

Diel, Seasonal and Spatial Drift Pattern of the Caddisfly (Trichoptera) Larvae in Two Medium-Sized Lowland Streams in Latvia

AGNIJA SKUJA

Institute of Biology, University of Latvia, Miera iela 3, LV-2169, Salaspils, Latvia; e-mail: agnija@lanet.lv

SKUJA A. 2010. DIEL, SEASONAL AND SPATIAL DRIFT PATTERN OF THE CADDISFLY (TRICHOPTERA) LARVAE IN TWO MEDIUM-SIZED LOWLAND STREAMS IN LATVIA. – *Latvijas Entomologs*, 49: 14-27.

Abstract: Diel, seasonal and spatial pattern of the caddisfly (Trichoptera) larvae drift was studied in two second-order lowland streams in Latvia (Tumšupe and Korģe). Samples were taken downstream and upstream of the riffles, with three drift nets. 30 min sampling was done every three hours during a 24-hour period, once in spring, summer and autumn in 2007. Taxa diversity and drift density were higher in the Tumšupe Stream (that had more stable water level) than in the Korģe Stream. The species composition in both streams was relatively similar. However, the differences in taxonomical composition among all seasons were low in the Tumšupe Stream and high in the Korģe Stream. The larvae were mostly day-active. Drift density downstream of the riffle was significantly higher than the upstream area only in the Korģe Stream in May. I expect that caddisfly larvae in the Korģe Stream might also be more impacted by predation of salmonids in the Korģe Stream, as compared to the Tumšupe Stream.

Key words: caddisflies, Trichoptera, larvae, drift, lowland streams, Latvia

Introduction

Drift (the downstream transport of benthic invertebrates in the water column) of the aquatic invertebrates in streams has been intensively studied since 1950s. Most of the studies were focused on mayflies (Waters 1972, Brittain, Eikeland 1988, Allan 1995), while investigations of the caddisflies in Europe have much shorter history (e.g. Otto 1976, Waringer 1989, Fjellheim, Raddum 1998).

Caddisfly larvae form a significant quantitative fraction of the macroinvertebrate drift (Brittain, Eikeland 1988). The order Trichoptera is among the most important and diverse of all aquatic insect taxa (e.g. Holzenthal et al. 2007, Mackay, Wiggins 1979, Balian et al. 2008). The larvae are essential participants of freshwater food webs and their presence and relative abundance are used in the biological assessment and monitoring of water quality (Holzenthal et al. 2007).

Most stream invertebrates are nocturnal and their increased activity at night often leads to an increase in upstream movements, and in downstream dispersal through the

mechanism of invertebrate drift (Elliott 2002a). Many results of studies have confirmed the diel periodicity of the drift. The highest density occurs just after sunset and another one (slightly lower) before sunrise (e.g. Waters 1972, Brittain, Eikeland 1988, Allan 1995). Nevertheless, the diel pattern is not unambiguous if different taxa are compared. The corresponding maxima of Ephemeroptera, Plecoptera, Simuliidae and amphipod *Gammarus* sp. drift generally occur at night (Waters 1972, Brittain, Eikeland 1988, Allan 1995). The most caddisflies show similar behaviour, although some Limnephilidae do drift mostly during the daytime (Brittain, Eikeland 1988). Waters (1972) also suggested that caddisfly larvae were mostly day-active. Many caddisfly species change their major diel drift pattern (Brittain, Eikeland 1988) and endogenous diel rhythm (Allan 1995) during their life cycle. Fjellheim (1980) studied free living *Rhyacophila nubila* larval drift at West Norwegian River and found that the 1st and the 2nd instar larvae possessed neutral phototaxis. Starting from the 2nd instar, the larvae become increasingly night-active and the last-instar larvae were generally night-active. Elliott (2002a) studied day-night changes in the spatial distribution of insects in a stony stream. These changes were an essential part

of the behavioural dynamics of 12 of the 21 species. The diurnal and nocturnal spatial distribution did not change significantly for one sedentary, case-building, Trichoptera species, and one net-spinning Trichoptera species (*Hydropsyche siltalai*). Aggregation reduced significantly at night for four species, all case-building Trichoptera larvae (*Odontocerum albicorne*, *Sericostoma personatum*, *Drusus annulatus* and *Potamophylax cingulatus*). Aggregation increased significantly at night, except at low densities, for the remaining eight macroinvertebrate species, one being a nocturnal predator and the others being herbivorous species; all occurred frequently in night samples of invertebrate drift (Elliott 2002a).

Young animals often predominate in the drift of caddisfly larvae that underlines the role of drift in dispersal (Waters 1972). Drift enables organisms to avoid unfavourable conditions and gives them the potential to colonize new habitats (Brittain, Eikeland 1988). Cereghino et al. (2004) studied mayfly *Rhithrogena semicolorata* (family Heptageniidae) drift under natural and hydropeaking conditions with aim to find out whether the larvae enter the drift in active or in passive way. Kohler (1985) interpreted the mayfly *Baetis* nocturnal activities mainly through the foraging activities. Wilzbach's (1990) observations did not support the hypothesis that *Baetis* drifted at night time, because they were hungry and were searching for food. Drift of aquatic invertebrates also may reflect intraspecific competition for space. Density-dependent drift occurs when animals are abundant enough to outbalance the capacity of their microhabitat. However, physical perturbation and predation may maintain population densities below this level (Bishop, Hynes 1969 after Ciborowski 1983).

A milestone of the drift studies was the "colonization cycle" hypothesis of population regulation, including the downstream drift of aquatic larvae and upstream flight of winged adults (Müller 1974, Waters 1972). Hence, upper reaches of streams remain populated by aquatic insects in spite of the tendency of larvae to drift downstream (Anholt 1995).

Benthic macroinvertebrates also may move upstream themselves (Allan 1995). The persistence of upstream populations despite the continuous drift is called "stream drift paradox" (Anholt 1995). Kopp et al. (2001) developed a simple stochastic model for competition of genotypes with different dispersal strategies in a stream habitat. They showed that exact compensation of larvae drift by upstream biased adult dispersal is an evolutionary stable strategy. They concluded that the upstream biased dispersal was not necessary for persistence at the population level, unless the reproductive rate was very low.

Natural drift is normally related to the abiotic factors – daylight, discharge, velocity, substratum, water temperature, turbidity, and moonlight. Abundance of food, predators, and especially its own benthic density are regarded as the most important biotic factors affecting the drift of a taxon (Statzner et al. 1985).

Walton's (1978) results suggest that substrate-specific associations may begin forming directly from the drift. Drift may occasionally function as a direct, one-way link connecting similar associations. Lowered energy cost of migration is a probable advantage to animals employing drift in this manner (Walton 1978). Shearer et al. (2002) summarized that hydraulic and substrate heterogeneity might influence spatial variability of drift indirectly through the effect of these factors on benthic invertebrate density. Stable substrates act as refugia from floods and may contribute to high local abundances in drift, while unstable areas may have low densities of benthic invertebrates and hence make smaller contribution to the drift (Shearer et al. 2002).

Robinson et al. (2004) found that floods reduced macroinvertebrate densities by 14% to 92%, averaged across habitat types, and the % reduction was related to flood magnitude. Fewer organisms were lost from bedrock habitats (43%) than from the other habitat types, and the most macroinvertebrates typically were lost from pools (>90%).

Holomuzki (1996) found that nocturnal drift of mayfly *Heptagenia hebe*, measured from enclosed substrates, was significantly lower from cobble/boulder substrates (0.1%) than from gravel/pebble and woody debris. Drift was strongly linked to substrate type, not predator type. Cobble/boulder substrates apparently

function as sinks (where immigration > emigration) for dispersing *H. hebe* nymphs in sandy streams with limited suitable habitat (Holomuzki 1996). Whereas Elliott (2002b) found that water depth and the type of substratum at the two investigated sites were two major factors affecting the time spent in the drift. The effect of the macrophytes and greater depth were to reduce the time to 39% of that at the shallower, stony site. Hay et al. (2008) found that macroinvertebrate drift increased in response to low-discharge events and reduced organic matter transport.

Drift density and size structure are important measures of productivity of rivers for salmonids (Hayes et al. 2000). Time spent in the drift may provide a useful measure for comparing the downstream dispersal of invertebrates in different streams, and may be a useful addition to models for the drift feeding of salmonids, because it represents the period over which a drifting invertebrate is available to drift-feeding fish (Elliott 2002b).

Salmonids in particular select and defend territories which are the best suited for the interception of drift; the size and location of the territory is determined by the drift density and patterns of drift in the water currents (Waters 1972).

Despite the long history of the drift studies, the further studies on drift pattern and mechanisms are in progress. In Latvia, drift of aquatic invertebrates was studied only fragmentarily. Preliminary studies on seasonal and diel drift dynamics were still conducted only for mayflies (Skuja et al.

2009). Further drift investigations are essential in the Baltic ecoregion in relation to the stream insect ecology and feeding of the salmonids.

I hypothesized that drift of caddisfly larvae changed among hours, seasons, and stream habitats and a fast-flowing section (riffle) could change the drift pattern. Thus, the aim of the paper was to study diel and seasonal drift pattern downstream and upstream to the riffle section at two medium sized lowland streams in Latvia.

Methods

Study area

Tumšupe and Korge streams are of the second order siliceous lowland streams with fast flow and well-oxygenated brownish water. Akal and different sized lithal habitats (pebbles, cobbles, medium size stones, with watermoss *Fontinalis* sp. and macroscopic algae cover) dominate on the bottom. Upstream to the riffle sections akal, FPOM, CPOM and macrophyte microhabitats were more characteristic.

The Tumšupe Stream is a tributary of the Lielā Jugla Stream in the Daugava River basin. The catchment area (106.4 km²) at the sampling site (24°35'03"E, 57°00'21"N) was covered by mixed forests (50%), cropland (30%), open grass/bushlands (10%) and pastures (10%) (Figure 1).

The Korge Stream is a tributary of the Salaca River. The catchment area (126.63 km²) at the sampling site (24°27'28"E, 57°45'43"N) was covered by mixed forests (60%), open grass/bushlands (10%), cropland (20%) and pastures (10%) (Figure 1).

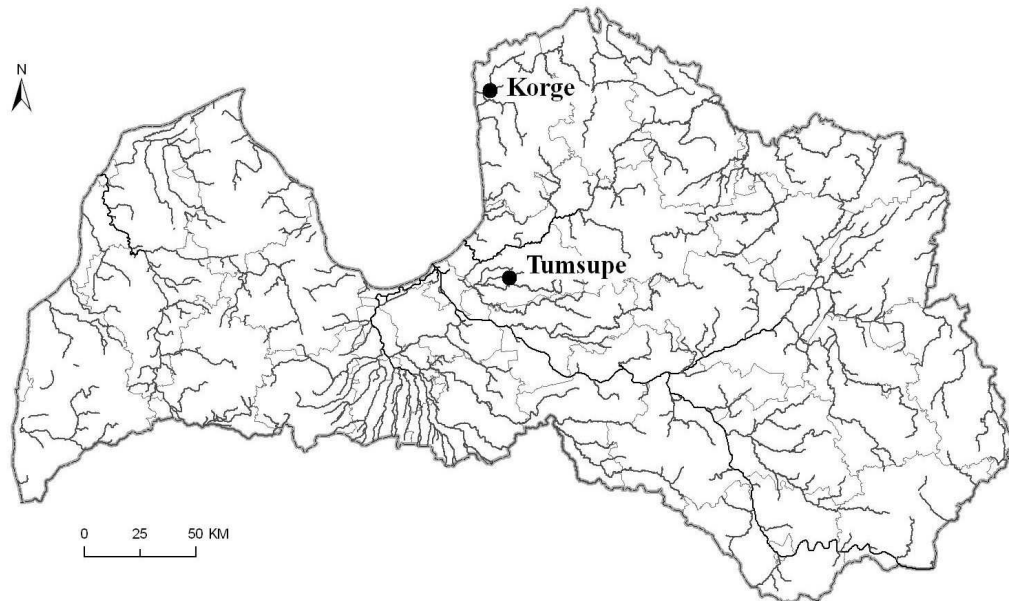


Figure 1. Sampling sites in the Korge Stream (Salaca River basin) and Tumsupe Stream (Daugava River basin) (used data layers developed by Envirotech Ltd.).

Drift sampling

The samples were collected downstream and upstream to the riffle section of the both streams.

Three drift nets (frame size of 0.25 x 0.25 m², mesh size of 0.5 mm) with exposition period of 30 minutes, at two cross sections at each stream were used eight times per 24-hour period (at 00.00, 03.00, 06.00, 09.00, 12.00, 15.00, 18.00 and 21.00 o'clock). As an exception, in the Tumsupe Stream on 30.10.2007, four times per 24-hour period were exposed only.

At the Tumsupe Stream, sampling was performed on 24/25.05, 21/22.08 and 30.10 in 2007. At the Korge Stream it was done on 18/19.05, 7/8.08 and 29/30.09 in 2007.

Current velocity (m/s) was measured, using "Mini" current meter, model "1205" in front of each drift net. The water depth for each drift net was measured. Water temperature (°C) and light intensity (lux) were measured, using luxmeter YK-2000 PLX for each sampling period.

Drift samples were preserved in 4% (final concentration) formaldehyde solution. Caddisfly larvae were identified to the species or higher taxonomic level, using the following keys: Wallace et al. (2003), Edington, Hildrew (2005), Waringer, Graf (1997), Lepneva (1964, 1966).

Drift data analyses

Drift density was calculated according to the following formula (Smock 1996):

$$\text{Drift density} = \frac{(n) \cdot (100)}{(t) \cdot (w) \cdot (h) \cdot (v) \cdot (3600s/h)}$$

where n is number of individuals, t is exposition period (h), w is net width, h is net height, v is mean current velocity, and "3600" is applied to convert hours to seconds.

Drift rate was defined as a number of collected individuals per 0.5 h.

Similarity of the species composition at studied streams was compared, by using Sørensen's similarity coefficient:

$$c_s = \frac{2C}{2C + A + B} \cdot 100,$$

where A, B is number of species in sample A and B, respectively, and C is the number of shared species (Krebs 1999).

A non-parametric Wilcoxon-Mann-Whitney test (synonym Mann-Whitney (Wilcoxon) W test) (Dytham 2003) was used to compare the medians, applying Statgraphics Plus software.

Results

Characteristics of abiotic parameters in the streams

In the Tumšupe Stream, the mean depth did not change significantly during the seasons.

The mean current velocity was significantly higher downstream of the riffle. The mean water temperature and the photoperiod changed seasonally (Table 1).

Table 1. Mean current velocity, mean depth, photoperiod, and mean water temperature upstream and downstream to the riffle section in the Tumšupe Stream in 2007. Explanations: * n=8, ** n=4.

Date	24/25.05*		21/22.08*		30/31.10**	
Stream section	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream
Mean depth (m)	0.21	0.25	0.23	0.23	0.23	0.25
Mean current velocity (m/s) (n=8)	0.3	0.6	0.2	0.7	0.5	1
Photoperiod (h)	17		15		9	
Mean water temperature (°C) (n=8)	15.3		17.5		8	

In the Korģe Stream, the mean depth did not change significantly likewise (except during low water period). The current velocity was insignificantly higher downstream of the riffle

section. In August, the water level reduced significantly while one could not measure the current velocity, and it was estimated to be 0.01 m/s (Table 2).

Table 2. Mean current velocity, mean depth, photoperiod, and mean water temperature upstream and downstream to the riffle section in the Korģe Stream in 2007.

Date	18/19.05		7/8.08		29/30.09	
Stream section	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream
Mean depth (m)	0.25	0.23	0.13	0.24	0.25	0.25
Mean current velocity (m/s) (n=8)	0.4	0.5	0.01	0.01	0.3	0.5
Photoperiod (h)	17		16		12	
Mean water temperature (°C) (n=8)	12.3		19.1		13.0	

Taxonomic composition and seasonal characteristics of caddisfly drift

Caddisfly larvae drift was richer in species in the Tumšupe Stream than in the Korģe Stream (Table 3). The total drift rate was also significantly higher in the Tumšupe Stream in May (565 ind. per 0.5 h) and August (227 ind. per 0.5 h), but it was relatively similar in October in the Tumšupe Stream and in September in the Korģe Stream (409 ind. per 0.5 h and 414 ind. per 0.5 h, respectively). In the Tumšupe Stream, the drift rate was the lowest in August. In the Korģe Stream, it was very low in May and August (39 ind. per 0.5 h and 29 ind. per 0.5 h, respectively).

A diel taxonomic composition of drifting species in the Tumšupe Stream

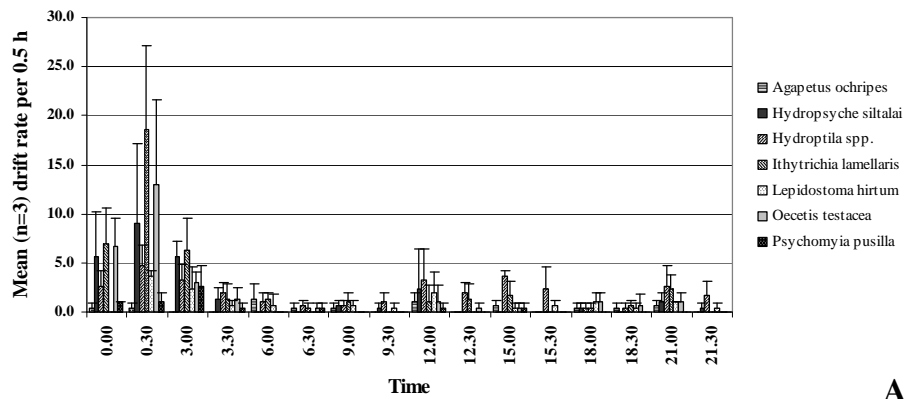
Ithytrichia lamellaris, *Hydroptila* spp., *Hydropsyche siltalai*, *Lepidostoma hirtum*,

Psychomyia pusilla were the most abundant taxa and *Lasiocephala basalis*, *Oecetis testacea*, *Agapetus ochripes* and *Athripsodes* spp. were also found frequently in May (the last instar larvae in relatively high abundances were observed mainly) (Figure 2A). *Hydropsyche* spp. juv., *Agapetus ochripes*, *Lasiocephala basalis*, *Hydropsyche pellucidula* were the most abundant taxa, and *Oecetis* spp. juv. and *Mystacides* spp. were observed the most frequently in the drift samples in August (Figure 2B). Limnephilidae gen. sp., *Hydropsyche* spp. juv., *Agapetus ochripes*, *Ithytrichia lamellaris*, *Lepidostoma hirtum* and *Athripsodes* spp. juv. were abundant in October (Figure 2C). The first instar larvae, especially *Hydropsyche* spp. and Limnephilidae gen. sp., were found in the drift samples in August and October.

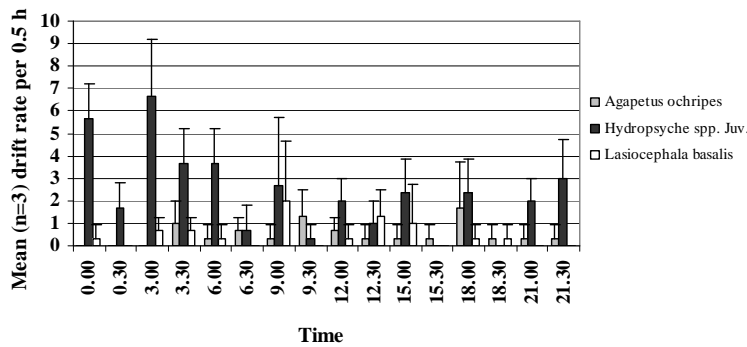
Table 3. A taxonomical composition of drifting caddisflies in Tumšupe and Korge streams in 2007.

Taxa	Stream name and sampling date					
	Tumšupe Stream			Korge Stream		
	24/25.05	21/22.08	30/31.10	18/19.05	7/8.08	29/30.09
BERAEIDAE						
<i>Beraeodes minutus</i> (LINNAEUS, 1761)						x
BRACHYCENTRIDAE						
<i>Brachycentrus subnubilus</i> CURTIS, 1834						x
ECNOMIDAE						
<i>Ecnomus tenellus</i> (RAMBUR, 1842)		x				
GOERIDAE						
Goeridae gen. sp.		x	x			
<i>Goera pilosa</i> (FABRICIUS, 1775)			x		x	x
<i>Silo pallipes</i> (FABRICIUS, 1781)	x	x	x			
GLOSSOSOMATIDAE						
<i>Agapetus ochripes</i> CURTIS, 1834	x	x	x			x
HYDROPSYCHIDAE						
<i>Cheumatopsyche lepida</i> (PICTET, 1834)	x		x			
<i>Hydropsyche siltalai</i> DOEHLER, 1963	x					
<i>Hydropsyche pellucidula</i> (CURTIS, 1834)	x	x	x			x
<i>Hydropsyche</i> spp. juv.	x	x	x		x	x
<i>Stactobiella risi</i> (FELBER, 1908)	x					
HYDROPTILIDAE						
<i>Hydroptila</i> spp.	x	x			x	x
<i>Ithytrichia lamellaris</i> EATON, 1873	x	x	x			x
LEPIDOSTOMATIDAE						
<i>Lasiocephala basalis</i> (KOLENATI, 1848)	x	x	x			
<i>Lepidostoma hirtum</i> (FABRICIUS, 1775)	x	x	x	x	x	x
Lepidostomatidae gen. sp.		x				
LEPTOCERIDAE						
Leptoceridae gen. sp.		x			x	x
<i>Athripsodes albifrons</i> (LINNAEUS, 1758)	x		x			
<i>Athripsodes aterrimus</i> (STEPHENS, 1836)	x					
<i>Athripsodes</i> spp. juv.	x	x	x	x	x	x
<i>Mystacides</i> spp. juv.	x	x	x			x
<i>Mystacides azurea</i> (LINNAEUS, 1761)	x	x	x			x
<i>Ceraclea</i> spp. juv.	x					x
<i>Oecetis</i> spp. juv.	x	x	x	x	x	x
<i>Oecetis testacea</i> (CURTIS, 1834)	x		x	x		
LIMNEPHILIDAE						
<i>Anabolia laevis</i> ZETTERSTEDT, 1840, juv.				x		
<i>Glyptotaelius pellucidus</i> (RETZIUS, 1783)			x			x
<i>Halesus tessellatus</i> (RAMBUR, 1842)	x			x		
Limnephilidae gen. sp. juv.	x	x	x	x		x
<i>Limnephilus</i> spp. juv.			x			x
ODONTOCERIDAE						
<i>Odontocerum albicorne</i> (SCOPOLI, 1763)			x			
POLYCENTROPODIDAE						
<i>Cyrnus trimaculatus</i> (CURTIS, 1834)				x		x
Polycentropodidae gen. sp. juv.		x	x		x	x
<i>Polycentropus flavomaculatus</i> (PICTET, 1834)						x
PSYCHOMYIIDAE						
<i>Lype reducta</i> (HAGEN, 1868)	x	x	x			
<i>Psychomyia pusilla</i> (FABRICIUS, 1781)	x	x	x			
RHYACOPHILIDAE						
<i>Rhyacophila nubila</i> ZETTERSTEDT, 1840			x			

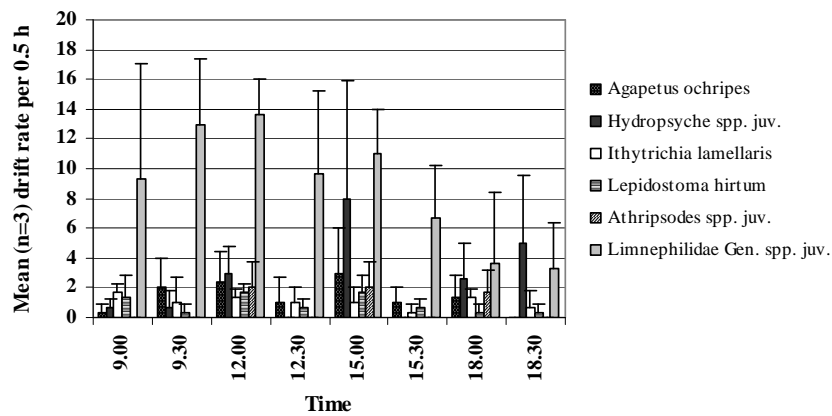
Taxa	Stream name and sampling date					
	Tumšupe Stream			Korģe Stream		
	24/25.05	21/22.08	30/31.10	18/19.05	7/8.08	29/30.09
<i>Rhyacophila</i> spp. juv.	X	X	X			X
SERICOSTOMATIDAE						
<i>Sericostoma personatum</i> (KIRBY, SPENCE, 1826)	X					
Trichoptera spp. indet. pupae/imago		X				X
Total number of taxa	25	21	25	8	8	22



A



B



C

Figure 2. Diel drift pattern of dominating caddisfly taxa in the Tumšupe Stream in 2007. A – 24/25.05, B – 21/22.08, C – 30.10. Error bars show standard deviations.

A diel taxonomic composition of drifting species in the Korĝe Stream

Few individuals were caught in May and August. *Lepidostoma hirtum*, *Oecetis* spp., and *Athripsodes* spp. were the most abundant taxa in May. *Athripsodes* spp. was the only frequently found taxon in August (Table 3). But

Limnephilidae gen. sp. juv., *Lepidostoma hirtum*, *Athripsodes* spp. were the most abundant taxa and *Mystacides* spp., *Oecetis testacea*, and *Polycentropodidae* gen. sp. were found frequently in September (Figure 3, Table 3).

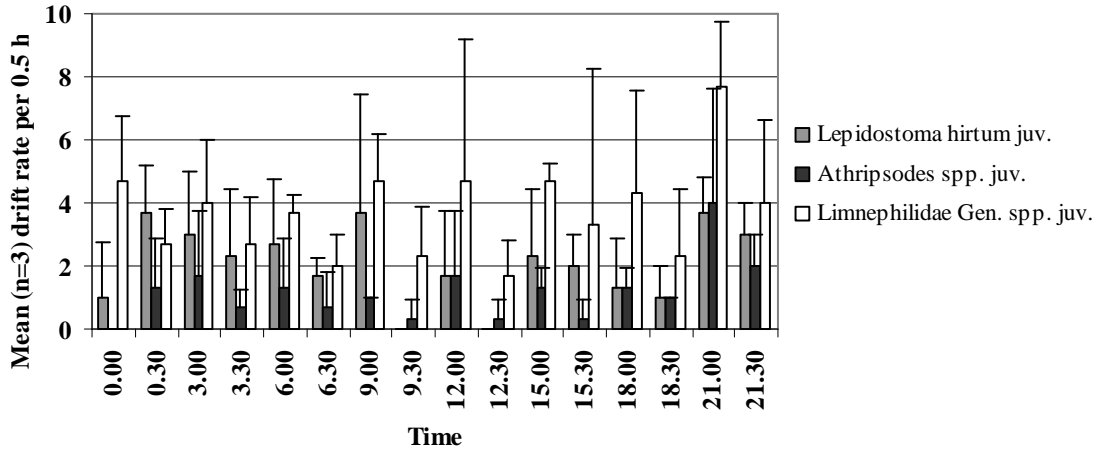


Figure 3. Diel drift pattern of the dominating caddisfly taxa in the Korĝe Stream on 29/30.09 in 2007. Error bars show standard deviations.

The species composition of caddisfly larvae drift was very similar during all seasons in the Tumšupe Stream. In the Korĝe Stream, a half of

the caddisfly taxa at least were different, as compared to the Tumšupe Stream (Table 4).

Table 4. Sørensen’s similarity coefficient (%) for the species composition in drift samples in Tumšupe and Korĝe streams between seasons in 2007.

Tumšupe Stream	21/22.08	30.10	Korĝe Stream	7/8.08	29/30.09
24/25.05	68	69	18/19.05	35	36
21/22.08		67	7/8.08		45

The species composition in drift samples of both streams was relatively similar. The Sørensen’s similarity coefficient of Tumšupe and Korĝe Streams was 69%.

Diel variation of caddisfly drift density

Increase in caddisfly drift density was observed in night time in May in the Tumšupe Stream. In the darkest time, drift density was higher even upstream of the riffle, but in the next period (during dusk) – downstream of the riffle. In general, the drift density during daytime was low in May (Figure 4A).

The drift density was low, and clear diel pattern was not found in August (Figure 4B). The density was higher upstream of riffle section with two small peaks at dusk in four cases. Significant differences were not observed in the drift density in light and dark time of the day in August (Figure 4B).

The drift density was higher in daytime than in night time in October. Then the drift density was higher than in August, and more frequently during the daytime than in May (Figure 4C).

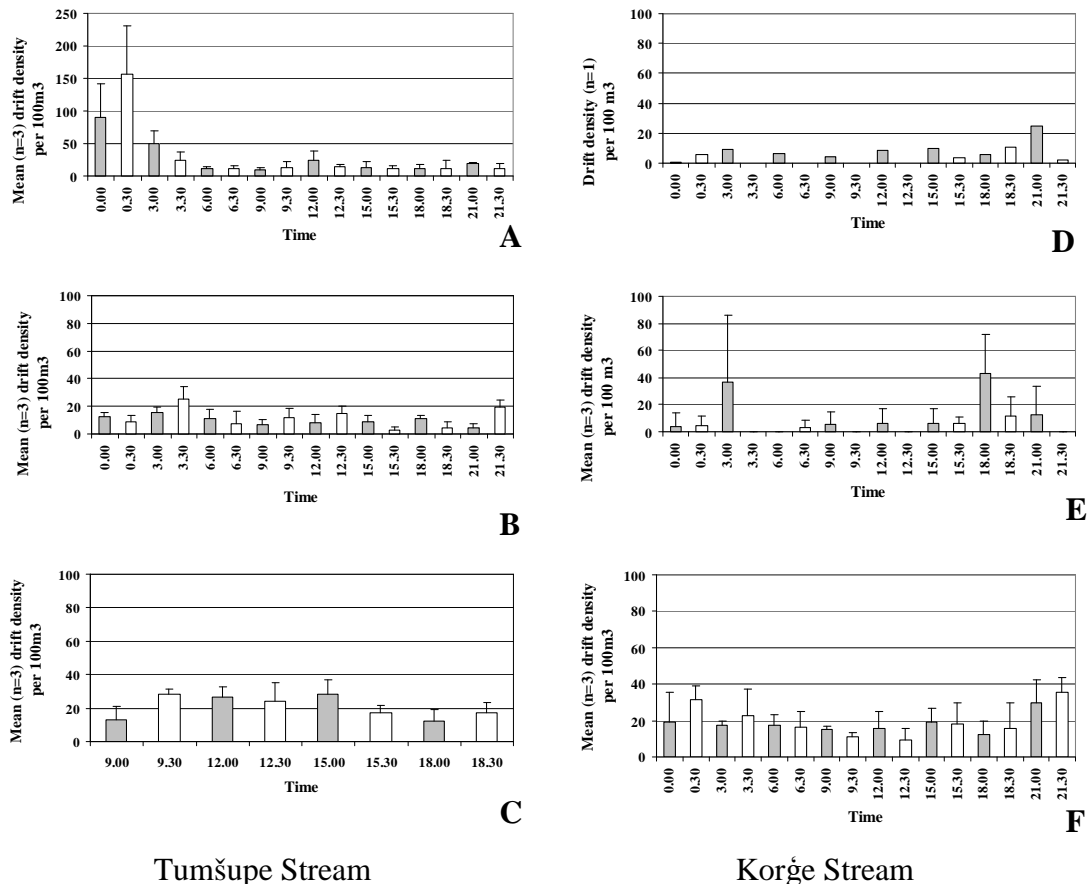


Figure 4. Mean drift density ($n=3$) per 100 m^3 in the Tumšupe Stream in 2007: A is 24-25.05, B is 21-22.08, C is 30-31.10* and in the Korgē Stream in 2007: D is on 18-19.05**, E is on 7-8.08, F is on 29-30.09. Grey columns – downstream of riffle, white columns – upstream of riffle. Error bars show standard deviations. *Sampling was done only four times per 24-hour period, ** $n=1$.

The drift density was comparatively low and higher downstream to the riffle section in May in the Korgē Stream. The maximum was observed during dusk (Figure 4D).

Similarly, the drift density was low and higher downstream to the riffle section in August. Two small maxima were observed during dusk (Figure 4E).

The drift density was significantly higher and more stable in September, comparing to May and August. Slightly higher caddisfly drift density was observed in night time (Figure 4F).

Spatial differences (upstream/downstream riffle)

Statistically significant difference between the medians at 95.0% confidence level for samples downstream and upstream to the riffle section were found in May ($p=0.04 < 0.05$), but not in August ($p=0.05$) and September ($p=0.87 > 0.05$) in the Korgē Stream (Figure 5A, 5B and 5C). Similarly, statistically significant difference between the medians at 95.0% confidence level for samples downstream and upstream to the riffle section in May ($p=0.79$), August ($p=0.87$) and October ($p=0.67$) were not found in the Tumšupe Stream (Figure 5D, 5E and 5F), since the corresponding p -value was greater than or equal to 0.05.

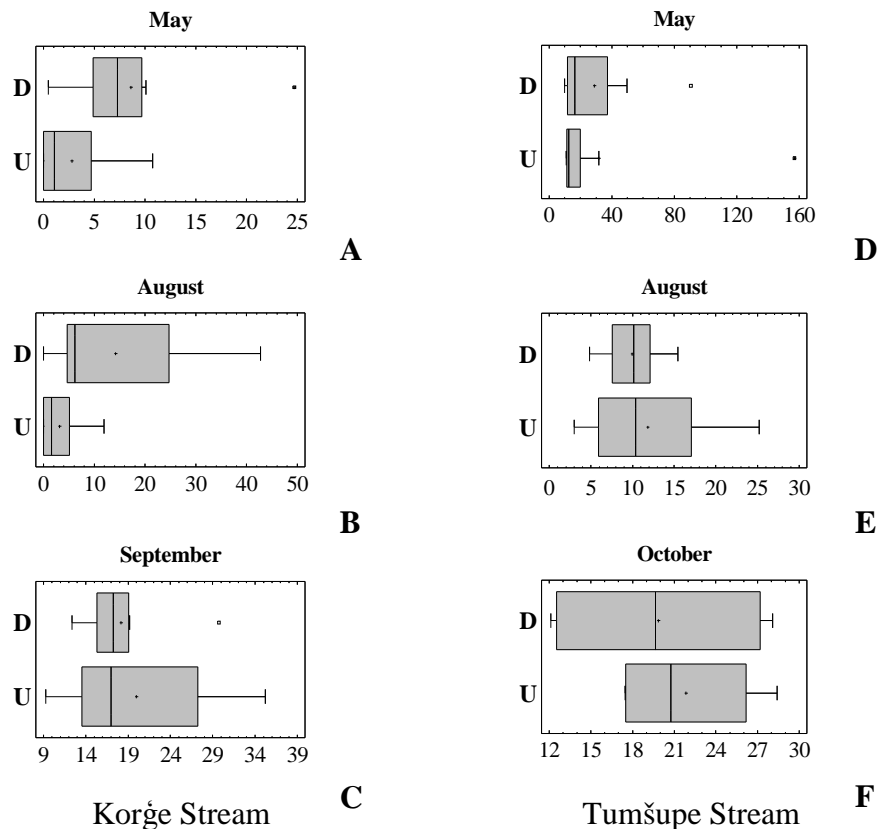


Figure 5. Box- and Whisker plots of the mean ($n=3$) caddisfly Trichoptera larvae drift density downstream (D) ($n=4$) and upstream (U) ($n=4$) to the riffle section in 2007: A is on 18-19.05, B is on 7-8.08, C is on 29-30.09 in the Korge Stream, D is on 24-25.05, E is on 21-22.08, F is on 30.10 in the Tumšupe Stream. Range bares show minimum and maximum, boxes are interquartile ranges (25 percentile to 75 percentile), bars in boxes are medians, and small crosses are the mean and small squares – outliers.

Discussion and conclusions

The drift density and the taxa diversity in drift samples were the highest in May, inconsiderably lower in October, but significantly lower in August, comparing to May in the Tumšupe Stream. Certainly, the spring drift pattern could be mainly linked with the individual life cycle characteristics of caddisfly species, because of predominance of the last instar larvae. In addition, there could be strong impact of hydrological conditions.

In contradiction to the Korge Stream, hydroptilids *Ithytrichia lamellaris* and *Hydroptila* spp., and *Agapetus ochripes* were characteristic for the Tumšupe Stream (especially in May).

Hydroptila spp. feeds, by sucking cells of filamentous green algae. *Ithytrichia lamellaris* larvae feeds on diatoms (Hickin 1968), while

Agapetus is grazer and feeds on periphyton (Allan 1995).

In general, caddisfly drift density and drift rate were low in the Korge Stream. The most abundant drift density occurred in September, while only few individuals were caught in May and August. The juveniles of limnephilids were the dominant, followed by *Lepidostoma hirtum* and *Athripsodes* spp. The drift rate tended to be insignificantly higher downstream of the riffle section and during the daytime, maximal light intensity and temperature.

Limnephilid juveniles dominated also in the Tumšupe Stream in October. Most of them feed on plant litter of terrestrial origin and emergent vegetation. The main growth of those species occurs between autumn and spring when leaf litter is the richest (Wallace et al. 2003). Detritivores that feed on coarse particulate organic matter (i.e. shredders) may account up

to 40% of the total invertebrates in low-order streams and they may be limited by food (Azevedo-Pereira et al. 2006).

Lepidostoma hirtum was the most frequently found species in the drift samples in both streams. This species is widespread throughout Europe. The other species of Lepidostomatidae – *Lasiocephala basalis*, was found only in the Tumšupe Stream. Lepidostomatidae have fairly long summer flight period and final-instar larvae can be found during the year. *Lepidostoma hirtum* was found overwintering at the 2nd to the 5th instar, and *Lasiocephala basalis* at the 4th and the 5th instar (Wallace et al. 2003). *L. basalis* possesses a univoltine life cycle. Adults emerge from June to August. Larvae are facultative xylophages (feed on wood), but also can use leaf litter (Hofmann 2000). Unlike *Lepidostoma hirtum*, whose last-instars cases consist of leaf fragments, *Lasiocephala basalis* constructs mineral cases in all larval instars. Its larvae exhibit striking aggregative behaviour prior to pupation, forming pupal aggregations of up to 500 individuals. The larvae are highly mobile and migrate to the root masses along the stream edge during periods of higher discharge. They prefer current velocities less than 15 cm/s (Hofmann 2000).

Hydropsychidae was the dominant taxon in the Tumšupe Stream (particularly *Hydropsyche siltalai* in May and *Hydropsyche* spp. juv. and *H. pellucidula* in August) comparing to the Korgė Stream. Holomuzki and Van Loan (2002) have summarized factors, which affect caseless, retreat builder hydropsychid drift. Abiotic factors include substrate availability and texture and flow disturbance, whereas biotic factors include predation risk, food availability, intraspecific aggressive encounters and life stage (developmental) changes (Holomuzki, Van Loan 2002). The behaviour of the net-spinning caddisflies could be also influenced by a limited number of suitable sites to construct their nets (Elliott 2002a) or low food abundances (Hay et al. 2008). Hypothetically, the salmonid predation pressure could be higher in the Korgė Stream, comparing to the Tumšupe Stream because Korgė is inhabited both by brown trout and Baltic salmon. The Korgė Stream is located

closer to the Baltic Sea, and there is minimal anthropogenic hydromorphological degradation of the River Salaca and no constraints for the migration of Baltic salmon.

Gallery-building larvae of *Psychomyia pusilla* (Edington and Hildrew 2005) were found only in the Tumšupe Stream.

Athripsodes spp. and *Oecetis testacea* to a lesser extent were frequently found in drift samples. Larvae of most Leptoceridae genera seem to be omnivorous feeders, but specialization as a predator is evident in the mandibles of *Oecetis* (Wiggins 1977).

The species composition of caddisfly larvae drift was very similar during all seasons in the Tumšupe Stream and less similar in the Korgė Stream. The species composition in both streams was relatively similar. The taxonomic diversity in macroinvertebrate drift at terminal ends of 10 riffles was similar across all riffles, although drift densities of the dominant taxonomic groups were spatially heterogeneous and significantly different (Hansen and Closs 2007). Moreover, there were no significant differences in the mean number of taxa drifting out of each riffle by month. Mayflies and terrestrial invertebrates entered the drift in significantly higher numbers during the summer compared to the winter, whereas caddisflies did not differ significantly.

Diel periodicity with nocturnal increase in drift density was found in the Tumšupe Stream only in May. A slight increase in drift density during dark time of the day or dusk was characteristic in May and August in the Korgė Stream. The obtained results approved that caddisfly larvae were mostly day-active (see also Waters 1972).

The caddisfly larvae drift rate could be also related to physical disturbance of substrate. The majority of caddisfly larvae, as compared to mayfly larvae, are weak swimmers. They may behave as passive particles and remain suspended until water velocity subsides (Lancaster et al. 1996).

Statistically significant differences upstream and downstream to the riffle section were found only for the Tumšupe Stream in May. There was no clear increase in drift density downstream to the riffle section for the Tumšupe Stream. Insignificant increase in drift

density was characteristic for the Korģe Stream in May and August. Densities of *Lepidostoma hirtum* were similar in riffles and pools in an Iberian stream, but production was higher in riffles than in pools Azevedo-Pereira et al. (2006). It could be related to additional food resources in riffles or to higher accumulations of leaf detritus in riffles than in pools. The total invertebrate and aquatic drift density (including caddisflies) was proportional to the riffle area and riffle length (Hansen and Closs 2007). The distance that invertebrates travelled appeared to be directly related to the length of riffles (1.0-12 m), because more larvae were collected at downstream ends of longer riffles if compared to shorter ones.

The main outcome of the current study was the general diel and seasonal pattern of the caddisfly drift, estimated upstream and downstream to the riffle in medium-sized lowland streams on hard bottom in Latvia. The future investigations are planned to describe drift pattern and ecological studies of dominant caddisfly taxa - *Lepidostoma hirtum* and *Athripsodes* spp. more thoroughly. These two species are significant decomposers of the leaf litter. To approve the hypothesis about the higher impact of salmonid predation on caddisflies in the Korģe Stream, now brown trout parr feeding selectivity study is carried out, using diel drift data and fish gut analyses, sampled in August of 2008.

Acknowledgements

I cordially thank Voldemārs Spuņģis (Faculty of Biology, University of Latvia, Rīga), the supervisor of my doctoral theses, for the advice and constructive comments during development of the manuscript and the help in fieldworks. I am grateful to Dāvis Ozoliņš for the help in fieldworks and sample processing and to Vjačeslavs Kuļikovs, Linda Eglīte, Laura Grīnberga, Oskars Purmalis, Ivars Druvietis (Institute of Biology, University of Latvia, Salaspils), Gundars Skuja, Dagnija Skuja and Augusts Skuja (family members) for the invaluable help in the fieldworks. I am particularly grateful to Dr Henn Timm (Centre for Limnology of the Institute of Agricultural and Environmental Sciences, Estonian

University of Life Sciences) for the constructive review and linguistic corrections on the earlier version of the manuscript. I thank MSc Lauma Gustiņa (Faculty of Geography and Earth Sciences, University of Latvia, Rīga) and Laura Grīnberga for the help in the preparation of the map. The material was collected in the framework of the National Research Program "Climate Change Impact on Water Environment in Latvia" (KALME), WP3 "Climate Change Impact on Freshwater Ecosystems and Biological Diversity".

The investigation was supported by European Social Fund (ESF), agreement No. 2009/0138/1DP/1.1.2.1.2/09/IPIA/VIAA/004.

References

- Allan J.D. 1995. *Stream ecology. Structure and function of running waters*. Chapman & Hall, London: 1–388.
- Anholt B.R. 1995. Density dependence resolves the stream drift paradox. - *Ecology* **76**, 2235–2239.
- Azevedo-Pereira H.V.S., Graça M.A.S, González J.M. 2006. Life history of *Lepidostoma hirtum* in an Iberian stream and its role in organic matter processing. - *Hydrobiologia* **559**:183–192.
- Balian E., Segers H., Lévêque C., Martens K. 2008. Freshwater animal diversity assessment. - *Hydrobiologia* **595**: 1–637.
- Brittain J.E, Eikeland T.J. 1988. Invertebrate drift – a review. - *Hydrobiologia* **166**: 77–93.
- Cereghino R., Legalle M., Lavandier P. 2004. Drift and benthic population structure of the mayfly *Rhithrogena semicolorata* (Heptageniidae) under natural and hydropeaking conditions. - *Hydrobiologia* **519**: 127–133.
- Ciborowski J.J.H. 1983. Influence of current velocity, density, and detritus on drift of two mayfly species (Ephemeroptera). - *Canadian Journal of Zoology* **61**: 119–125.
- Dytham C. 2003. *Choosing and Using Statistics. A Biologist's Guide*, 2nd edition. Blackwell Publishing, Oxford: 1–248.
- Edington, J.M., Hildrew, A.G. 2005. *A Revised Key to the Caseless Caddis Larvae of the*

- British Isles, with notes on their ecology.* FBA, Scientific Publication **53**: 1–134.
- Elliott J.M. 2002a. A quantitative study of day-night changes in the spatial distribution of insects in a stony stream. - *Journal of Animal Ecology* **71**: 112–122.
- Elliott J.M. 2002b. Time spent in the drift by downstream-dispersing invertebrates in a Lake District stream. - *Freshwater Biology* **47**: 97–106.
- Fjellheim A., Raddum G.G. 1998. Life cycle and drift of *Glossosoma intermedia* (Trichoptera: Glossosomatidae) in western Norway. - *Internationale Vereinigung für Theoretische und Angewandte Limnologie* **26**: 2048–2052.
- Fjellheim A. 1980. Differences in drifting of larval stages of *Rhyacophila nubila* (Trichoptera). - *Holarctic Ecology* **3**: 90–103.
- Hansen E.A., Closs G.P. 2007. Temporal consistency in the long-term spatial distribution of macroinvertebrate drift along a stream reach. - *Hydrobiologia* **575**: 361–371.
- Hay C.H., Franti T.G., Marx D.B., Peters E.J., Hesse L.W. 2008. Macroinvertebrate drift density in relation to abiotic factors in the Missouri River. - *Hydrobiologia* **598**: 175–189.
- Hayes J.W., Stark J.D., Shearer K.A. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. - *Transactions of the American Fisheries Society* **129**: 315–332.
- Hickin N.E. 1968. Caddis larvae. Larvae of British Trichoptera. Associated University Press, Inc, Cranbury, New Jersey: 1–480.
- Hoffmann A. 2000. The Association of the Stream Caddisfly *Lasiocephala basalis* (KOL.) (Trichoptera: Lepidostomatidae) with Wood. - *International Review of Hydrobiology* **85**, No. 1: 79–93
- Holomuzki J.R., Van Loan A.S. 2002. Effects of structural habitat on drift distance and benthic settlement of the caddisfly, *Ceratopsyche sparna*. - *Hydrobiologia* **477**: 139–147.
- Holomuzki J.R. 1996. Effects of substrate and predator type on microdistributions and drift of a lotic mayfly. - *Journal of the North American Benthological Society* **15**, No. 4, 520–528.
- Holzenthal R.W., Blahnik R.J., Prather A.L., Kjer K.M. 2007. Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. - *Zootaxa* **1668**: 639–698.
- Kohler S.L. 1985. Identification of Stream Drift Mechanisms: An Experimental and Observational Approach. - *Ecology* **66**, No. 6: 1749–1761.
- Kopp M., Jeschke J.M., Gabriel W. 2001. Exact compensation of stream drift as an evolutionarily stable strategy. - *Oikos* **92**: 522–530.
- Krebs C.J. 1999. *Ecological methodology*. 2nd edition. Addison Wesley Longman, New York: 1–620.
- Lancaster J., Hildrew A.G., Gjerlov C. 1996. Invertebrate drift and longitudinal transport processes in streams. - *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 572–582.
- Lepneva S.G. 1964. *Trichoptera. Larvae and Pupae of the Annulipalpia*. Fauna of the USSR **2**, No. 1. Nauka, Leninograd: 1–562 (in Russian).
- Lepneva S.G. 1966. *Trichoptera. Larvae and Pupae of the Integripalpia*. Fauna of the USSR **2**, No. 2. Nauka, Leninograd: 1–562 (in Russian).
- Mackay R.J., Wiggins G.B. 1979. Ecological diversity in Trichoptera. - *Annual Review of Entomology* **24**: 185–208.
- Müller K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. - *Annual Review of Ecology and Systematics* **5**, 309–323.
- Otto C. 1976. Factors affecting the drift of *Potamophylax cingulatus* (Trichoptera) larvae. - *Oikos* **27**: 93–100.
- Robinson C.T., Aebischer S., Uehlinger U. 2004. Immediate and habitat-specific responses of macroinvertebrates to sequential, experimental floods. - *Journal of the North American Benthological Society* **23**, No. 4: 853–867.
- Shearer K.A., Hayes J.W., Stark J.D. 2002. Temporal and spatial quantification of aquatic invertebrate drift in the Maruia River, South Island, New Zealand. - *New*

- Zealand Journal of Marine and Freshwater Research* **36**: 529–536.
- Skuja A., Ozoliņš D., Poppels A. 2009. Seasonal and diel pattern of mayfly (Ephemeroptera) drift in Korge stream in Latvia. - *Aquatic Insects: International Journal of Freshwater Entomology* **31**, No. 1, Supplementum 1: 293–299.
- Smock, L.A. 1996. Macroinvertebrate movements: drift, colonization, and emergence. In: Hauer F.R., Lamberti G.A. (eds). *Methods in Stream Ecology*. Academic Press, San Diego: 371–406.
- Statzner B., Elouard J.M., Dejoux C. 1985. Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). II. *Cheumatopsyche falcifera* (Trichoptera: Hydropsychidae). - *Journal of Animal Ecology* **55**: 93–110.
- Wallace I.D., Wallace B., Philipson G.N. 2003. *Keys to the Case-Bearing Caddis Larvae of Britain and Ireland*. Sutcliffe D.W. (ed.). Freshwater Biological Association, Scientific publication **61**, Liverpool: 1–259.
- Walton E.O. Jr. 1978. Substrate attachment by drifting aquatic insect larvae. - *Ecology* **59**, No. 5: 1023–1030.
- Waringer J., Graf W. 1997. *Atlas der österreichischen Köcherfliegenlarven: unter Einschluss der angrenzenden Gebiete*. Facultas-Universitätsverlag, Wien: 1–286.
- Waringer J.A. 1989. Resistance of a cased caddis larva to accidental entry into the drift: the contribution of active and passive elements. - *Freshwater Biology* **21**: 411–420.
- Waters T.F. 1972. The drift of stream insects. - *Annual Review of Entomology* **17**: 253–272.
- Wiggins G.B. 1977. *Larvae of the North American Caddisfly Genera (Trichoptera)*. University of Toronto Press, Toronto and Buffalo: 1–401.
- Wilzbach M.A. 1990. Nonconcordance of Drift and Benthic Activity in Baetis. *Limnology and Oceanography* **35**, No. 4: 945–952.

Received: May 20, 2010.