 1).

Water velocity was measured at the start and end of each 20 minute sample using a velocity meter (FLO-MATE 2000, Marsh-McBirney, Inc.) placed in the centre of the net.

Table 1. Relative abundance of adult fish species assessed by electro-fishing in the lower 4 km stretch of the River Mehaigne (Belgium) during daytime in late March 2003. An asterisk denotes species that contributes less likely to larval drift species assemblage due to their lower occupation in the river, their autumnal spawning period or catadromous status.

Common name	Scientific name	N	%
Roach	*Rutilus rutilus* (Linnaeus, 1758)	1139	62.5
Chub	*Leuciscus cephalus* (Linnaeus, 1758)	307	16.8
Gudgeon	*Gobio gobio* (Linnaeus, 1758)	145	8.0
Bleak	*Alburnus alburnus* (Linnaeus, 1758)	70	3.8
Dace	*Leuciscus leuciscus* (Linnaeus, 1758)	52	2.9
Nase	*Chondrostoma nasus* (Linnaeus, 1758)	35	1.9
Brown trout	*Salmo trutta* (Linnaeus, 1758)*	29	1.6
Barbel	*Barbus barbus* (Linnaeus, 1758)	9	0.5
Bullhead	*Cottus gobio* (Linnaeus, 1758)	9	0.5
Silver bream	*Abramis bjoerkna* (Linnaeus, 1758)*	5	0.3
Rudd	*Scardinius erythrophthalmus* (Linnaeus, 1758)	4	0.2
Carp	*Cyprinus carpio* Linnaeus, 1758*	3	0.2
Tench	*Tinca tinca* (Linnaeus, 1758)*	3	0.2
Grayling	*Thymallus thymallus* (Linnaeus, 1758)	2	0.1
Ide	*Leuciscus idus (*Linnaeus, 1758*)*	2	0.1
Common bream	*Abramis brama* (Linnaeus, 1758)*	2	0.1
Crucian carp	*Carassius carassius* (Linnaeus, 1758)*	2	0.1
Riffle minnow	*Alburnoides bipunctatus* (Bloch, 1782)	1	0.1
Ruffe	*Gymnocephalus cernuus* (Linnaeus, 1758)	1	0.1
Pike	*Esox lucius* Linnaeus, 1758	1	0.1
European eel	*Anguilla anguilla* (Linnaeus, 1758)*	1	0.1
Stone loach	*Barbatula barbatula* (Linnaeus, 1758)	1	0.1
Σ		1823	

As sampling durations were short and the amount of drifting debris was low during the study, we did not consider the non-linear net clogging model developed by Faulkner & Copp (2001), but instead used the mean water velocity to estimate drift density. Drift density was defined as the number of individuals counted per 1000 m^3 of filtered water (n 1000 m^{-3}), as is commonly used in other studies. Water turbidity (Formazine Attenuation Unit, FAU) was assessed before each sampling using a portable spectro-photometer (HACH, DR/2010). Light intensity (in Lux) was recorded by a data logger (Onset StowAway® LI) every 5 min. Night was considered to be the stabilised duration of darkness between decreasing and increasing intensities of the twilight periods. During dusk, light intensity decreased from > 1000 Lux around 1 h before sunset and to < 0.1 Lux about 1 h after sunset. The same pattern was observed with increasing values for dawn. Consequently, the last dusk sample (Ss+1) and the first dawn sample (Sr-1) were always collected under a 1 Lux illumination (Fig. 1). Data on hourly river discharge were provided by the SETHY MET of the Walloon Region. A data logger (Onset StowAway® Temp) recorded the temperature (°C) every hour 5 km upstream of the study site.

Pinder's (2001) identification key was used to determine the larval development stages and species, which are based on the 'integrated ontogenetic' approach described by Balon (1975), with a collection of digital pictures of roach *Rutilus rutilus*, nase *Chondrostoma nasus*, dace *Leuciscus leuciscus* and chub *L. cephalus* larvae obtained from artificial reproduction used to increase the accuracy of species identification.

The influence of environmental factors on drift density was examined using Spearman's correlation. Differences between drift densities were compared using the Kruskall-Wallis and Mann-Whitney U tests. Differences among mean value of environmental variables and larval total body lengths (TL, ± 0.5 mm) were compared using analysis of variance (ANOVA) coupled with Fisher's PLSD test.

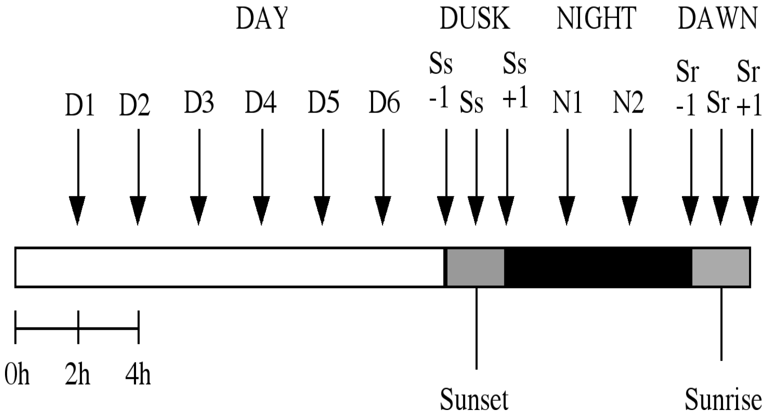

Fig. 1. Sampling protocol applied during the ten 24 h drift investigations in the River Mehaigne in 2003 and 2004. Arrows indicate sample timing during the 4 periods of the day. D1-6 = day samples every 2 h; Ss-1 = sample 1 h before sunset, Ss = sample at sunset, Ss+1 = sample 1 h after sunset, N1-2 = night samples every 2 h, Sr-1 = sample 1 h before sunrise, Sr = sample at sunrise, Sr+1 = sample 1 h after sunrise. Each sampling lasted 20 minutes.

Results

Seasonal drift patterns

In drift net samples conducted in 2003 and 2004, roach and chub were found to be the most abundant species, with chub being considerably less abundant in 2004 than in 2003 (Table 2). Other species, such as bleak *Alburnus alburnus*, dace and barbel *Barbus barbus* were present occasionally. During both years, mean larval abundance increased significantly (Kruskall-Walis test, $P = 0.0017$, $H = 12.742$, df = 2) from the first to the third 20 minute sample during the first hour after sunset (sample 1 = 39.2 ± 12.3 fish 1000 m^{-3}, sample 2 = 81.9 ± 20.1 1000 m^{-3}, sample 3 = 165.1 ± 39.3 1000 m^{-3}). Consequently, we used the mean drift density of these three dusk samples in our further analysis and graphs.

In 2003, the highest mean drift density (Fig. 2a) was observed on 6 June. This peak occurred a few days after a significant increase in water temperature (+ 4 °C), and ten days after a major peak in river discharge. A second drift peak was observed on 27 June, after a small temperature increase. The third main drift peak appeared on 7 July, two days after a decrease in the water temperature associated with an increase in river discharge. The drift density remained relatively low during the rest of the study period.

In 2004, the highest drift density was observed on 4 June (Fig. 2b), under a progressive increase in water temperature and a stable discharge and turbidity. During the following weeks, drift peaked on five other sampling dates coinciding with successive temperature increases. Considering only the period from 7 June to 5 July, a positive correlation was observed between drift density and the daily change in temperature ($T°_{day} – T°_{day-1}$) (Spearman correlation, $r_s = 0.762$, $P = 0.0115$). We were not able to sample on 23 July because of

Table 2. Mean water temperature (T° ± SE), river discharge (RD, ± SE) and water turbidity (Turb, ± SE) from 15 May to 31 July 2003 and 2004. Mean drift density (DD ± SE), relative abundance (%) and numbers (in brackets) of larval fish species in the lower part of the River Mehaigne estimated by three weekly drift net samples from 15 May to 31 July in 2003 and from 21 April to 31 July in 2004 and by five 24h cycles in 2003 and 2004, in respect with their larval development stages (L1-L5) as defined by Pinder (2001).

	2003					**2004**					
T° (°C)	16.7 ± 0.2					14.8 ± 0.2					
RD ($m^3 s^{-1}$)	1.3 ± 0.1					1.1 ± 0.1					
Turb (FAU)	22.3 ± 5.0					18.0 ± 4.0					
				Weekly dusk samples							
Species	**All St**	**L1**	**L2**	**L3**	**L4**	**All St**	**L1**	**L2**	**L3**	**L4**	**L5**
Roach	74.5 (449)	74.4	25.6			83.0 (331)	87.2	12.8			
Chub	17.9 (108)	61.1	35.2	3.7		5.5 (22)	43.5	21.7	21.7	8.7	4.3
Bleak	1.0 (6)	33.3	66.7			1.3 (5)	100				
Dace						0.3 (1)		100			
Barbel	0.5 (3)	33.3			66.7	0.3 (1)			100		
Unidentifiable	6.1 (37)					9.8 (39)					
N	603	403	157	4	2	399	303	48	6	2	1
Mean DD (n $1000m^{-3}$)		152.7 ± 49.1					105.2 ± 25.8				
				24 h cycles							
Species	**All St**	**L1**	**L2**	**L3**	**L4**	**All St**	**L1**	**L2**	**L3**	**L4**	**L5**
Roach	41.4 (135)	45.9	54.1			77.5 (165)	75.8	24.2			
Chub	41.7 (136)	2.2	95.6	2.2		16.0 (34)	79.4	20.6			
Bleak	7.1 (23)	56.5	43.5			0.5 (1)	100.0				
Barbel	1.8 (6)			50.0	50.0	1.4 (3)		33.3	66.7		
Three-spined stickleback	0.3 (1)	100.0									
Unidentifiable	7.7 (25)					4.6 (10)					
N	**326**	**79**	**213**	**6**		**326**	**153**	**48**	**2**		

a major increase in river discharge due to a local storm event. For this reason, we are not able to describe larval drift under extremely high discharge conditions. Drift abundance remained low during the rest of the study period.

When the entire study period (15 May to 31 July) is compared between years (Table 2), no differences were found in mean drift density (Mann-Whitney U-test, $P = 0.2370$), river discharge or turbidity but mean water temperature was significantly lower (ANOVA, $F = 17.046$, df = 60, $P = 0.0001$) in 2004 than in 2003.

Diel drift patterns

In 2003, roach and chub were the most abundant species, in an almost equal proportion (Table 2), but in 2004, roach were more abundant than chub, with barbel and bleak again being in low abundance. All 24 h cycles in both years revealed similar diel drift patterns (Fig. 3) in which drift densities were significantly lower during the day than at dusk and night (Fig. 4: Kruskal-Wallis test, $P < 0.0001$, H = 42.06, df = 3), though overall dusk and dawn densities did not differ statistically (M-W, $P = 0.2772$). However, under the same light intensity, mean drift density was significantly higher during late dusk (Ss+1, decreasing light intensity < 1 Lux) than early dawn (Sr-1, increasing light intensity < 1 Lux) (M-W, $P = 0.0233$) for both years. In 2003 (Fig. 5), no significant difference was observed between roach drift density during the four periods of the day (K-W, df = 3, $P = 0.1647$). Whereas, chub drift

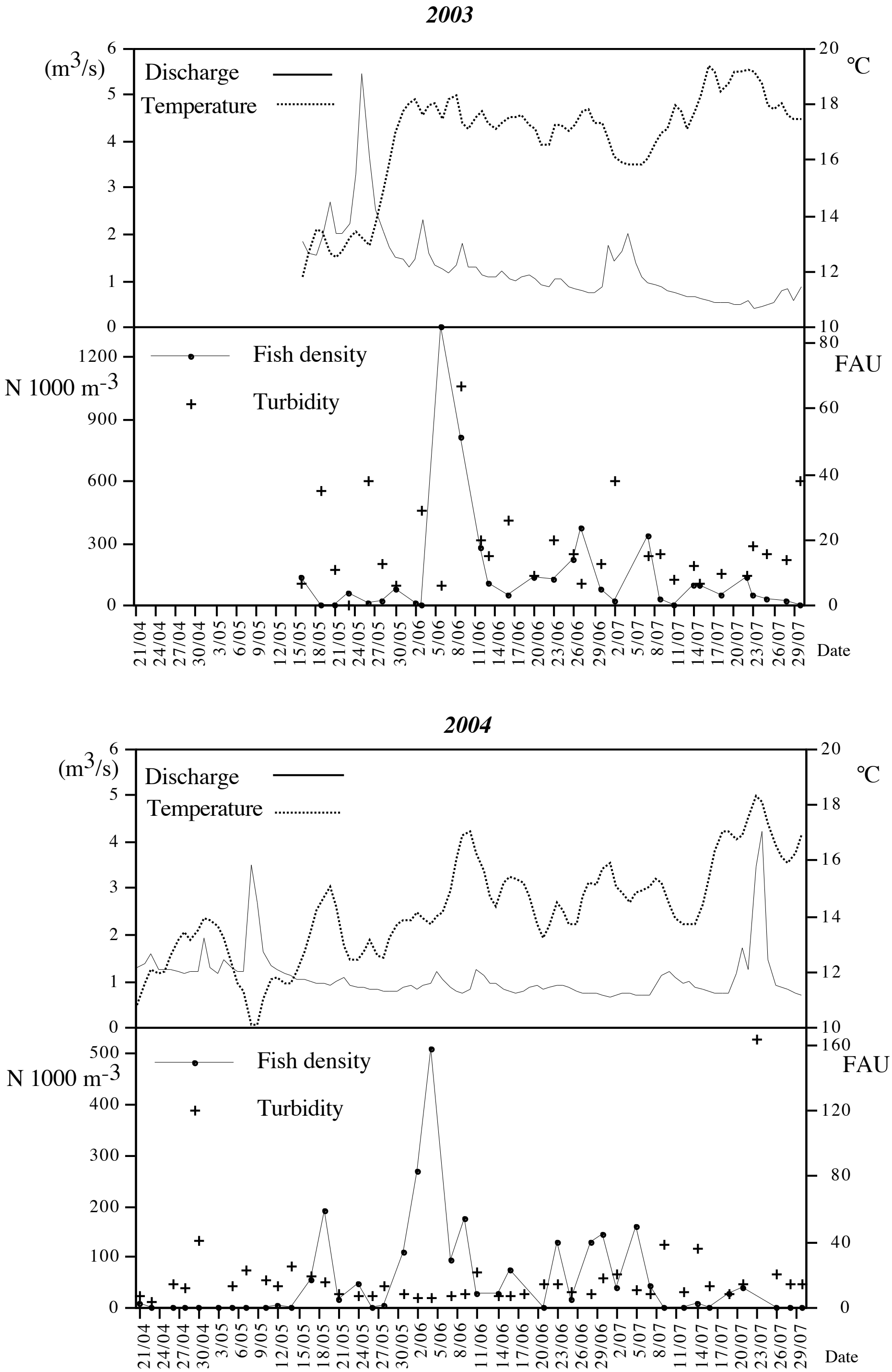

Fig. 2. Mean river discharge (m3 s-1), water temperature (°C), water turbidity (FAU) and drifting fish density (N 1000 m-3) in the River Mehaigne from 15 May to 31 July 2003 (Fig. 2a) and from 21 April to 31 July 2004 (Fig. 2b).

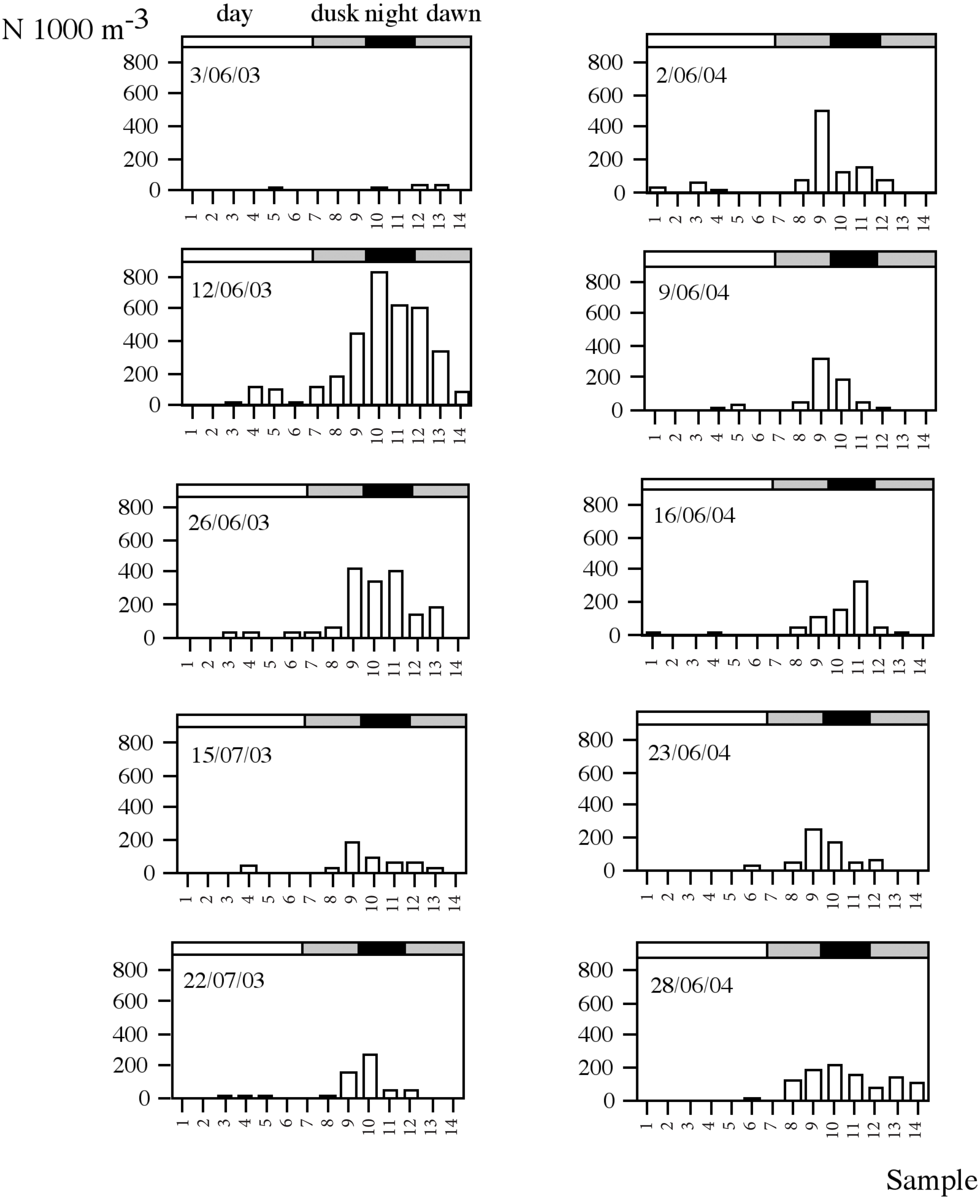

Fig. 3. Mean larval fish drift densities (N 1000 m-3) collected during the 14 samples of each 24h periods in 2003 and 2004.

density varied significantly between night, dusk, dawn and day ($P = 0.0014$), as it also did in 2004 (Fig. 5; $P = 0.0095$), when roach drift densities also varied ($P < 0.0001$).

As regards fish size, when both years are pooled (Table 3) the mean TL of drifting roach larvae was significantly greater (ANOVA, $F = 15.430$, df = 240) at dawn than during the day, dusk and night (Fisher PLSD, Ps < 0.0002), whereas they were significantly shorter during dusk than during the night ($P = 0.0120$). Chub larvae were significanlty shorter

(*F* = 3.396, D.F. = 135) during the night than during dusk (*P* = 0.0185) and dawn (*P* = 0.0156), whereas no difference in chub mean TL was observed between dawn and dusk (*P* = 0.5603).

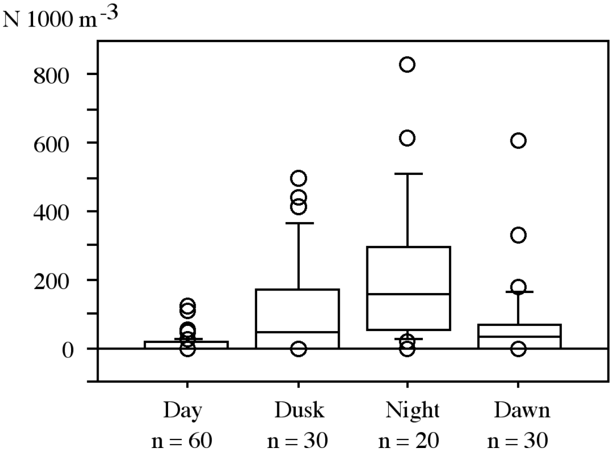

Fig. 4. Box and whiskers plots of the mean larval fish drift density (N 1000 m^{-3}) during the 4 periods of the day of the ten 24h cycles conducted in 2003 and 2004. The centre line denotes the median value, the box encloses the inner two quartiles, error bars indicate the 90th and 10th percentiles, and ○ indicate outliers, n = total number of samples collected during each period of the day.

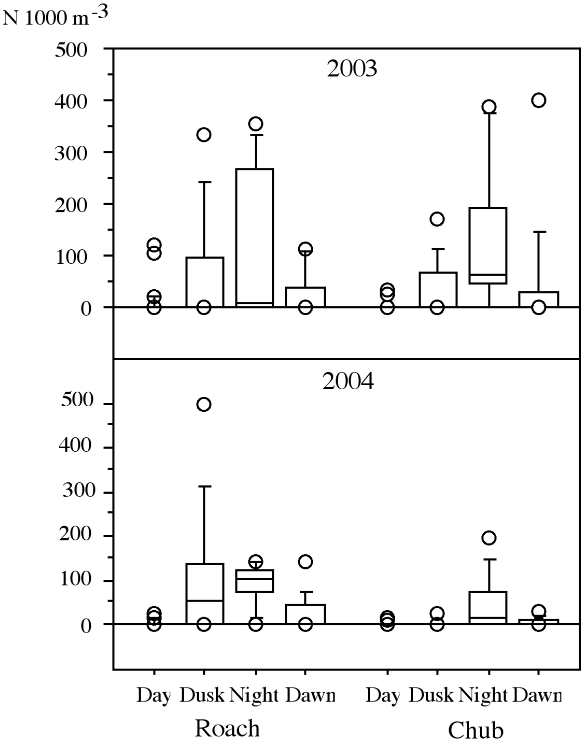

Fig. 5. Box and whiskers plots of the mean larval drift density (N 1000 m^{-3}) of roach and chub during the 4 periods of the day of the ten 24h cycles conducted in 2003 and 2004. The centre line denotes the median value, the box encloses the inner two quartiles, error bars indicate the 90th and 10th percentiles, and ○ indicate outliers. The number of sample was the same than in Fig. 4.

Table 3. Fish mean total length (TL, mm) and standard error (SE) of roach and chub caught in the drift net samples from the River Mehaigne during the different periods of the day in 2003 and 2004 combined.

	Roach			Chub		
	n	TL (mm)	SE	N	TL (mm)	SE
Dawn	40	7.112	0.132	33	9.076	0.173
Day	17	6.147	0.299	5	8.400	0.731
Dusk	96	6.000	0.085	14	9.286	0.172
Night	91	6.324	0.090	87	8.511	0.129

Discussion

The relative abundance of larval drift in the lowest stretch of the River Mehaigne reflects the dominance in the adult fish assemblage of roach and chub, which migrate in large numbers into this stretch from the River Meuse to spawn (Philippart, unpublished data). The relative density of chub larvae was lower in 2004 than in 2003 (Fig. 5). Although we have no information about the adult chub relative abundance in 2004 compared to 2003, the lower abundance of larvae in the drift may have resulted from the effect of lower mean water temperatures in 2004 on chub spawning success (Reichard et al. 2002a, Zitek et al. 2004b). The dominance of roach and variable abundance of chub in larval drift have been observed elsewhere in Europe (Peňáz et al. 1992, Jurajda 1998, Reichard 2001, Reichard et al. 2002a, Zitek et al. 2004a,b), but chub have also been described as avoiding drifting (Garner 1999). Gudgeon *Gobio gobio* was the third most abundant species in the adult fish community of the River Mehaigne (Table 1), but we did not observe any gudgeon larvae in our samples. Although an important component of larval drift in some studies (Jurajda 1998, Reichard et al. 2001, 2002a, Zitek et al. 2002b), gudgeon has been described by other authors as a non-drifter, since gudgeon larval development happens in close association with the substratum of its spawning site (Bardonnet 2001). The absence of gudgeon in our samples could be related to the presence of suitable spawning site, or nursery areas upstream the sampling site were drifting larvae could drop out of the drift. Barbel drifting larvae probably came from upstream well-established barbel populations.

Drifting roach in 2003 and 2004 were mainly of developmental state L1(Table 2), which is characterised by the onset of exogenous feeding, reduction of the yolk sac and filling of the posterior chamber of the swim bladder (Copp 1990). This suggests that reproduction takes place somewhere just upstream of the drift sampling area, in spawning areas close enough to the main flow for the larvae to be take as drift, leaving insufficient time in the drift for L3 roach to appear in our drift samples. As for chub, L1 stages also dominated but with a higher proportion of L2 chub than of L2 roach (Table 2), which could suggest that chub spawning grounds were further upstream.

The lack of correlation between river discharge and drift density in the River Mehaigne was similar to other sites (Copp et al. 2002, Reichard et al. 2002a, Zitek et al. 2004b), though rapid increases in discharge can incite peaks in larval drift (Reichard et al. 2001), conditions during which our drift net could not be used.

In the 24 h samples collected in 2003 and 2004, the observed diel pattern of cyprinid drift was similar to that observed in previous studies elsewhere (e.g. Pavlov et al. 1978, Peňáz et al. 1992, Jurajda 1998, Reichard et al. 2001, 2002b, Copp et al. 2002, Zitek et al. 2004b). As expected from rheotaxis studies in roach (of 8–9 mm), whereby the critical current velocity decreases under the light threshold of 1 Lux (Pavlov

1994), the greatest drift densities were observed when decreasing light levels were < 1 Lux, and decreased progressively during night and dawn with increasing fish TL. The numbers of chub in the drift at night were higher than those of roach and also exhibited a smaller body size during the night, compared to dusk and dawn, resembling studies elsewhere (Peňáz et al. 1992, Zitek et al. 2004b). L1 larvae of rheophilic cyprinids like chub have a large yolk sac inducing a negative buoyancy and a probable burial of larvae (Prokeš & Peňáz 1980, Çalta 2000, Bardonnet 2001). Drifting step by step in darkness in the gravel of the river is a good way to avoid predation during early stages in benthic larvae of rheophilic cyprinids (Bardonnet 2001). The smaller body size of chub larvae at night may be explained by a dispersal from spawning grounds during the night, a behaviour observed in nase *Chondrostoma nasus* (Persat & Olivier 1995), a typical representative of rheophilic cyprinids. However, a potential influence of the clogged substratum of the Mehaigne River on the drift pattern is not excluded, by obstructing hatched larvae burying (Bardonnet 2001), exposing them to drift.

The passive and/or active nature of larval cyprinid drift behaviour continues to be discussed among authors. Recently, as they observed no difference in drifting TL between dusk and night, Reichard et al. (2002b) concluded that "drift in cyprinid fishes is a temporally sensitive behavioural decision rather than passive displacement". The fish TL differences observed in the present study between dawn, dusk and night tend to associate drift with a behavioural decision, and that drift strategies differ between species. Authors agree that the nocturnal dominance of drift allow fishes to limit exposition to predation (Pavlov 1994, Copp et al. 2002).

In the present study, the three weekly 1 h sampling method provided a complementary element to diel sampling as regards species composition and the influence of environmental variables on the drift density of cyprinid larvae. Zitek et al. (2004b) found that 2 h samples collected in the evening were sufficient to predict the total 24 h drift of cyprinid species. However, the results of the present study suggest that 24 h cycles in a drift study bring essential elements when it is aimed to characterise different diel drifting patterns among species in respect with morphological and behavioural interactions during larvae ontogeny.

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