

Diel patterns of drift by macroinvertebrates in the River Lee (Hertfordshire) during low discharge

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Summary	145
Introduction	145
Study site, material and methods.....	146
Results	148
Discussion.....	151
Acknowledgements	155
References.....	155

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Summary

The present study aimed to determine the periodicity of invertebrate drift and its relation to environmental factors. Macroinvertebrate drift samples from Woolmer's Park on the River Lee were collected every three hours over twenty-four-hour periods, once a week between 10 May and 13 July 1995 inclusive. Samples were collected every three hours along with measurements of water velocity, luminosity and water temperature. The most abundant taxa recorded in the drift samples were the Ephemeroptera, *Caenis robusta*, *Baetis rhodani*, *Ephemerella ignita*, *Asellus aquaticus* and Chironomidae. *C. robusta* and *B. rhodani* exhibited night-time maxima, *E. ignita* and Chironomidae had diel patterns of drift during daylight hours. Chironomid drift was significantly, positively correlated with discharge, whereas *E. ignita* was inversely correlated with discharge. *A. aquaticus* peaks in drifting densities occurred at 12.00 and 03.00 hours indicating that for this species, light was not a factor. No correlation between numbers of *A. aquaticus* drifting and discharge and water temperature were found. Note is made of the fact that correlations between drift densities, which are often reported in ecological studies, are spurious in that the drift densities are derived from water velocity measurements at the net's entrance.

Introduction

Immature stages of most rheophilous species of invertebrates, as well as some adults, are known to drift downstream with the current at some stage of their lives (Waters 1972). Drift behaviour of benthic stream organisms has been well documented, in particular with reference to diel periodicity (e.g. Müller 1965, Elliott 1968). Many of these early investigations highlighted both biotic and abiotic influences on drift. The 'types' of drift have been investigated extensively (e.g. Corkum and Clifford 1980, Lancaster 1990), exhibiting several intriguing patterns (Kohler 1984). The following groups of drift are recognized: behavioural, distributional, background and catastrophic (Minckley 1964, Waters 1965). Also, Müller (1982) endeavoured to explain drift behaviour within a life cycle context and proposed the term 'colonization cycle' for downstream drift of insect larvae and nymphs with a compensatory upstream

flight by adult female insects that lay eggs in the headwaters. The concept was later refined to include seasonal movement into more favourable habitats.

Until the 1970s, most studies suggested that macroinvertebrates drifted passively, either as a result of accidental dislodgement during periods of high activity (often with pronounced diel rhythms), or due to increased discharge rates. Although accidental dislodgement undoubtedly accounts for a portion of invertebrate drift, more recent work indicates that other factors are also responsible. Increases in discharge will lead to increased drift, however, water velocity may influence other abiotic factors such as temperature and water chemistry, which may also influence drift (e.g. Brittan and Eikeland 1988). A review of invertebrate drift by Greenwood and Richardot-Coulet (1996) agreed that drift might be a response to environmental constraints and also influenced by resource partitioning.

Invertebrate drift certainly occurs as a response to predation pressure (e.g. Peckarsky and Penton 1989, Lancaster 1990). Questions have arisen as to prey responses to predation. Is prey activity nocturnal in the presence of predators? Does this nocturnal shift occur because of reduced daytime activity rather than increased nocturnal activity? (Douglas et al. 1994). The nocturnal drift of *Baetis rhodani* was due to the presence of trout *Salmo trutta* (Malmquist 1988), whereas higher ratios of night:day drift density of several Ephemeroptera have been reported in streams containing drift-feeding fishes (Flecker 1992, Douglas et al. 1994). Drift periodicity is thought to be genetically fixed, occurring both in the presence and absence of chemical cues (Forrester 1994). Nonetheless, most studies agree that invertebrates exhibit diel periodicity in their drift rates, with the most commonly observed patterns having nocturnal maxima (Barnes and Mann 1991). Indeed, total drift densities may be three times greater at night than during the day. Possible explanations include the effect of light levels and changes in oxygen concentrations (oxygen levels typically reach late-night minima).

Conflicting views exist regarding the factors that induce drift and the reasoning behind drift for different invertebrate components, so no single hypothesis is likely to explain the drift of all taxa at all times (Wiley and Kohler 1981). Changes in ambient light intensity may not be the ultimate reason for drift behaviour, and they do not seem to serve as the trigger or phase-setting agent for drift (Smock 1996). Studies on the threshold level below which drift commences include levels of 0.1-1 lux (Tanaka 1960), 1 lux (Holt and Waters 1967) and 1.57 lux (Chaston 1971). No definitive threshold level has been established, but there is general agreement that light levels of approximately 1 lux and above will reduce drift sufficiently. The majority of drift studies having been carried out in either clean upland streams (e.g. Malmquist 1988, Peckarsky and Cowan 1995) or artificial streams systems (e.g. Hildebrand 1974, Lancaster 1990), with few addressing nutrient-enriched water courses. So the potential impact of elevated nutrients and suspended solids levels on invertebrate activity has received insufficient study. The aim of the present study was to determine whether the drift of invertebrates in the River Lee, a nutrient-rich chalk stream with elevated levels of suspended matter (Faulkner and Copp 2001), follows the similar diel periodicity as reported in other streams. We examine invertebrate drift densities in relation to water temperature, water velocity and light intensity, thus complementing related research of fish drift (Copp et al. 2002) and diel fish distributions (Copp 2004, Copp et al. 2004). The River Lee is of particular interest because the majority of its flow emanates from treated sewage outfalls, especially in periods of reduced discharge (Pilcher and Copp 1997).

Study site, material and methods

The River Lee, with a catchment area of 1,420 km² and a human population of two million, is one of the most heavily impacted river systems in the UK. A major tributary of the River Thames in south-eastern England, the River Lee is

of chalk origin (north-west of Luton: Nat. Grid Ref. TL058248), but receives a majority of its discharge as treated sewage effluent, especially during low flow. Water quality in the reach from Essendonbury Farm (TL272098) to Bayfordbury (TL314111) has been designated as 1B (NRA 1994). Sampling was undertaken in a private estate, Woolmer's Park (TL 288 100), which is near the village of Essendon. The study site at Woolmer's Park (Figure 1) has received limited river channel management, mainly the removal of overhanging or fallen trees and bushes (see Copp and Bennetts 1996). The channel varied between 3 and 12 metres wide, in places depth exceeded 2 m, and the width of the riparian border varied from 2 to > 40 m. The river contains riffle, pool and run sequences (for greater detail, see Copp and Bennetts 1996 and Copp et al. 2002).

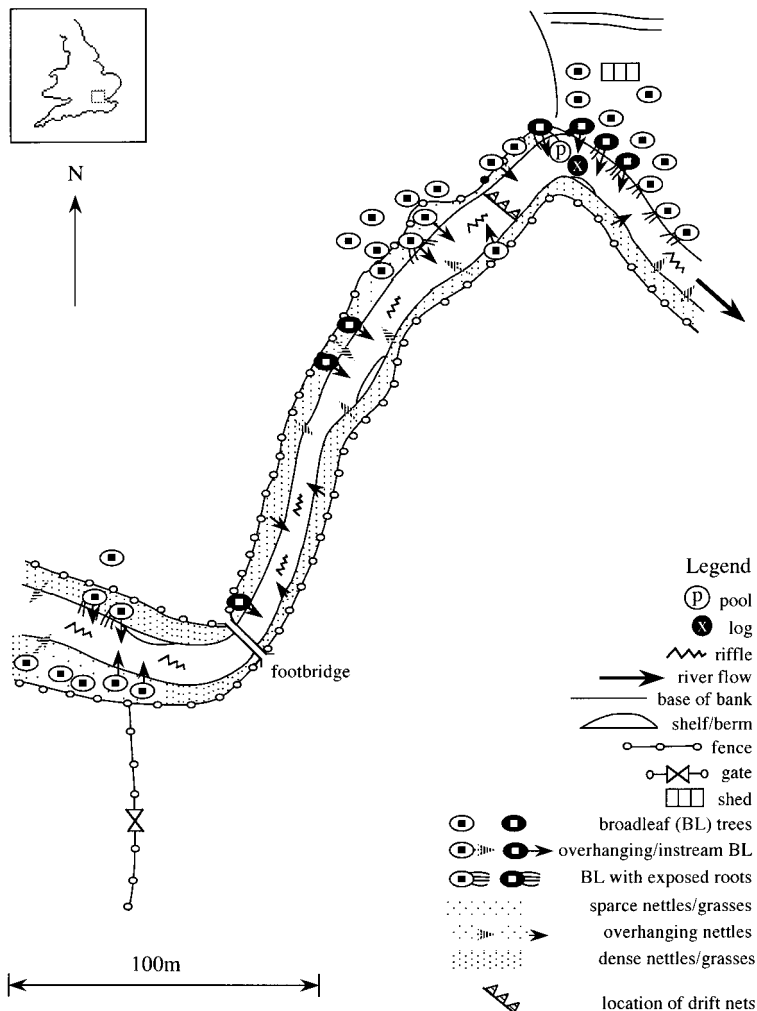


FIGURE 1. Study site on the River Lee at Woolmer's Park, Hertfordshire (UK), with location of drift nets and riparian vegetation indicated.

Drift samples were collected each third hour over twenty-four-hour periods once each week from 10 May to 13 July 1995 using the drift nets and methods described in Copp et al. (2002). The nets (square-to-conical shaped: 0.5 m in total length and 50 µm mesh) were set at 09:00 and the following variables were measured at each sampling time: water temperature, light intensity (lux) and water velocity at the mouth of each net. The drift nets were situated on the left and right banks and centre channel to collect across a range of flow types (for details, see Faulkner and Copp 2001). Invertebrates were sorted from each sample within one to six hours after sampling. Samples of fish and invertebrates were separated and preserved in vials with 4 per cent formaldehyde. Owing to the elevated amounts of debris captured in the nets, the sorting of each samples was limited to thirty minutes to provide an equal unit of effort (see Copp et al. 2002).

The invertebrates collected were counted and identified to order, family, genus or species where possible, using a binocular microscope (10× or 30× magnification) and a variety of identification keys (e.g. Edington and Hildrew 1981, Wallace et al. 1990, Tachet et al. 1991). Drift densities were calculated using the volumes of water filtered estimated for each sample interval using the model presented by Faulkner and Copp (2001), which accounts for the decreased filtering efficiency encountered due to the high amounts of suspended matter carried by the River Lee. We tested for correlations (using Spearman's r) calculated between the densities of taxonomic groups with respect to three variables and the position of the nets in the channel (significance at 95 per cent), as well as for differences between sampling times using StatView SE© on Apple Macintosh© and CSS Statistica© on PC.

Results

The most abundant taxonomic group of invertebrates in the drift was arthropods; they comprised 97.5 per cent of the animals collected (Table 1) of which 84 per cent were insects, with Ephemeroptera and Diptera being the most important groups and Isopoda being the third largest order. The remaining invertebrates consisted of Tricladida and Oligochaeta. We concentrated our analysis on the most abundant species (Table 1): *Ephemerella ignita*, *Caenis robusta*, *Baetis rhodani* (Ephemeroptera), *Chironomus* sp. larvae and *Asellus aquaticus*.

From May to July, there were large differences in the numbers of animals collected. *Caenis robusta* had highest densities in late May, whereas *E. ignita* exhibited greatest densities throughout June, declining towards the end of the month. *B. rhodani* had low densities throughout the sampling period, but displayed a small peak in early June (Figure 2). The variation over this period could be explained by individual species' life cycles (emergence and early instar dispersal).

Over a twenty-four-hour period, peak densities for *C. robusta* and *B. rhodani* occurred at night (Figure 3). *Asellus aquaticus* and Chironomidae (Figure 4) and *E. ignita* (Figure 5) also displayed two peaks in density, at 12.00 and 03.00 for *A. aquaticus* (Figure 4) and at 12.00-15.00 and 06.00 hours for Chironomidae and *E. ignita* (Figures 4 and 5). Overall invertebrate drift density was not correlated with water temperature, but certain species were significantly correlated with water temperature and light intensity with regard to specific net locations within the stream (Table 2). On the left bank, *E. ignita* was inversely correlated with discharge, the Chironomidae and *Hydropsyche siltalai* were inversely correlated with temperature and the Ephemeroptera and *H. siltalai* with light levels. On the right bank, all significant correlations with discharge were positive, apart from *E. ignita*, for which it was negative. For the mid-channel net, *E. ignita*, and *H. angustipennis* were inversely correlated with discharge, whereas all Chironomidae, all Diptera and *H. siltalai* were positively correlated. All Trichoptera and Chironomidae were inversely correlated with water temperature, whereas *E. ignita* was positively so. All correlations with light levels were positive in all species except for *Caenis robusta* in the centre net.

TABLE 1. Percentage contribution of taxa (**PHYLUM**, CLASS, ORDER, SUBORDER, Family, *Genus, species*) in drift samples collected in the River Lee (England) during May, June and July in 1995.

Taxon			%
ARTHROPODA			
INSECTA	EPHEMEROPTERA (48.5 %)	<i>Ephemera ignita</i> <i>Caenis robusta</i> <i>Baetis rhodani</i>	32.0 11.0 5.5
	DIPTERA (29.5 %)	Chironomidae (24 %) larvae pupae Simuliidae Ceratopogonidae Chaoboridae Tipulidae Empipidae	21.5 2.5 4.5 <1.0 <0.5 <0.1 <0.1
	TRICHOPTERA (3.5 %)	<i>Hydropsyche siltalai</i> <i>Hydropsyche angustipennis</i> Hydroptilidae <i>Agapetus fuscipes</i>	2.5 <1.0 <0.1 <0.1
	COLEOPTERA (2.5 %)	Coleoptera sp. <i>Elmis aena</i> <i>Haliplus</i> sp.	1.5 1.0 <0.1
	HEMIPTERA	<i>Sigara</i> sp.	larvae <0.5 adults <0.5
	ODONATA (<0.1 %)		
	ZYGOPTERA	Calopterygidae	<0.1
	ANISOPTERA		<0.1
CRUSTACEA (10.5 %)	ISOPODA (10 %)	<i>Asellus aquaticus</i> <i>Asellus meridianus</i>	10.0 <0.1
	AMPHIPODA	<i>Gammarus pulex</i>	<0.5
	BRANCHIURA	<i>Argulus coregoni</i>	<0.1
CHELICERATA (3 %)	HYDRACARINA		2.5
	ARANEAE	<i>Argyroneta aquatica</i>	<0.5
PLATYHELMINTHES			
	TRICLADIDA		1.5
ANNELIDA			
	OLIGOCHAETA		1.0
MOLLUSCA			
	BIVALVIA		<0.1

TABLE 2. Correlations (Spearman's r corrected for ties) and probabilities (P) between invertebrate drift densities collected in three nets (left bank, centre, right bank) and environmental factors in the River Lee during May to July 1995. Comparisons of all nets combined for all taxa combined and the most abundant taxa only (*Ephemera ignita*, *Caenis robusta*, *Baetis rhodani*, all Chironomidae, Simuliidae). *Hy.* = *Hydropsyche*.

Variable versus Taxa	net: left		centre		right		combined		
	r	P	r	P	r	P	r	P	
Discharge									
<i>Ephemera ignita</i>	-0.363	0.005	-0.378	0.001	-0.258	0.050	-0.370	0.001	
<i>Baetis rhodani</i>			0.291	0.010			0.293	0.010	
All Ephemeroptera			-0.263	0.050					
Chironomidae larvae	0.360	0.005	0.458	0.001	0.352	0.005			
Chironomidae nymphs	0.386	0.001	0.329	0.005					
All Chironomidae	0.444	0.001	0.481	0.001	0.365	0.005	0.539	0.001	
Simuliidae					0.227	0.050			
All Diptera	0.332	0.005	0.483	0.001	0.385	0.001			
<i>Hy. angustipennis</i>			-0.230	0.050					
<i>Hy. siltalai</i>			0.578	0.001	0.373	0.005			
All Trichoptera			0.394	0.001	0.301	0.010			
Coleoptera larvae	0.249	0.050			0.241	0.050			
<i>Elmis aena</i>	0.235	0.050	0.245	0.050	0.303	0.010			
All Coleoptera	0.261	0.050			0.227	0.050			
Hydracarina					0.264	0.030			
Oligochaeta	0.263	0.050			0.255	0.050			
Tricladida	-0.302	0.010							
All invertebrates			0.213	(0.06)	0.270	0.050	0.229	0.050	
Water temperature									
<i>Ephemera ignita</i>	0.235	0.050	0.325	0.005			0.228	0.050	
<i>Baetis rhodani</i>			-0.293	0.050	-0.271	0.020	-0.222	0.050	
All Ephemeroptera			0.378	0.001					
Chironomidae nymphs	-0.342	0.005	-0.237	0.050	-0.237	0.050			
All Chironomidae	-0.235	0.050	-0.227	0.050	-0.254	0.050	-0.307	0.010	
All Diptera			-0.225	0.050					
<i>Hy. siltalai</i>	-0.263	0.050	-0.496	0.001	-0.348	0.005			
All Trichoptera			-0.338	0.003	-0.363	0.005			
<i>Elmis aena</i>					-0.364	0.005			
<i>Gammarus pulex</i>					-0.241	0.050			
Tricladida	0.223	0.050	0.229	0.050					
Light level									
<i>Caenis robusta</i>	-0.449	0.001	-0.212	(0.06)	-0.378	0.001	-0.363	0.002	
<i>Baetis rhodani</i>	-0.429	0.001			-0.275	0.050	-0.247	0.030	
All Ephemeroptera	-0.260	0.050							
Chironomidae larvae	0.259	0.050	0.377	0.001	0.286	0.050			
All Chironomidae	0.231	0.050	0.349	0.005	0.29	0.050	0.380	0.001	
All Diptera			0.338	0.005	0.254	0.050			
<i>Hy. siltalai</i>	-0.358	0.005			-0.244	0.050			
All Trichoptera	-0.296	0.010			-0.258	0.050			
Coleoptera larvae			0.330	0.005					
<i>Elmis aena</i>					-0.300	0.010			
<i>Asellus aquaticus</i>	-0.326	0.005			-0.321	0.010			
All invertebrates	-0.243	0.050			-0.237	0.050			

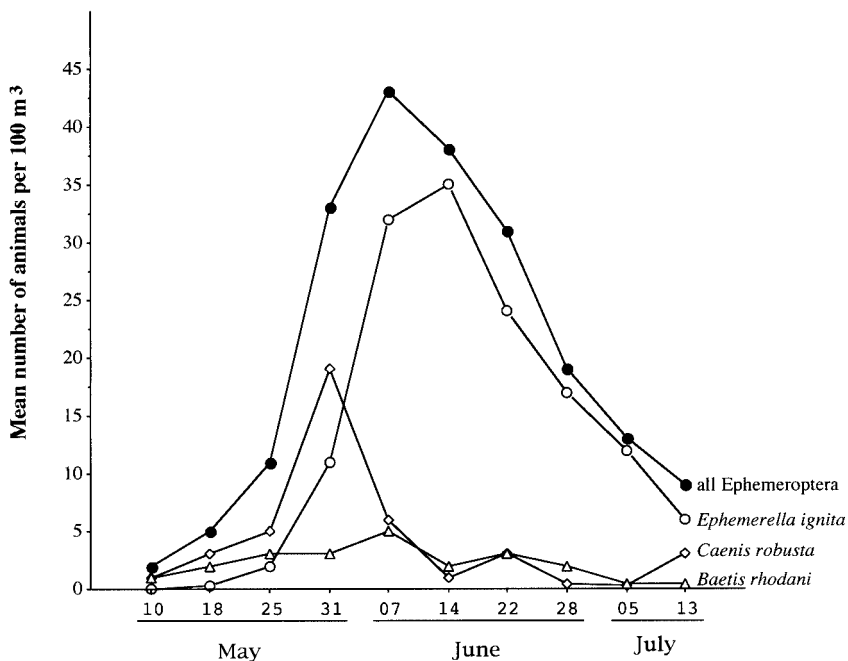


FIGURE 2. Mean density of *Ephemera ignita*, *Caenis robusta* and *Baetis rhodani*, separately and combined (all Ephemeroptera), at each sampling occasion in the River Lee.

With all samples combined, *E. ignita* and Chironomidae densities were inversely and positively correlated with discharge, respectively. *C. robusta* and *B. rhodani* appeared to drift in a manner inversely correlated with light, as their densities decreased as light levels increased. The opposite was true for Chironomidae, which had densities inversely correlated with water temperature.

Discussion

The asymmetrical gradient of drift density across the channel observed in the River Lee has been reported in large rivers (e.g. Obi and Connor 1986, Grzybkowska 1992). The high proportion (43 per cent) of mayfly nymphs, particularly *E. ignita* and *C. robusta*, observed in drift samples from the River Lee (Table 1) may reflect the fact that the early instars of many Ephemeroptera are recorded drifting in large numbers from early spring until well into the autumn, with some species being plentiful right through the year (Harker 1989: 27–34). The presence of *E. ignita* in such high densities is not unusual; Elliott (1968) reported that they had the highest mean activity of the five species he studied.

Manipulative field experiments of the effects of water temperature, discharge and the presence of predatory fish in relation to drift density have revealed that amongst the various factors (different invertebrate groups, different times of the day), light intensity was the most important factor conditioning the distribution of activity (Williams 1990). Mayfly nymphs in particular appear to adhere closely to light intensity (Greenwood and Richardot-Coulet 1996), demonstrating in some cases (e.g. *E. ignita*) strong negative phototaxis from 5 to 500 lux as well as increased movement at night up onto the upper surface of stones (Elliott 1968).

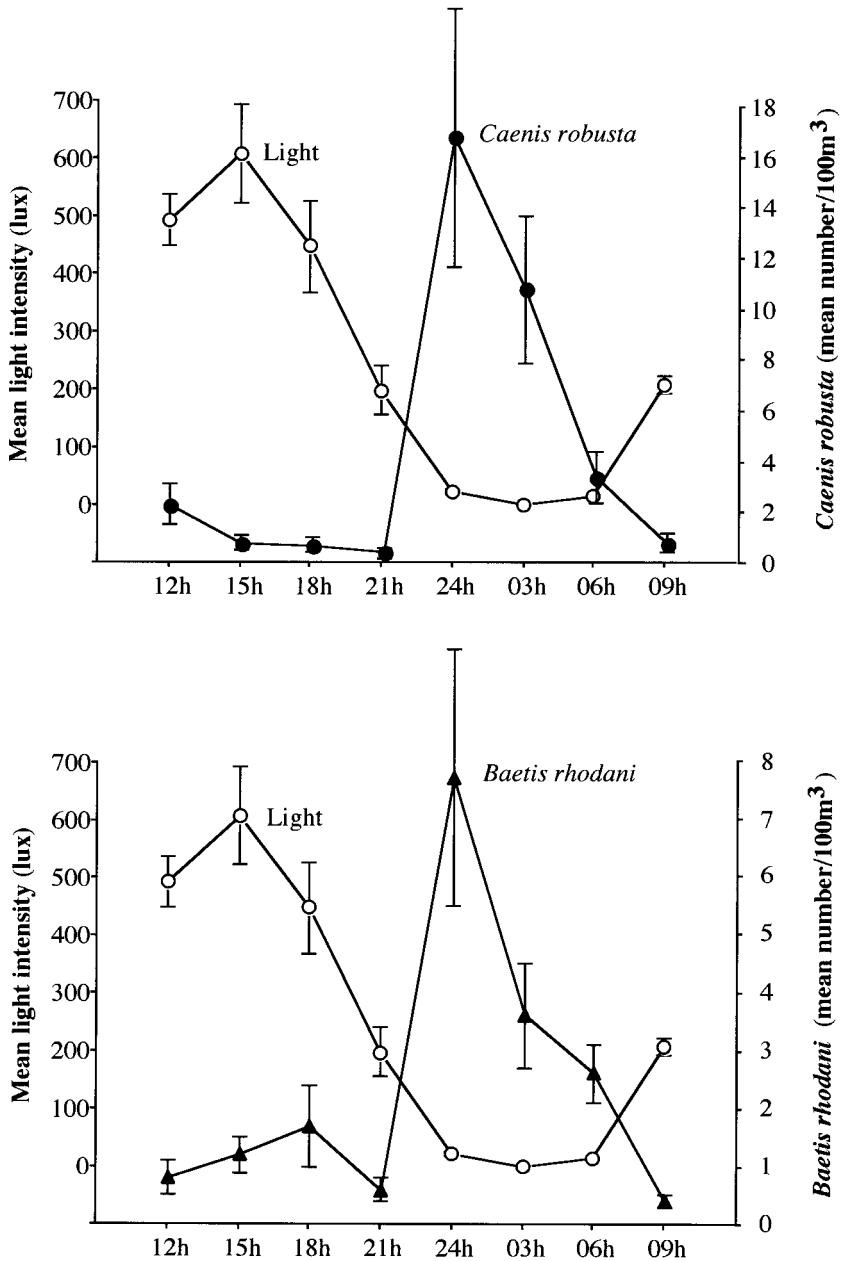


FIGURE 3. Mean light intensity and mean density (note different scales), with standard error, of *Caenis robusta* and *Baetis rhodani* recorded at each sampling occasion over ten 24-hour periods from 10 May to 13 July 1995 in the River Lee.

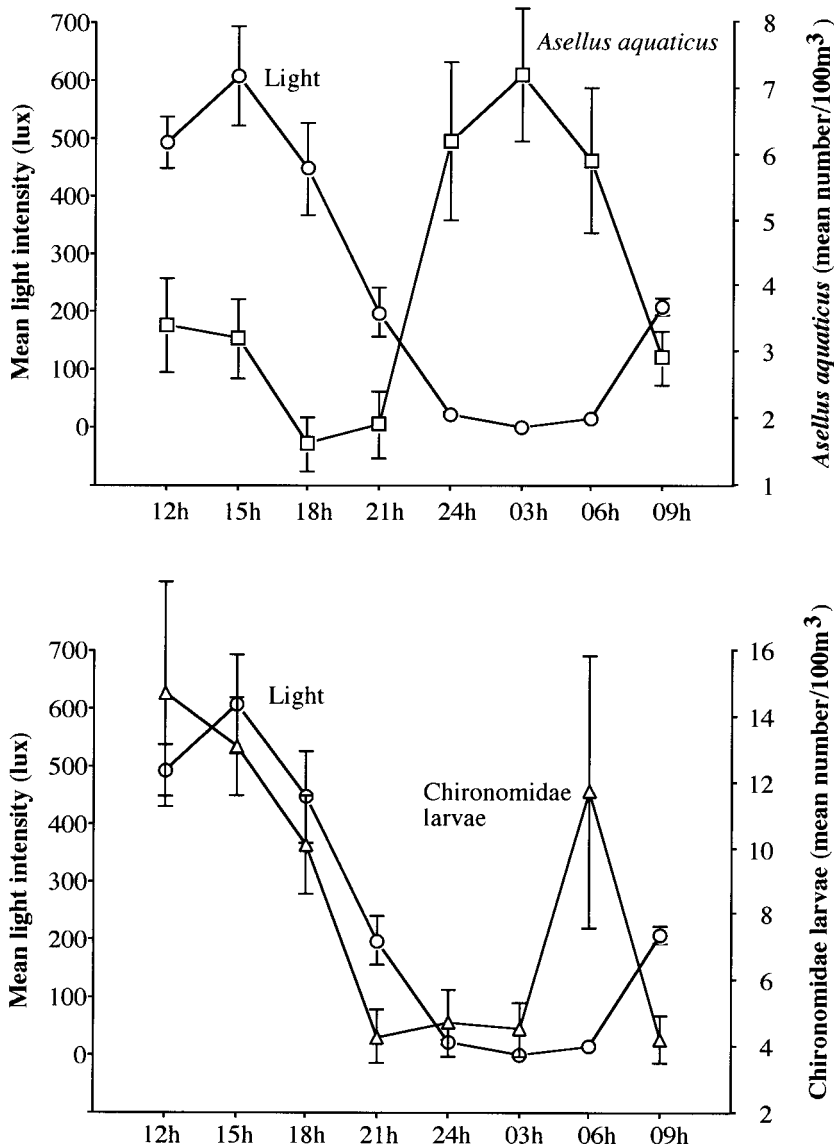


FIGURE 4. Mean light intensity and mean density (note different scales), with standard error, of *Asellus aquaticus* and Chironomidae larvae recorded at each sampling occasion over ten 24-hour periods from 10 May to 13 July 1995 in the River Lee.

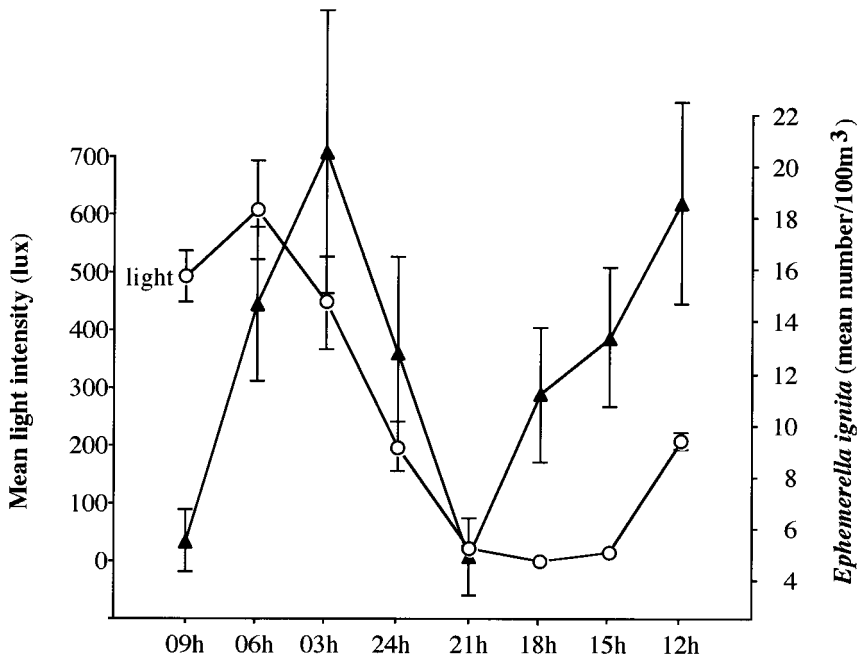


FIGURE 5. Mean light intensity and mean number of *Ephemerella ignita* (with standard error) recorded at each sampling occasion over ten 24-hour periods from 10 May to 13 July 1995 in the River Lee. Densities increase with a decrease in lux.

Traditionally, this increase in the nocturnal use of stone surfaces was believed to lead to an increase in accidental dislodgement and an associated increase in drift density. Whereas several studies have highlighted that light intensity is an important factor, few studies have produced statistically significant evidence to demonstrate that a single factor is responsible for the initiation of mayfly drift. Harker (1953) suggested that mayfly activity cycles were controlled not by one, but a number of factors acting simultaneously and, despite the numerous studies on mayfly activity that followed, this suggestion generally appears to hold true. For example, Allen et al. (1986) acknowledged that light intensity is a contributing factor, but disagreed with the passive entry theory and proposed instead that other factors (such as water velocity) may induce behavioural drift. This concept was strengthened by work carried out by Koetsier and Bryan (1995), which demonstrated that mayfly nymph densities were inversely related to discharge and positively related to water conductivity and water velocity. Note, however, that correlations between drift densities and water velocity are spurious because the drift densities are calculated using water velocity measurements taken at the net's entrance.

With regard to *E. ignita* (Figure 5), the peak densities we observed at 12.00 and 06.00 hours in the River Lee are contrary to the drift patterns recorded by Elliott (1968); the patterns we observed may well reflect fish predation pressures (McIntosh and Peckarsky 1996), and initial results from subsequent studies of diel fish predation activity support this assumption (Copp et al. 2004). The night time drift patterns of *C. robusta* and *B. rhodani* may also be indicative of the presence of fish, coupled with night-time foraging movements.

This explanation does not, however, account for the high densities of Chironomidae drifting during daylight hours. In the Lee, we also observed a positive correlation between drift densities and increases in discharge and an inverse correlation with water temperature. As the Chironomidae were generally small individuals, there may well be additional size/weight associations (as yet unexplored) related to the physical entrainment of the organisms. Because Chironomidae larvae are abundant and taxonomically diverse in most freshwater benthic communities, these dipterans are also the major macroinvertebrate groups found drifting in rivers, especially during summer. But the high density of drifting chironomids is usually dominated by first and second instars, which are the major dispersive agents in all taxa, independent of the life mode of older instars, including pelophilous *Chironomini* (Soponis and Russell 1984, Williams 1989). The behaviour of early instars enables them to seek suitable habitats for further development or/and recolonization of areas of stream bed after a spate (Grzybkowska et al. 1996), drought or heavy pollution (Brittan and Eikeland 1988). It is difficult to add anything to the knowledge of chironomid propensity to drift when these midges are identified to family level, as in our investigations, because drift patterns of chironomid species and genera vary spatially and temporally. As shown by Ferrington (1984) and Grzybkowska (1992), some chironomid taxa exhibited diel drift patterns and they may vary with hydrologic and geomorphic conditions.

An alternative explanation might be prey selection by invertebrate predators. Predator invertebrate species are few and include Zygoptera, Coleoptera and Hemiptera in low numbers, with less than one per cent of the drift consisting of predatory species. Similarly, the densities of benthic predators at the same site (though sampled in the subsequent year), were also low (Copp et al. 2004). Thus, the impact of invertebrate predation at this location is probably negligible compared to that of fish. The classic diel pattern was not exhibited in our study for the most abundant taxonomic groups, but there is some evidence of a bigeminus pattern for *C. robusta* and *B. rhodani* as (Figure 3). As a complement to the ongoing fish-invertebrate interactions studies in nutrient-rich streams, the present study has provided important baseline information. However, future work on invertebrate drift in nutrient-rich streams needs to address the difficulties of sampling invertebrate drift in the face of high levels of suspended matter (Faulkner and Copp 2001), as well as invertebrate size relationship patterns, particularly those of the Chironomidae.

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