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Effects of flow and refugia on drift loss of benthic macroinvertebrates: implications for habitat restoration in lowland streams

DIETRICH BORCHARDT
Fachgebiet Siedlungswasserwirtschaft, Universität/Gesamthochschule Kassel, Postfach 10 13 80, D-3500 Kassel, Germany

SUMMARY

1. Current stream restoration practices are rarely based on sufficient knowledge of the physical-habitat requirements of the biota. In this study the drift loss of two lowland stream benthic macroinvertebrates, *Gammarus pulex* (L.) (Amphipoda, Crustacea) and *Ephemerella ignita* (Poda) (Ephemeroptera, Insecta), was investigated over gradients of flow forces and abundance of woody debris in laboratory flume experiments.
2. The losses by drift of *E. ignita* and *G. pulex* increased significantly at median flume shear stresses of approximately 11 and 31 dyn cm^{-2}, respectively.
3. Above these critical shear-stress values the population losses of both species significantly decreased with increasing abundance of stationary woody debris.
4. *Ephemerella ignita* exhibited high population loss in the first period of hydraulic disturbance. *Gammarus pulex* was affected in a different way, showing an almost constant population loss over time. In contrast to *E. ignita, G. pulex* used the refugium 'woody debris' actively and more efficiently.
5. Restoration concepts of lowland running waters have to consider hydraulic disturbance by flow as a key element for potential benthic community recovery.
6. Woody debris in the baseflow channel of lowland streams appears to mitigate the impact of hydraulic disturbance to benthic macroinvertebrates caused by rising discharge.

Introduction

Water flow and related hydraulic phenomena are major determinants of the physical environment in lotic ecosystems and have both benign and critical impacts on aquatic communities (Ambühl, 1959; Statzner, Gore & Resh, 1988). The drag force of flowing water can cause dislodgement and subsequent downstream transport of individuals. Such species-specific population losses appear to be compensated by various migration strategies (Williams, 1981). Because most running waters are characterized by high seasonal fluctuations in discharge, the hydraulic environment shifts over time. Such shifts are primarily dependent on meteorological events and catchment characteristics (Hynes, 1970; Mangelsdorf & Scheurmann, 1980). Fluctuations in discharge and the corresponding potential changes in flow forces can have dramatic effects on lotic organisms and community structure (e.g. Welcomme, 1985), especially during spates. In rivers or streams with a bottom of coarse inorganic material, interstitial spaces within the stream bed serve as important refugia during such critical hydraulic periods (Schwoerbel, 1964; Tilzer, 1968), even under sudden changes of discharge (Borchardt & Statzner, 1990). However, in lowland running waters the stream bed often consists of fine inorganic material with very narrow interstices within the substrata. Therefore, this habitat offers little refugial space to most benthic macroinvertebrates while other habitat structures, such as woody debris, fulfil this function.

Although these basic principles are generally accepted, little information is available about critical hydraulic situations for single species, their resistance to hydraulic disturbances and links to habitat structures in terms of refugial space. For restoration projects this information is badly needed, because the construction or rehabilitation of the hydraulic environment has to cover a wide range of discharge situations and their return periods. Additionally, in catchments influenced by man, both discharge and discharge fluctuations are often increased (Beard & Chang, 1979), whereas woody debris is usually removed from the river channel by current management practice.

In order to investigate the response of single macroinvertebrate organisms and population over gradients of near-bottom flow forces at different abundances of refugial space provided by woody debris, experiments in laboratory flumes with *Gammarus pulex* (L.) (Amphipoda, Crustacea) and *Ephemerella ignita* (Poda) (Ephemeroptera, Insecta) were performed. These two species are often abundant in lowland streams of northern Europe. The objectives of this paper are: (i) to describe the drift response of these two benthic macroinvertebrates at increased flow forces, (ii) to derive critical levels of hydraulic disturbance for different morphological structures in their habitat, (iii) to demonstrate the potential contribution of experimental approaches to the ecological basis of stream restoration concepts and measures.

Materials and Methods

The experiments were performed in two laboratory flumes described by Borchardt & Statzner (1990). These flumes (length, 300 cm; width, 20 cm) can be operated under both circulating and flow-through conditions. Experimental animals were allowed to acclimatize to the imposed shear-stress regime while the flume was in recirculating mode (thus avoiding accumulation at an outlet) before switching to flow-through mode when animals could be captured as they drifted out of the flume.

The flume bottom used for the simulation of the lowland stream environment consisted of defined amounts of gravel and sand (0.05–60 mm, $d_{50} = 6$ mm) with a surface layer formed by sand fractions. The abundance of refugial space was determined by placing different quantities of fixed, waterlogged branches (length, 15–25 cm; diameter, 1–2 cm) on top of the inorganic material (approximately 800, 1600 and 3200 g wet weight m^{-2}). This woody debris was not moved under the hydraulic conditions tested, but at the highest hydraulic values the surface layer of sand started to move in parts of the flumes. One experimental series with approximately 800 g m^{-2} woody debris was performed without fixing the material. The results from this series represent the zero values of woody debris in Figs 1 and 2, because the woody material started to move at median flume shear stresses above 11.2 dyn cm^{-2} (cf. Table 1) and was almost completely washed

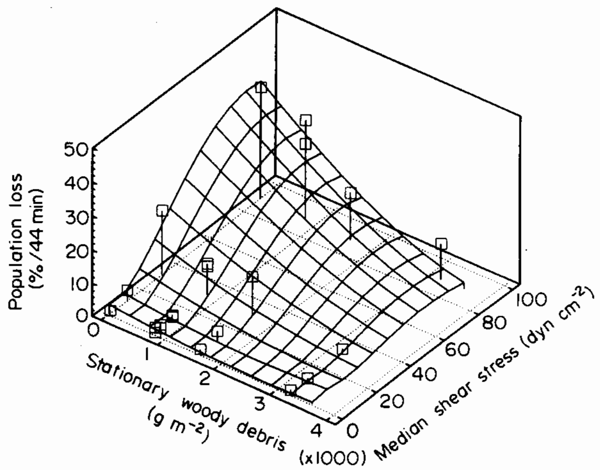

Fig. 1 Population loss of *Gammarus pulex* by drift as related to shear stress and abundance of stationary woody debris. Data points are shown together with a surface plot of multiple-regression model given in Table 2.

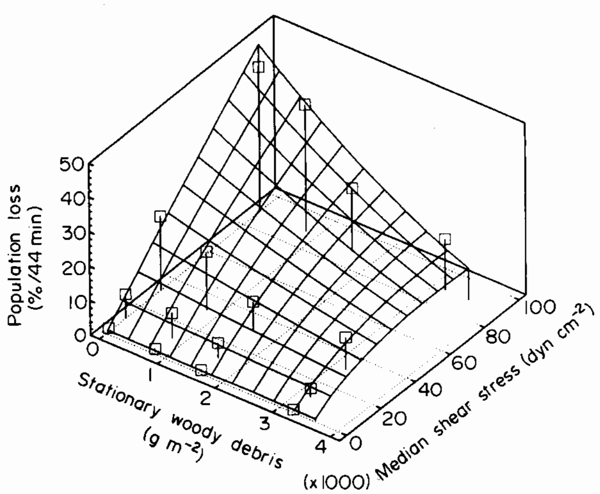

Fig. 2 Population loss of *Ephemerella ignita* by drift as related to shear stress and different abundance of stationary woody debris. Data points are shown together with a surface plot of multiple-regression model given in Table 2.

Table 1 Statistics of depth, flow velocity and shear stress at five different hydraulic levels (circulating flow, FTH1–FTH4 = Flow Through mode) used for experiments with *Gammarus pulex* and *Ephemerella ignita*. Measurements were performed in steps of 15 cm in the longitudinal direction of the flume ($n = 21$). Depth was measured with a metre stick, flow velocity with a current meter 'Ott C2 10.150' and shear stress estimated with FST-hemispheres (Statzner & Müller, 1989; Statzner, Kohmann & Hildrew, 1991)

	Circulating flow	FTH1	FTH2	FTH3	FTH4
Depth (cm)					
Arithmetic mean	7.8	7.9	7.1	5.5	5.2
Median	7.0	7.5	7.0	5.0	5.0
Standard deviation	1.7	1.6	1.8	1.2	1.5
Minimum	6.0	5.5	4.5	3.5	3.5
Maximum	11.5	11.5	10.5	9.0	9.0
Flow velocity (cm s^{-1})					
Arithmetic mean	6.63	6.89	15.5	23.8	46.1
Median	6.43	6.64	15.3	27.9	46.0
Standard deviation	1.04	1.04	3.4	8.8	11.2
Minimum	5.50	5.50	10.3	13.1	23.6
Maximum	9.00	9.00	21.5	47.8	65.1
Shear stress (dyn cm^{-2})					
Arithmetic mean	1.34	1.39	11.3	31.3	104.0
Median	1.19	1.19	11.2	31.7	89.5
Standard deviation	0.43	0.46	6.92	9.61	66.7
Minimum	1.04	1.04	3.98	11.2	44.8
Maximum	2.82	2.82	31.6	44.8	251.8

out of the flumes at the highest hydraulic levels tested (31.7–89.5 dyn cm^{-2}).

The macroinvertebrate drift response to flow conditions tested refers to shear stress, the flow force acting per unit area of stream bottom.

The hydraulic environment in the experimental flumes under control conditions was constructed on the basis of *in-situ* measurements of near-bottom flow forces in a quasi-natural German lowland stream at base flow (Kleine Örtze; Lower Saxony [Statzner & Sperling, 1993]). Because these results and the hydraulic data for the experimental flumes used in this study deviate significantly from normal distributions, the hydraulic environment is described by frequency distributions and their parameters (Table 1).

The specimens of *G. pulex* and *E. ignita* were collected in the Esse and Losse, two small streams situated in the vicinity of Kassel (51°24′N, 9°34′E). After their transport to the laboratory the test organisms were kept under flow conditions comparable to those in their natural habitat and fed with detritus *ad libitum* for up to 5 days prior to the experiments. The experimental runs started with preparation of the physical structures within the flumes followed by a 24-h period when the flumes were in circulation mode. Speciments of *G. pulex* used in the experiments were size-selected by gentle wet sieving (mean dry weight ±1 SD, 1.9 ± 0.6 mg); those of *E. ignita* were larvae with a length of 5.7 ± 0.4 mm (mean ± 1 SD without cerci). Each experiment involved 500 individuals for *G. pulex*, corresponding to a density of 833 ind. m^{-2}, or 80–120 individuals for *E. ignita*, corresponding to a density of 133–200 ind.m^{-2}, in separate trials for each species. The experimental phase with its changing hydraulic environment (increased shear stress) started between 09:00 and 10:00 h and lasted for 44 min under quasi-natural light conditions. The channel flow mode was changed smoothly from circulation to flow-through mode during a period of a minute. During the experimental period visual observations were made of behaviour and movements of the organisms in selected areas of the flume and population loss by drift at the outlet of the flume was measured at 4-min intervals. The first time interval of drift sampling started after target hydraulic values were reached. Water temperatures were within a range of 16–19°C and oxygen saturation varied between 98 and 100%.

Models of population loss in relation to quantities of woody debris and increasing shear stress were derived by multiple stepwise forward regression analysis. Drift loss data required arcsin ($\sqrt{p}$) transformation, because observed values exceeded the range of 30–70% (Hartung, 1989). The independent variables, woody debris and shear stress, were also transformed in order to improve the fit of models.

These were entered or removed in the selection process at a significance level of 95%. Graphical presentations of model estimates are based on retransformed data (Figs 1 and 2) in order to achieve equal scales of observed and fitted data.

Results

The drift losses of *G. pulex* and *E. ignita* were significantly influenced both by increasing shear stress and the abundance of refugial space in terms of the amount of woody debris that was not moved by flow (Figs 1 and 2 with statistical models given in Table 2).

At a median shear stress of 1.2 dyn cm^{-2}, representing conditions with a hydraulic environment comparable to the natural habitat of both organisms at base flow, drift loss was very low (0.2–1% of population/44 min for both taxa). Drift loss increased significantly at a median bottom shear stress of 31.7 dyn cm^{-2} for *G. pulex* and at 11.2 dyn cm^{-2} for *E. ignita*, indicating a lower threshold of drift induced by flow forces for the latter.

At 31.7 dyn cm^{-2} and with lower quantities of woody debris the loss of *G. pulex* was high (18.9, 11.2 and 7.4%/44 min), but decreased to 1.2% at the highest abundance of refugial space (Fig. 1). This loss was in the same range as the values under hydraulic conditions with a lower shear stress. At a median shear stress of 11.2 dyn cm^{-2} the population loss of *E. ignita* decreased from 6.9 to 2.4%/44 min with an increase in refugial space from the minimum to maximum offered (Fig. 2). This loss was higher than for *G. pulex* (3.2 to 0.4%/44 min). At 31.7 dyn cm^{-2} the population loss of both species was of the same order of magnitude, but the drift reduction due to increased refugial space for *E. ignita* was less obvious than for *G. pulex* (Figs 1 and 2).

At the highest median shear stress tested in the experiments (89.5 dyn cm^{-2}), population losses further increased to 33.1%/44 min for *G. pulex* and 42.0%/44 min for *E. ignita* at the lowest refugial space. For *G. pulex* the population loss again was reduced by increasing amounts of woody debris. At 1600 g m^{-2} of wood, this loss was approximately half that at 800 g m^{-2} (13.6 and 26.4%/44 min), whereas a further increase of wood to 3200 g m^{-2} had little additional effect on population loss (10.6%/44 min). *E. ignita* population losses also decreased with increasing amounts of woody debris, but this effect was less obvious when compared to the *G. pulex* responses. An increase in woody debris by a factor of four (800 to 3200 g m^{-2}) reduced the population loss of *E. ignita* from 22.4 to 14.8%/44 min.

The temporal pattern of drift loss indicated additional differences in the responses of the two species under hydraulic disturbance with different refugial space (Fig. 3). *G. pulex* losses decreased continuously and in an approximately linear fashion with increasing refugial space. On the other hand, the majority of the *E. ignita* population losses occurred in the first 12 minutes. After this time few organisms entered the drifted and were washed out of the flume.

For both taxa, significant population losses by drift were achieved in relatively short periods and started immediately after critical values of hydraulic disturbance were reached (Fig. 3).

Table 2 Multiple regression analysis of population loss of *Gammarus pulex* and *Ephemerella ignita* by drift as related to shear stress [τ_o (dyn cm^{-2})] and woody debris (g m^{-2}) not moved by flow. Drift loss estimates = arcsin ($\sqrt{p}$). Woody debris transformed by ($x + 1$)

Independent variable	Coeff.	95% conf. limit	*t*-value	Sig. level
Gammarus pulex				
$\sqrt{\tau}$	0.1758	0.0700	5.38	0.0003
ln τ_o	−0.1625	0.1000	−3.44	0.0063
τ_o^3	−3.6E-7	1.4E-7	−2.51	0.0312
woody debris	−6.3E-5	5.0E-5	−2.45	0.0342
τ_o woody debris	−8.4E-7	7.9E-7	−2.93	0.0150
R^2 (model) = 0.9715; df = 18				
Ephemerella ignita				
$\sqrt{\tau_o}$	0.0749	0.0060	26.82	0.0000
τ_o woody debris	−1.3E-6	3.1E-7	−6.84	0.0000
R^2 (model) = 0.9872; df = 14				

Discussion

The drift of benthic macroinvertebrates is a well-known phenomenon in lotic ecosystems. Its ecological significance has been subject to much debate since the works of Müller (1954) and Waters (1972). Most work in the past 30 years has focused on single physical, chemical and biotic factors that affect drift patterns in running waters (e.g. Müller, 1954, 1974; Hughes, 1966; Woijtalik & Waters, 1970; Waters, 1972;

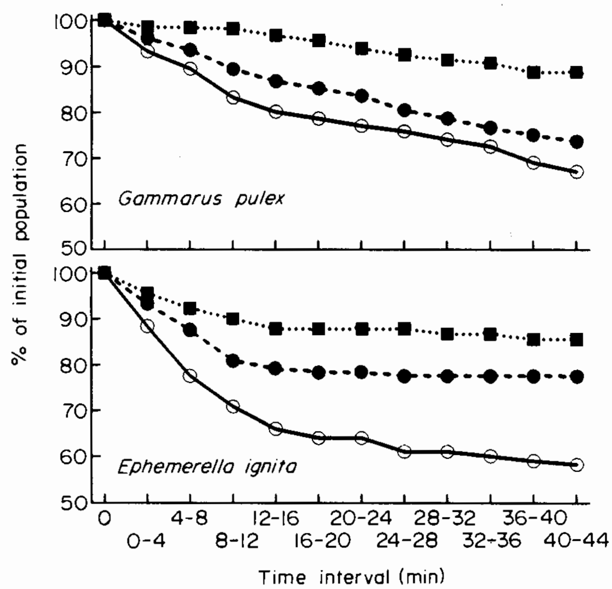

Fig. 3 Temporal pattern of drift loss of *Gammarus pulex* and *Ephemerella ignita* at different abundance of stationary woody debris ($0\,g\,m^{-2}$ = ○; $800\,g\,m^{-2}$ = ●; $3200\,g\,m^{-2}$ = ■) at a median shear stress of $89.5\,dyn\,cm^{-2}$. See Table 1 for other pertinent hydraulic conditions.

Cadwallader & Eden, 1977; Gore, 1977; Statzner & Stechmann, 1977; Bohle, 1978; Walton, 1978; Stoneburger & Smock, 1979; Peckarsky, 1979; Irvine, 1985; Andersson *et al.*, 1986). However, little information is yet available about the interactions of factors (e.g. flow and the physical structure of the habitat) that result in drift of single species and their significance for benthic communities. Therefore, the functional understanding of drift and the assessment of its ecological significance is still limited (Brittain & Eikeland, 1988). This is of special interest in the context of hydraulic disturbance of habitats during high flow, its crucial impact on macroinvertebrates having been shown in several studies (e.g. Weninger, 1968; Irvine, 1985) and termed 'catastrophic drift' by Waters (1972). These 'catastrophic drift' events can be viewed as significant decreases in benthic densities resulting from population loss in short time intervals, a definition that will be adopted in the following discussion.

The results of the experiments presented here indicate that both near-bottom flow forces, expressed as shear stress, and the physical characteristics of the habitat, in terms of refugial space, are of great importance during periods of hydraulic disturbance. A general pattern of increased population loss with increasing shear stress for *G. pulex* and *E. ignita* was observed in experimental streams. Increased abundance of refugial space (woody debris not moved) reduced the amount of loss in populations of both species and resulted in mitigated impacts of critical flow forces. Except for the highest abundance of woody debris used, critical values of hydraulic disturbance were achieved at a median shear stress of approximately $11\,dyn\,cm^{-2}$ for *E. ignita* and 30 $dyn\,cm^{-2}$ for *G. pulex*. The 'critical shear stress' of $11-30\,dyn\,cm^{-2}$ for a significant population loss of *E. ignita* and *G. pulex* is well below values required for the movement of the surface layer of the inorganic substrate (approximately $60-70\,dyn\,cm^{-2}$ for a mixture of cobbles and sand, given by Mangeldorf & Scheurmann, 1980). Consequently, in lowland rivers with little refugial space 'catastrophic drift' events caused by hydraulic disturbance can be expected before significant substrate movement begins.

Above critical hydraulic conditions, *G. pulex* and *E. ignita* appear to be affected in different ways. The drift of *E. ignita* appears to be primarily dependent on the site where the individuals are located when the hydraulic environment becomes critical. Individuals that are exposed on surfaces or structures that offer little protection against flow are washed away because of their low resistance to flow, as described by Ambühl (1959). This is confirmed by the very high drift losses, observed within the first 12 min of hydraulic disturbance, followed by very low values. Furthermore, from other laboratory studies *E. ignita* is known to drift almost passively from the substrate at current velocities above $10\,cm\,s^{-1}$, with poor ability to prevent transport (Butz, 1973). These observations may explain the abundance of this species in drift samples at base flow (Elliott, 1967, 1968) and the dramatic increase of its drift at high-flow conditions (Weninger, 1968), resulting in decreased population densities after such events.

Compared to *E. ignita*, *G. pulex* is a mobile species and known to resist high current velocities of up to $99\,cm\,s^{-1}$ for short time periods (Dorier & Vaillant, 1953), although this species is considered to be 'ill-adapted' for life in lotic environments (Hynes, 1970). Upstream movements of the species have been shown at current velocities up to $44\,cm\,s^{-1}$ (Dorier & Vaillant, 1953). However, *G. pulex* prefers slowly moving water with a current velocity of $5-25\,cm\,s^{-1}$ (Ambühl, 1959). Under hydraulic conditions with high flow forces and with abundant refugial space, *G. pulex* seems to use the refugia very efficiently and to greater extent than *E. ignita*. It is reasonable to assume that *G. pulex* reaches the refugia actively. This was confirmed by observations of specimens visible at the surface of the substrate; these were abundant at 1.2 dyn cm^{-2} median shear stress, but almost invisible during high-flow conditions, hiding themselves in patches of the woody debris. Furthermore, even when there are sudden changes in discharge and shear stress *G. pulex* is known to move immediately into the interstices of coarse substrate surface layers (Borchardt & Statzner, 1990). Therefore, the mechanisms of reduced population loss at critical hydraulic disturbance and refugial space appear to be different for the two species tested in this study.

Evidently, restoration projects of lowland running-water ecosystems should consider hydraulic disturbances at high flow to be of significance for benthic macroinvertebrates and their populations. Every increase in refugial space (e.g. amount of wooden structures not moved) appears to mitigate the impact of critical hydraulic stress. Although the channel periphery, backwaters and bankside debris can be important as 'potential refugia' in lowland running waters (Townsend, 1989), certain species of the macroinvertebrate community, like *E. ignita* in this study, appear to exhibit no or little ability to reach these refugia by active movements. Therefore, habitat restoration should involve careful consideration of 'refugia' or 'dead zones' (Lancaster, Hildrew & Townsend, 1990) in the stream channel. Ecologically sound management of the hydraulic environment has to consider both base flow (Gore, 1978; Gore & Juday, 1981; Campbell & Scott 1984; Gore & Nestler, 1988) and high-flow periods (this study), to address minimum flow requirements and critical maximum values of hydraulic disturbance.

The 'meandritis' and 'bath-tubitis' that are common in the restoration of stream channel morphology (Statzner & Sperling, 1993) have to be replaced by a functional concept with a quantitative ecological basis. Such a concept should be developed using both existing knowledge and careful addition of specific missing facts derived from experimental work in the field and laboratory. As shown in this study, the latter may help to identify quantitative relationships that might never be elucidated by field studies alone.

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