Invertebrate drift in a glacial river and its non-glacial tributary

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SUMMARY

1. Invertebrate drift was studied in a glacially fed river and a non-glacial tributary in western Norway. Samples were taken during two consecutive 24-h periods in May, July and October 1997. The 3 months are characterized by snowmelt, ice melt and rainfall runoff, respectively. The main glacial river has colder, more turbid water, especially during the period of maximum ice melt during summer.

2. Chironomidae, especially the genus *Diamesa*, dominated the drift in the main river in May and October, constituting 97 and 99% of total numbers, respectively. Simuliidae, Plecoptera, Ephemeroptera and Trichoptera were the other main components.

3. A comparison of drift and benthos data revealed that the tributary was of little significance for colonization of the main glacial river. Only some additional species in very low numbers were recorded downstream of the confluence.

4. During July significant differences in diel drift pattern of Chironomidae and Simuliidae existed between the glacial and non-glacial reaches. There was a mid-day peak independent of discharge in the glacial river, but this peak was not noted in the tributary. Species of the genus *Diamesa* appear to be adapted for daytime drift, possibly evolved through the absence of predators and competitors that are typical of rhithral systems where nocturnal drift is more usual.

Keywords: Chironomidae, colonization, *Diamesa*, diel rhythms, glacial river, invertebrate drift

Introduction

Invertebrate drift is a common phenomenon in running waters and has been widely studied (see Waters, 1972; Müller, 1974; Statzner *et al.*, 1984; Brittain & Eikeland, 1988; Faulkner & Copp, 2001), although until recently no studies of drift ecology in glacier-fed rivers have been undertaken (Ilg *et al.*, 2001). Drift is important in terms of the redistribution and colonization of benthic insects (Waters, 1972; Williams & Feltmate, 1992) and Townsend & Hildrew (1976) showed that up to 82% of the invertebrates colonizing experimentally denuded areas of a stream bed arrived via the drift.

Streams originating from the meltwater of glaciers are characterised by maximum temperatures below 10 °C, a main seasonal peak in discharge during summer, diel fluctuations in flow which usually peak in late afternoon and high summer turbidity (Milner & Petts, 1994). Fishes are typically absent. Food resources are sparse, but include benthic algae and below the tree line allochthonous organic matter (Ward, 1994; Zah & Uehlinger, 2001). This environment contrasts with snowmelt/rainfall streams, particularly in summer (see Ward, 1994). Consequently, different drift patterns may exist between glacial and non-glacial rivers, on account of major differences in discharge, temperature and turbidity characteristics.

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Many studies have shown that drift is characterized by a distinct diel periodicity, with nocturnal drift being greater than daytime drift (Waters, 1962, 1968; Müller, 1974). However, the diel pattern can become more complicated if the drift is divided into different taxa and life cycle stages. Ephemeroptera, Plecoptera, Simuliidae and most Trichoptera usually have their drift maximum during the night (Brittain & Eikeland, 1988). Chironomidae, however, have been reported to show either little diel variation in drift densities (Anderson & Lehmkuhl, 1968; Waters, 1972; Armitage, 1977), or a drift maximum when light intensity peaks (Clifford, 1972a; Ali & Mulla, 1979; Allan, 1987) or a maximum at night (Ali & Mulla, 1979; Stoneburner & Smock, 1979).

Discharge is one of the main factors affecting the magnitude of invertebrate drift (Brittain & Eikeland, 1988). Waters (1972) separated drift into passive and active components. Passive (catastrophic) drift results from sudden increases in current velocity or stream discharge. Active entry into the current (behavioural drift) was viewed as a mechanism to avoid predators, competitors or overcrowded conditions (Waters, 1972), or presumably moving to a better habitat or food source. The characteristic conditions of glacier-fed rivers, low temperatures, high diel flow fluctuations and absence of predators, may influence drift strategies.

In the conceptual model proposed by Milner & Petts (1994) for predicting the longitudinal distribution of macroinvertebrate benthic assemblages in streams downstream of glacial margins, non-glacial tributary streams were proposed to play an important modifying role. Where a clear-water non-glacial tributary joins a glacier-fed river close to its source, the tributary temperatures may be higher than the main river and the fauna more abundant and diverse. Below tributary confluences maximum temperature of the main channel may increase, allowing species from the non-glacial tributary to colonize the colder glacier-fed river.

The main objectives of our study were to evaluate the role of drift from non-glacial tributaries in colonizing downstream reaches of glacier-fed streams and to identify possible differences in macroinvertebrate drift patterns between glacial and non-glacial streams. To accomplish these objectives macroinvertebrate drift was studied in a glacier-fed river system in the western part of Norway. This was part of a wider study of glacier-fed rivers across Europe (Brittain & Milner, 2001).

Methods

The study area comprised of a glacial-melt dominated river and a small non-glacial tributary, Vålefossen. They are situated in the valleys, Briksdal and Olde-dalen (61°41′N, 6°51′E) in Sogn og Fjordane County, western Norway (Fig. 1). River Dalelva originates from the glacier, Briksdalsbreen (350 m a.s.l.), a western outlet from an extensive ice cap, the Joste-dalsbreen (area 487 km^2, Østrem, Dale & Tandberg, 1988). After about 8 km downstream the river runs into a lake, Oldenvatnet (40 m a.s.l.), and
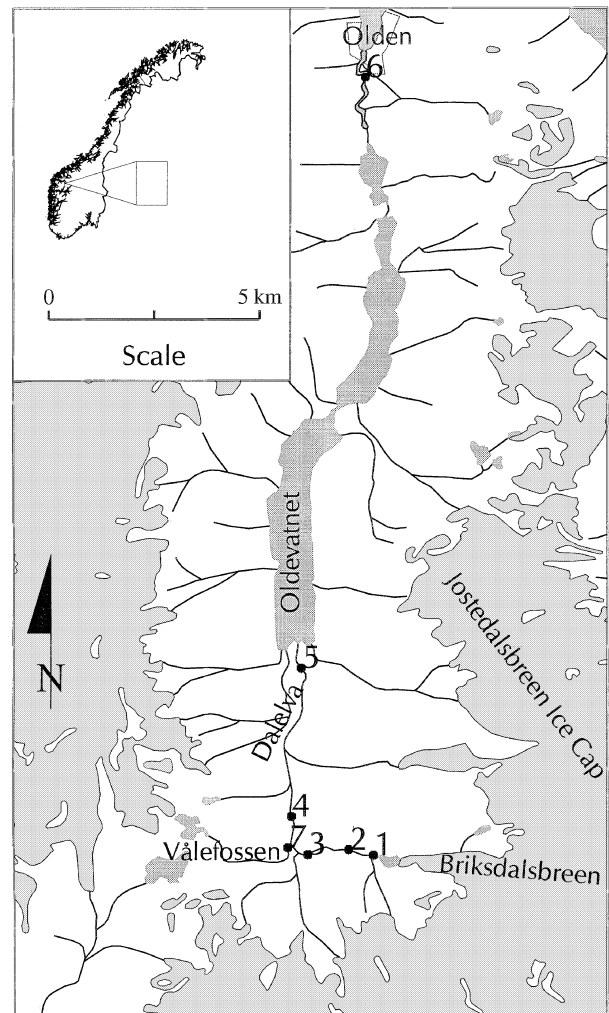

Fig. 1 Location of sampling Stations 1–7 in the glacial river, Dalelva, Briksdal, and its tributary, Vålefossen. Glacial areas are shaded.

subsequently into the fjord at the village of Olden after *c.* 19 km. Further details of the river are provided in Brittain *et al.* (2001).

The sampling stations (1–7) for benthos and drift were situated from 100 m below the glacier snout of Briksdalsbreen (340 m a.s.l.) to about 500 m from Oldenvatnet, with altitudinal intervals of about 50 m. Drift density, composition and periodicity was investigated at three of these locations; Station 3b in the main glacial stream, Daleelva, 3 km downstream of the glacier and 10 m before its confluence with the non-glacial tributary, Vålefossen (180 m a.s.l.); Station 4 in Dalelva 1 km after the confluence with Vålefossen (70 m a.s.l.); and Station 7 in the non-glacial tributary Vålefossen, 10 m before its confluence with Dalelva (180 m a.s.l.). The glacier, Briksdalsbreen, is advancing and all stations were bordered by deciduous woodland (mainly birch and alder) and/or farm pasture.

Discharge varied considerably in the glacial river throughout the ice-free period. Low flows were recorded during the spring and autumn (Brittain *et al.* 2001). For example the mean discharge recorded in October was 2.9 m^3 s^{-1}. whereas in July the mean was 20.4 m^3 s^{-1}, although with large diel flow fluctuations. Near the glacial snout, water temperatures were around 0.1 °C. There were small differences in water temperature between night and day, and during July and October there was no significant diel temperature variation. Temperatures in the non-glacial tributary were 5–10 °C higher than in the glacial river, especially during July.

Sampling was carried out during three periods in the ice-free season of 1997; (1) before the onset of glacial ice melt (27–30 May), (2) during peak ice melt in mid-summer (26–30 July) and (3) at low flows in the autumn prior to freeze-up (13–17 October). Invertebrate drift was sampled during daylight at Stations 1, 2, 3b, 4 and 7 (Fig. 1). Diel periodicity in drift was investigated at three stations, 3b, 4, and 7. Sampling was undertaken for a 1-h period at six hourly intervals over two 24-h periods: 18:00, 00:00, 06:00 and 12:00 hours, with one overlapping period. Each sampling period started at 18:00 (GMT + 2 h).

The drift samplers used were cylindrical plastic tubes (150 mm long with inner diameter 98 mm) fitted with a 1-m long bag with a mesh-size of 250 μm. At each station three drift samplers were placed on iron bars about 5 cm under the water surface. Water temperature and water velocity were both measured with a Höntzsch μP Flowtherm (Höntzsch GmGH, Walblingen, Germany) fitted with a 18-mm diameter propeller in front of the drift samplers at the beginning and end of each sampling period. Drift samplers were emptied after 1 h and the organisms preserved in 70% ethanol for later identification and counting. Longer sampling period than 1 h would also have resulted in clogging of the drift samplers, especially during summer with high sediment loads.

On each sampling occasion, five benthic samples were also taken at all stations during daytime using a standardized kicking technique (see Brittain *et al.*, 2001). Drift and benthic samples from stations before and after the confluence were used to evaluate the importance of potential colonization from the tributary.

Macroinvertebrates were sorted into the following groups: Chironomidae, Simuliidae, Plecoptera, Ephemeroptera, Trichoptera and 'other taxa'. The latter group included Tipulidae, Oligochaeta, Collembola and Staphylinidae. Plecoptera, Ephemeroptera and Trichoptera were identified to species, and *Diamesa* were separated from other chironomids.

Occasionally drift samples were lost because of high discharge and drifting ice. In such cases, drift was expressed as the mean of the drift samples remaining. However, all morning samples were lost at Station 4 during the second 24-h period in July.

Drift density was expressed as numbers per 100 m^3 water filtered using the equation:

$$N_t = \frac{n \cdot 60}{\left(\frac{v_1 + v_2}{2}\right)At} \cdot 100$$

where N_t = number of invertebrates filtered per 100 m^3 water, n = total number of invertebrates filtered, v_1 = water velocity (m s^{-1}) at the beginning of sampling, v_2 = water velocity (m s^{-1}) at the end of sampling, A = cross sectional area of the drift sampler (m^2) and t = filtration time (s).

One-way repeated measure analysis of variance (one-way RM ANOVA) was used to test temporal differences between drift densities. Non-normal data were log$_{10}$ transformed or Friedman repeated measures analysis of variance (RM ANOVA on ranks) applied. To isolate the group or groups that differed from the others, a pairwise multiple comparison procedure was used (Student–Newman–Keuls method). The relationship between drift density and discharge was examined by regression (Pearson product moment correlation).

Results

Drift density and composition

Chironomidae dominated the drift samples, on average constituting 95% of all taxa collected during the three sampling periods (Table 1). *Diamesa* constituted 92% of all Chironomidae and their contribution was especially high in the glacial river during May and October (97 and 99%, respectively). However, in the tributary *Diamesa* constituted a low percentage during May (57%) and July (10%). The other major taxa in the glacial river were Simuliidae, 57% of those remaining, Plecoptera (16%), Ephemeroptera (8%) and Trichoptera (2%).

Chironomidae were recorded in high densities in the drift in both the tributary and the glacial river upstream and downstream of the confluence, although typically densities were higher in the glacial river (Fig. 2). Plecoptera and Simuliidae were found in both benthos and drift of the glacial river above the confluence with the tributary in May and October (Fig. 3). However, Ephemeroptera were only recorded in the benthos. Plecoptera and Simuliidae were recorded in the benthos as far up as Station 1 just below the glacial snout, while Ephemeroptera first appeared at Station 2. Drifting Ephemeroptera were only recorded in the tributary. In July, no benthic invertebrates other than Chironomidae were recorded in the glacial river. The few Chironomidae caught in the drift were all taken below the confluence. Trichoptera were only found in the benthos in the nonglacial tributary (except in October) and were never recorded in the drift.

During May, the stonefly, *Brachyptera risi*, occurred in the benthos at all stations from the glacier downwards (Table 2), while *Capnia bifrons*, was only recorded in the drift. In addition, the mayfly, *Baetis rhodani*, and the stoneflies, *Amphinemura sulcicollis*,

Table 1 Mean density (No. 100 m^{-3} ± SE) of major invertebrate taxa in drift from Briksdal through the sampling periods May, July and October

| Taxon Station	May			July			October		
	3b	7	4	3b	7	4	3b	7	4
Chironomidae	18142 ± 290	1372 ± 13	8852 ± 179	3801 ± 41	1750 ± 30	3616 ± 64	5498 ± 128	653 ± 7	5620 ± 59
Simulidae	181.5 ± 2.6	162.4 ± 3.4	89.6 ± 1.7	11.2 ± 0.5	330.8 ± 5.4	29.2 ± 0.8	82.3 ± 2.3	750 ± 12	67.4 ± 2.3
Plecoptera	55 ± 1.2	134.3 ± 2.3	39.4 ± 1.1	3.7 ± 0.2	57 ± 1.6	9.6 ± 0.4	3.2 ± 0.2	168 ± 4	8.5 ± 0.4
Diura nanseni		1.5			9.4		1.7	107.1	
Brachyptera risi	46.9	8.6	26.4	3.7		4.9		35.3	2.3
Amphinemura standfussi					41.1	1.1			1.1
Amphinemura sulcicollis		49.0	1.1			1.2	1.5	16.4	
Nemoura cinerea	0.5	9.6	1.1		2.8	2.4		2.7	
Nemurella pictetii	6.4	2.2	0.8						
Protonemura meyeri		10.9	2.6		3.6			4.0	
Capnia sp.								1.4	
Capnia bifrons	0.7		3.2						5.1
Leuctra sp.								1.4	
Leuctra nigra	0.6	52.7	4.3						
Ephmeroptera		44.9 ± 1.6	3.2 ± 0.4		10.5 ± 0.6	1.1 ± 0.1		170.2 ± 4.8	
Baetis rhodani		44.9	3.2		10.5	1.1		170.2	
Trichoptera		10.5 ± 0.4		2.0 ± 0.3	31.9 ± 2.4	2.8 ± 0.2		1.3	
Limnephilidae		2.8							
Chaetopteryx sp.				1.2					
Heptagenia digitatus		0.4							
Potamophylax sp.								1.3	
Potamophylax cingulatus		8.5							
Others				0.8	31.9	2.6			
Other taxa	82.1 ± 0.6	72.9 ± 1.4	51.6 ± 1.0	67.0 ± 2.0	105.0 ± 1.8	45.9 ± 1.2	8.0 ± 0.4	76.8 ± 3.9	10.1 ± 0.6
Total	18461 ± 291	1798 ± 15	9035 ± 180	3884 ± 41	2286 ± 39	3705 ± 77	5591 ± 129	1820 ± 16	5706 ± 61
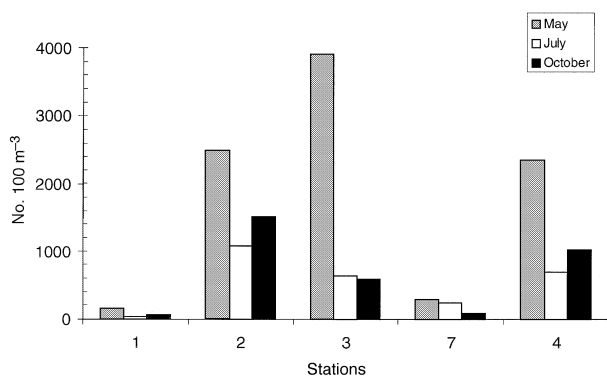
Fig. 2 Density of Chironomidae in the drift (no. 100 m^{-3}) in the river, Dalelva, at stations downstream from the glacier and in the tributary stream (Station 7).

Nemoura cinerea, *Nemurella pictetii*, *Leuctra nigra* and *Leuctra fusca* were all recorded above the confluence during May. In July only the stoneflies, *N. cinerea* and *B. risi*, occurred in the drift in the glacial river upstream of the tributary. Below the tributary at Station 4, some more species appeared in the drift, but were not recorded in the benthos, except in the tributary itself. In October, four species, *Diura nanseni*, *A. sulcicollis*, *C. bifrons* (in the benthos up to Station 2) and *B. risi*, were recorded either in the drift or in the benthic samples upstream of the tributary. The two species found in the benthos upstream of the tributary, *C. bifrons* and *B. risi*, were also found in benthos below the tributary, but they were only recorded drifting in the glacial river downstream of the tributary, which was not the case for the two species found in the drift (Table 2). *Baetis rhodani*, *N. cinerea* and *Protonemura meyeri* were only recorded in the tributary, and in the benthos downstream of the confluence.

Diel periodicity in drift

Chironomidae showed a significant peak in drift density at mid-day in the glacial river over all three sampling periods ($P < 0.01$) (Fig. 4). In the tributary, chironomid drift density peaked during the middle of the day in May, although it was not statistically significant from that during other time periods ($P > 0.05$) (Fig. 4). In July drift peaked at night in the tributary ($F = 11.2$, $P < 0.01$), whereas in October the only statistically significant variation was a decrease in densities in the 18:00 hours samples ($F = 5.5$, $P < 0.01$).

Differences in drift pattern between *Diamesa* and other Chironomidae were not significant, except during July (Fig. 5). *Diamesa* peaked significantly in density during the daytime in both the tributary and the glacial river ($P < 0.05$), while other Chironomidae drifted most at midnight in the tributary and displayed one midday peak and one midnight peak in the glacial river. The latter peak was not statistically significant.

In the glacial river, drift of Simuliidae peaked significantly in daytime during the first 24-h period in both May ($F = 4.5$, $P < 0.01$) and October ($F = 2.9$, $P < 0.05$), whereas there was no obvious diel pattern during the second period (Fig. 6). In July, there seemed to be two peaks in density, but densities were too low to draw any conclusions concerning diel variation. In the tributary the highest simuliid density was recorded at mid-day during the first 24-h period in May. This peak was significantly different from the night sample ($F = 3.9$, $P < 0.05$) (Fig. 6). In the second period the midnight and 06:00 hours densities were significantly different from the 12:00 and 18:00 hours samples ($F = 7.5$, $P < 0.05$). In July there were two peaks in drift density in the tributary; one at mid-day ($F = 6.2$, $P < 0.05$) and one at midnight ($F = 7.6$, $P < 0.05$). In October, the simuliids showed no obvious diel variation during the first period, but a highly significant midnight peak during the second period ($F = 9.9$, $P < 0.01$).

Ephemeroptera, Plecoptera and Trichoptera, the EPT taxa, peaked at night in May, whereas in July and October drift densities were too low to draw any conclusions concerning diel variation (Fig. 7). In the tributary there was generally a peak in density in the evening or at midnight (Fig. 7). The midnight peak was highly significant during the second period in July ($F = 21.2$, $P < 0.01$), and the first period in October ($F = 9.6$, $P < 0.01$).

Total drift of Plecoptera and that of *B. risi* were similar in the glacial river, with a significant peak at midnight during all months (Fig. 8). *Amphinemura sulcicollis* and *L. nigra* were the most abundant Plecoptera in the tributary during May, where they displayed a drift peak at mid-day (Fig. 8). *Amphinemura standfussi* drifted most in the tributary in July, peaking at 12:00 hours during the first 24-h and at 24:00 hours during the following 24-h period. In October, *D. nanseni* (Fig. 8) was by far the most common Plecoptera, and with a highly significant peak in density at night
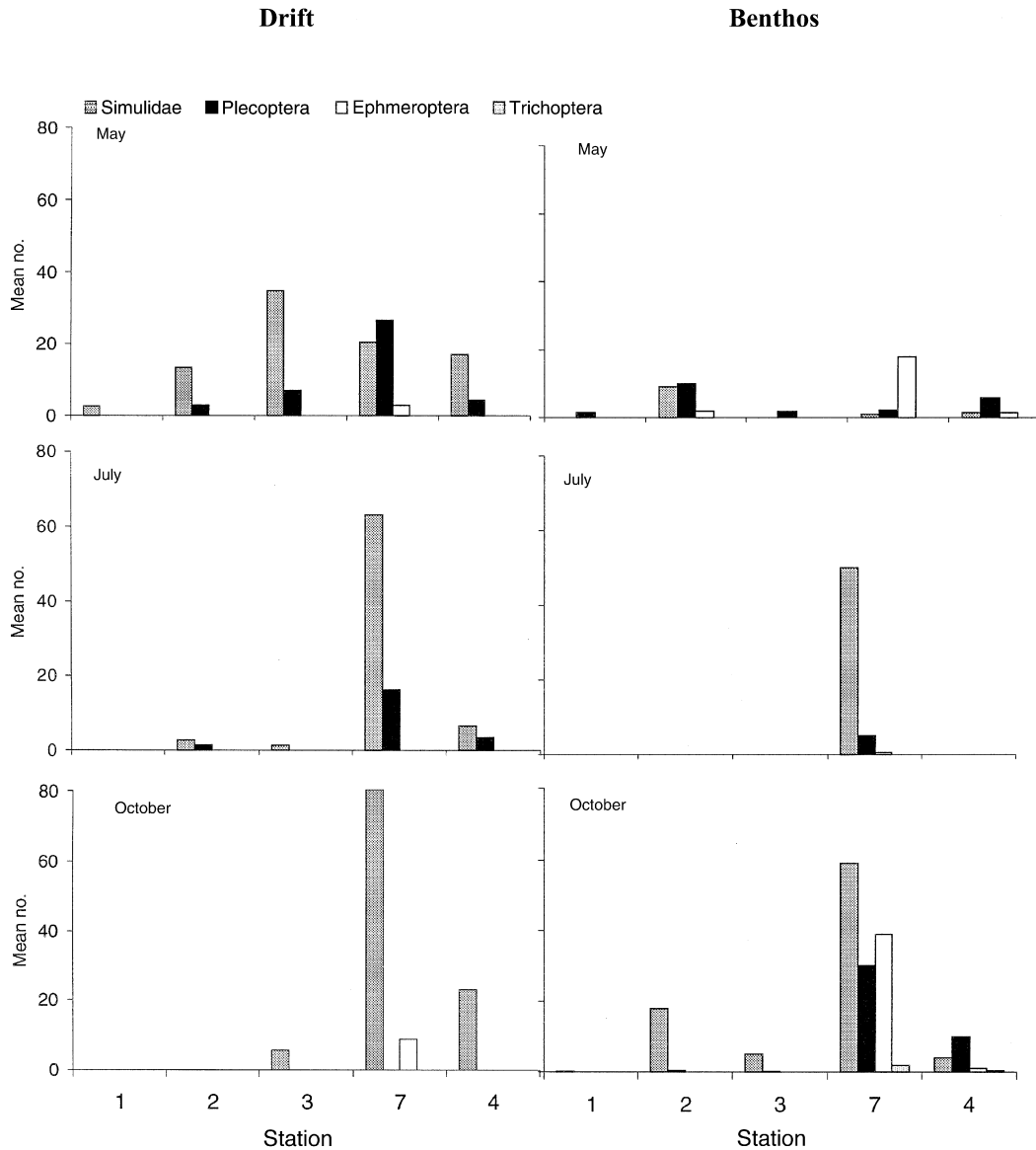
Drift   **Benthos**

Fig. 3 Density of Simuliidae, Plecoptera, Ephemeroptera and Trichoptera in the drift (mean numbers 100 m^{-3}) and in the benthos (mean no. per kick sample) in Dalelva (Stations 1–4) and a non-glacial tributary (Station 7) during the three sampling periods.

($F = 28.4$, $P < 0.001$). *Baetis rhodani* was the only ephemeropteran recorded in the drift, with significantly drifting at night in all sampling months (Fig. 8).

No significant correlation was evident between drift density and discharge measured during the same hour, during the previous hour, or during the mean of the last 3 h in either July or October. In July, there were differences in drift patterns between *Diamesa* and other Chironomidae (Fig. 5). However, there were still no significant relationships between density of *Diamesa* and discharge, or between density of other Chironomidae and discharge (Fig. 9).

Discussion

Invertebrate drift varies both spatially and temporarily. Several authors have stated that peaks in drift density generally correspond to periods of rapid growth, prepupation and emergence (e.g. Elliott, 1967; Müller, 1973; Stoneburner & Smock, 1979). The densities observed in Briksdal during May, which were high compared with reported drift densities (Armitage, 1977; Allan, 1995), were probably distributional drift (Müller, 1973) of species that had overwintered as eggs or larvae. This is

Table 2 Ephemeroptera and Plecoptera recorded in the benthos (B) and drift (D) at different stations in the glacial river, Dalelva (Stations 1–4) and its tributary stream (Station 7)

	Station									
	1		2		3		4		7	
	B	D	B	D	B	D	B	D	B	D
Baetis rhodani Pictet										
May			+				+	+	+	+
July								+	+	+
October							+		+	+
Brachyptera risi Morton										
May	+		+	+	+	+	+	+	+	+
July						+		+	+	
October			+				+	+	+	+
Nemoura cinerea Retzius										
May			+			+		+	+	+
July										
October									+	+
Capnia bifrons Newman										
May		+				+		+		+
July										
October			+		+		+		+	
Amphinemura sulcicollis Stephens										
May			+					+	+	+
July										
October								+		
Amphinemura standfussi Ris										
May										
July								+	+	+
October								+		+
Leuctra nigra Olivier										
May						+		+	+	+
July										
October										
Nemurella pictetii Klapálek										
May						+		+		+
July										
October										
Protonemura meyeri Pictet										
May								+	+	+
July									+	+
October									+	+
Diura nanseni Kempny										
May									+	+
July						+			+	+
October							+		+	+
Leuctra fusca Linnaeus										
May			+							
July										
October									+	

supported by the high number of early instar Simuliidae recorded in the tributary during October. They probably spend the winter as larvae (Ulfstrand, 1968), and emerge as adults after snowmelt during spring.

Diamesa, the dominant taxon throughout the snow-free period, is normally the predominant, if not the only, taxon occurring in the upper reaches of glacial rivers (Sæther, 1968; Steffan, 1971; Slack *et al.*, 1979; Milner, 1994; Milner & Petts, 1994; Ward, 1994).
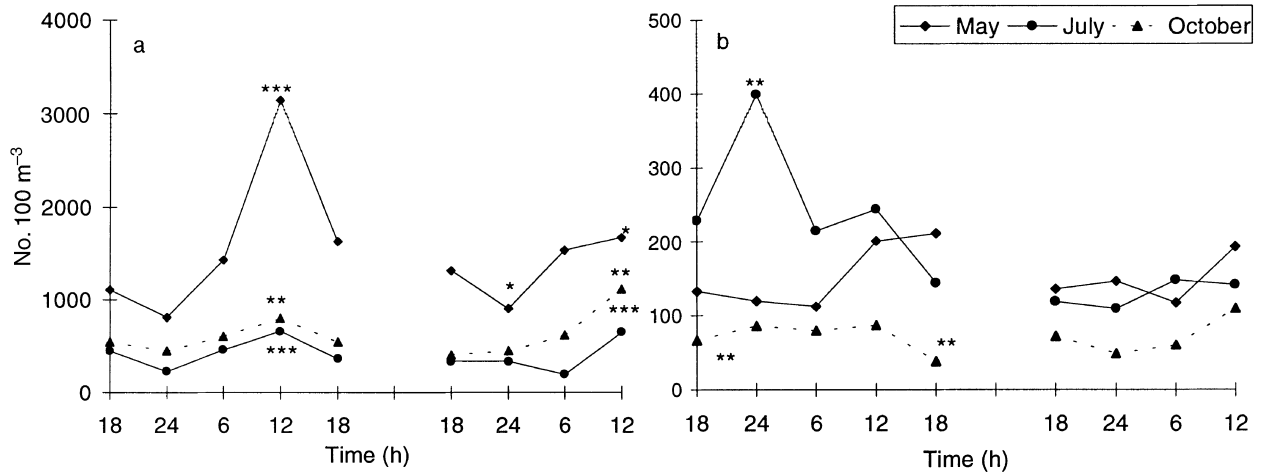
Fig. 4 Diel variation of Chironomidae (mean no. 100 m^{-3}) in May, July and October in (a) the glacial river (mean of Stations 3b and 4) and (b) the tributary (Station 7) during two 24-h periods. Note the difference in scale. Statistical differences between adjacent sampling periods are indicated: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

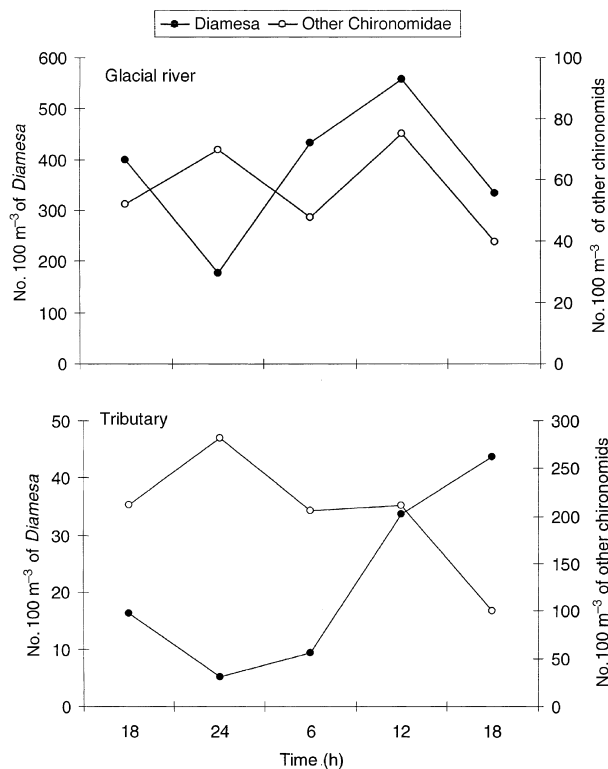**Fig. 5** Drift density (mean no. 100 m^{-3}) of *Diamesa* and other chironomids in the glacial River Dalelva (Station 3b) and its non-glacial tributary (Station 7) in July.

Milner (1994) suggested that *Diamesa* species dominate in unstable environments because of lack of competitors, but may be eliminated in more stable environments by interspecific competition; an idea

that may explain the low numbers of *Diamesa* in the non-glacial tributary.

Besides the Chironomidae, species from several other invertebrate taxa were recorded in both drift and benthic samples in the glacial river upstream of the tributary confluence, especially during May and October. The record of the stoneflies *B. risi* and *C. bifrons* only 100 m below the snout of the glacier both prior to and after the glacial melt was unexpected. In the conceptual model of Milner & Petts (1994), Plecoptera were suggested to first appear when T_{max} exceeds 4 °C. However, the mean temperatures were 1.7 °C at Station 1 and 3.4 °C at Station 2 during the sampling period in May before the onset of glacial melt. During winter, Dalelva is completely covered with snow and ice, but because of the lack of glacial water inputs, non-glacial and groundwater sources predominate. This provides conditions more suitable for species that would normally not survive glacial meltwater conditions. We suggest as originally indicated by the authors, that the conceptual model of Milner & Petts (1994) is only valid during the summer period when glacial meltwater dominates.

Taxa other than Chironomidae, not recorded in the benthos and only rarely in the drift of the main glacial river during summer, must avoid the severe glacial melt conditions by different strategies (Füreder, 1999). Some taxa may have groundwater/hyporheic refugia (Stanford & Ward, 1993; Malard *et al.*, 2001), while others are cold adapted species with their main
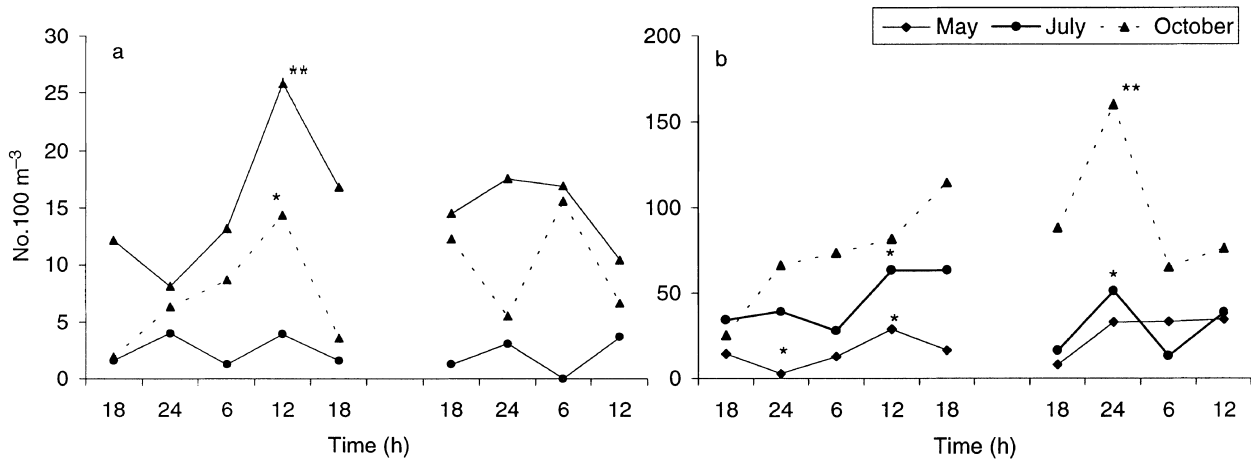
Fig. 6 Diel variation of Simuliidae (mean no. 100 m^{-3}) in May, July and October in (a) the glacial river (mean of Stations 3b and 4) and (b) the tributary (Station 7) during two 24-h periods. Note the difference in scale. Statistical differences between adjacent sampling aperiods are indicated: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
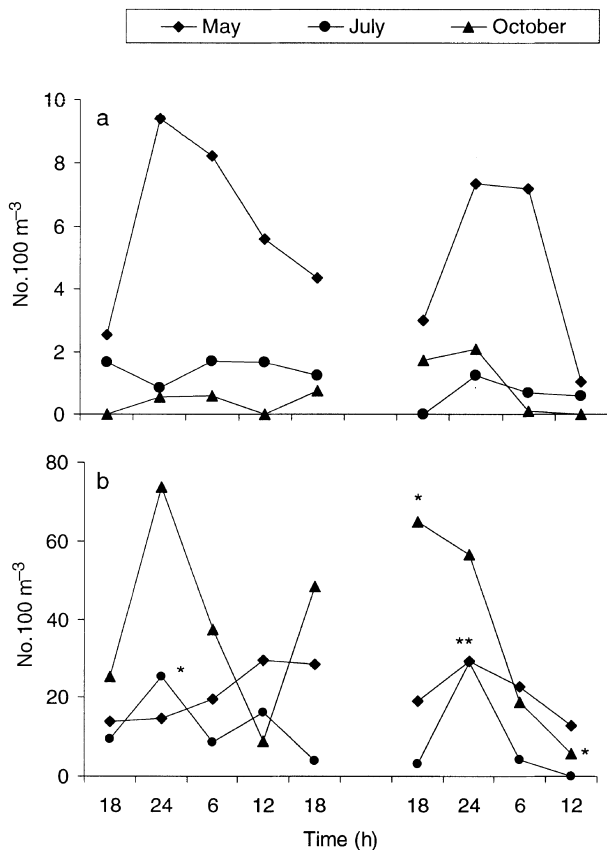

Fig. 7 Diurnal variation (mean no. 100 m^{-3}) of Ephemeroptera, Plecoptera and Trichoptera in the glacial river, Dalelva (a) (mean of Stations 3b and 4) and (b) its tributary (b) (Station 7). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

nymphal growth during the winter months. Some species also have their egg incubation period during winter (Lillehammer *et al.*, 1989), but *C. bifrons* is the only plecopteran in Norway where all embryonic development occurs within the female's body (ovovivipary), and the eggs hatch shortly after oviposition (Lillehammer *et al.*, 1989). The nymphs diapause within the substrate during the warm summer months and emerge next spring when the ground is still snow-covered (Lillehammer *et al.*, 1989). This explains their absence in drift samples during July and their availability to survive in glacial streams.

The non-glacial tributary was of little importance for colonization of the main glacial river. When a species colonises a new habitat, it has to establish juvenile stages within the stream benthos before it can be considered a part of the species pool within the river (Milner, 1994). During spring and autumn several species were present in the main channel, independent of tributary colonization. Nevertheless, some species were restricted to the main rivers downstream of the tributary confluence. These species may have colonized from the tributary via drift. Environmental conditions were extreme in the glacial river during July, and species occurring at that time in the drift below the tributary would probably have difficulties in establishing a population. A similar pattern was also documented in another glacial, Leirungsåi, in the Jotunheimen Mountains, central Norway, although colonizing species from that tributary had a greater chance of establishment in this
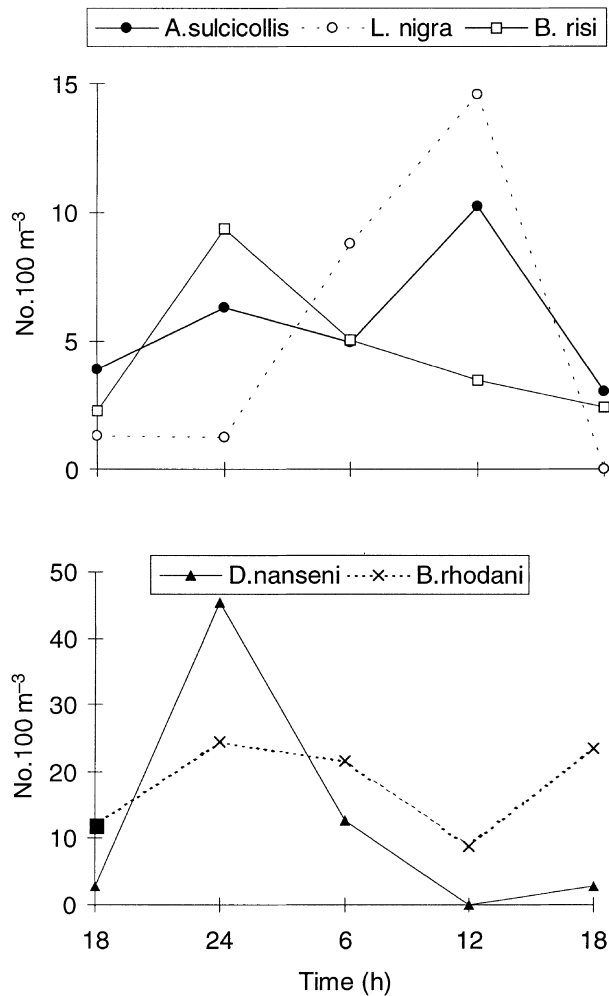
Fig. 8 Diurnal variation of some common taxa in the drift (mean no. 100 m^{-3}). *Brachyptera risi* from Station 3b in May, *Amphinemura sulcicollis* and *Leuctra nigra* from Station 7 in May, *Diura nanseni* from Station 7 in October and *Baetis rhodani* from Station 7 in October.

glacial river as the tributary was farther from the glacier (I. Haug, unpublished data).

The difference in drift patterns between the glacial river and non-glacial stream was demonstrated for Chironomidae in July. Discharge in the glacial river was high, the waters were highly turbulent and turbidity levels high. The drift density of Chironomidae showed a highly significant peak during daytime in the glacial river, whereas there was a significant night time peak in the non-glacial tributary. However, even in May and October, when the physical conditions in the main river were very different compared with July (low discharge and no significant diel fluctuations), Chironomidae drift density still displayed
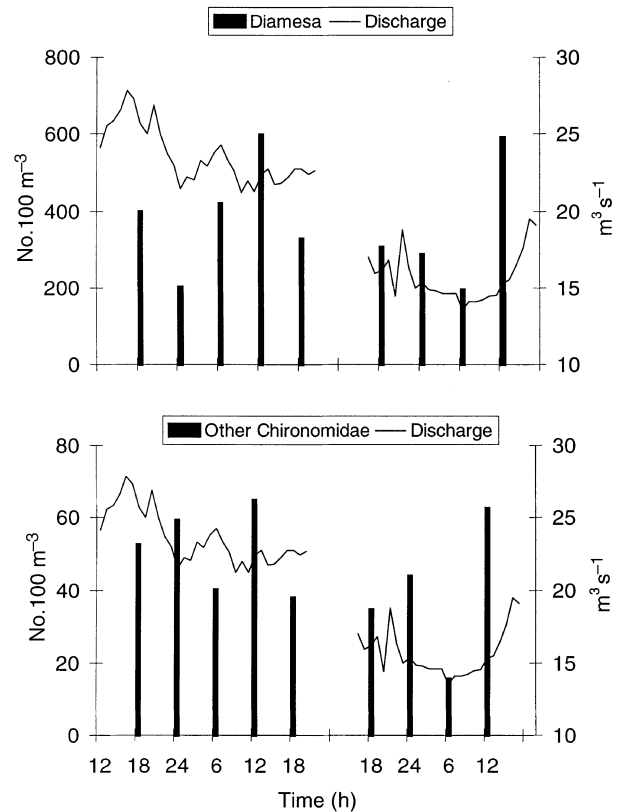

Fig. 9 Relationship between density of *Diamesa* and other Chironomidae (mean no. 100 m^{-3}) and discharge (m^3 s^{-1}) in Dalelva during July.

a daytime peak, whereas in the tributary no periodicity was apparent. Factors other than discharge must be influencing chironomid drift strategy. *Diamesa* constituted more than 90% of all the chironomids during the ice-free season, except for the tributary in July. It appears that *Diamesa* is adapted to drift during daytime. This could be a genetically determined response to factors like photoperiod, UV-light, benthic density, predation and avoidance of competition with nocturnal drifters. In the tributary in July, when the other Chironomidae taxa dominated, they displayed a significant midnight drift peak. In another Norwegian glacier-fed system the percentages of *Diamesa* were low in June and July, but high in September (I. Haug, unpubl. data), explaining the distinct mid-day increase in drift density found in this glacial river during September.

Chironomids often drift more in a response to the discharge regime than other invertebrates (Brittain & Eikeland, 1988). However, the correlation between Chironomidae drift density and discharge was not

significant in the present study, although discharge may still have had some effect on chironomid drift densities in July. Drift density is known to be independent of discharge, in contrast to drift rate (Elliott, 1970), and several authors have suggested that drift density tends to correct for seasonal variations in discharge (e.g. Elliott, 1967; Allan, 1987). This may be the underlying cause of the non-correlation between chironomid drift density and discharge observed in this study.

The predominately daytime drift of Simuliidae in the glacial river differed from other studies where Simuliidae have been typically reported as nocturnal drifters (e.g. Clifford, 1972b; Armitage, 1977). However, these studies were from non-glacial streams and the different species composition in glacier-fed systems may explain the differences in drift pattern. It is also possible that the differences are the result of different life cycle stages or to species that change their drift strategy when living in a colder, more unstable environment.

There were no significant differences in drift patterns for EPT taxa between the glacial and non-glacial river. However, in the glacial river the density of these taxa was low, and their apparent diel periodicity may not be real. These taxa usually have their drift maximum during the night (Waters, 1972; Brittain & Eikeland, 1988). This trend was also apparent in the present data. However, some species differed. For example *A. sulcicollis* and *L. nigra* were found drifting in high densities during daytime in May. Waters (1968) indicated that day-active periodicities may be the result of a greater activity related to increased metabolism at higher water temperatures. *Amphinemura sulcicollis* and *L. nigra* were found as pre-emergence nymphs or newly emerged images. The mature nymph may move by drift to more suitable emergence habitats (Waters, 1972).

Periodicity in drift is thought to be the result of predator avoidance to minimize fish (Allan, 1978; Flecker, 1992) or invertebrate predation (Peckarsky, 1979). Studies in fishless rivers have found no evidence of consistent diel periodicities (Turcotte & Harper, 1982; Flecker, 1992). Allan (1978) found that nocturnal drift was most pronounced in larger size classes, which is in accordance with size-selective feeding of daytime predators. The risk of predation as an explanation of nocturnal drift is difficult to test directly, because nocturnal drift behaviour is almost

certainly determined genetically (Allan, 1995). Fish are lacking or present in very low numbers in the upper reaches of our study river. However, many EPT taxa still showed significant nocturnal drift, whereas the Chironomidae and Simuliidae had their drift maximum during daytime, suggesting a behavioural drift in EPT taxa. Patterns in Chironomidae and Simuliidae drift are related more to catastrophic and passive drift. Drift of invertebrates may also be density dependent, and reflect production in excess of the carrying capacity (Waters, 1961). In some rivers, however, physical perturbation, such as increasing discharge and floods, may maintain population densities below this level, with the result that drift in glacial rivers may be density independent at most times (Bishop & Hynes, 1969). Steffan (1971) claimed that neither predation nor competition influenced the fauna of kryal biotopes; predators are absent and population densities so low that it is unlikely that food competition occurs, despite limited organic resources. The main reason for the diurnal periodicity shown in this study, is therefore probably passive drift because of increasing discharge during daytime and drift patterns evolved through lack of predators.

Acknowledgments

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