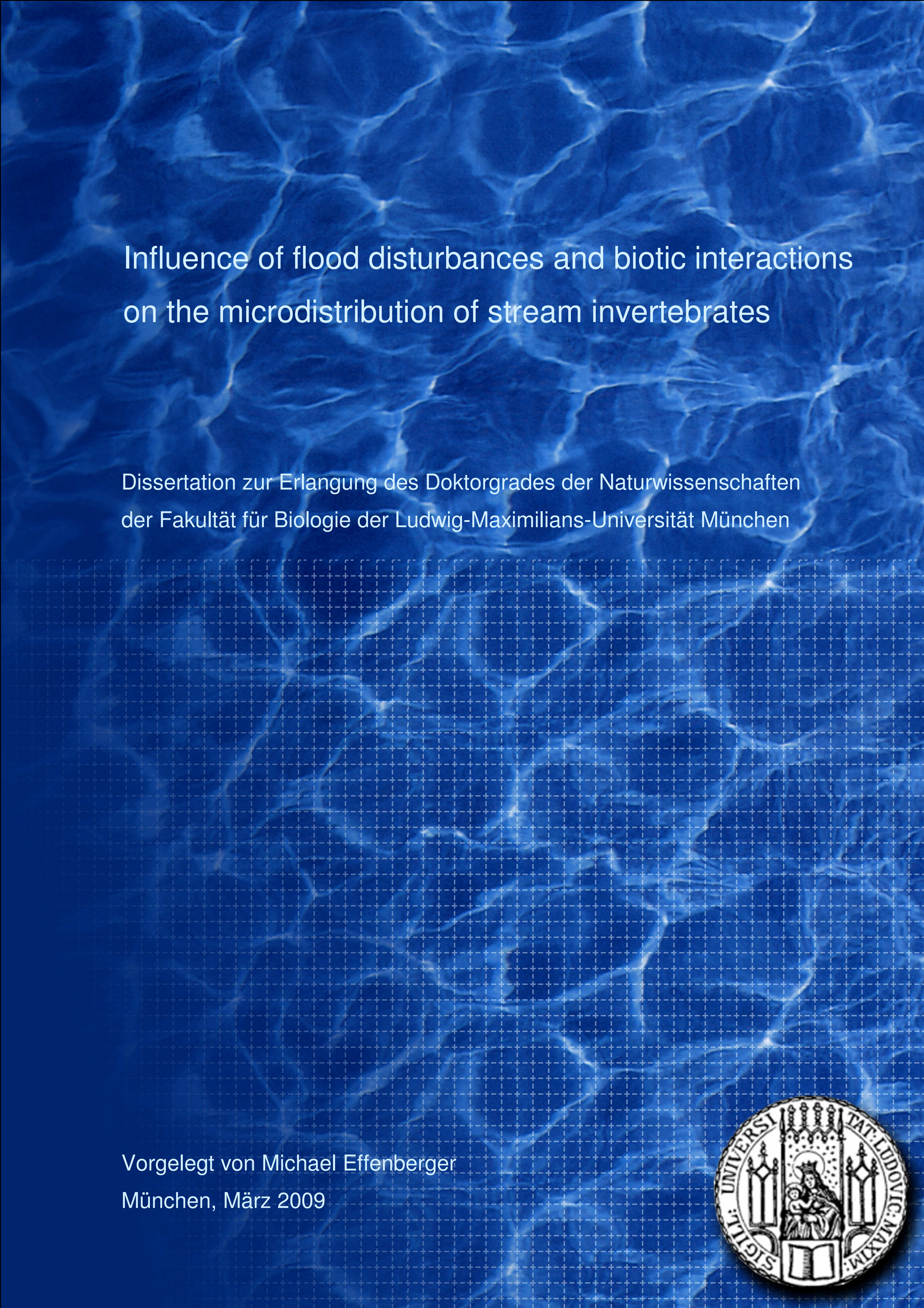

Influence of flood disturbances and biotic interactions on the microdistribution of stream invertebrates

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Vorgelegt von Michael Effenberger
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Erstgutachter:	Prof. Sebastian Diehl
Zweitgutachter:	Prof. Florian Siegert

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FÜR JULIAN UND RAINER EFFENBERGER

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SUMMARY

Most living communities form a temporally shifting patchwork of irregularly distributed organisms. Besides many habitat-specific biotic and abiotic environmental conditions, two key drivers are known to shape community structure: abiotic disturbance and biotic interactions (most notably competition and predation). Few other ecosystems possess either the frequency or intensity of disturbances observed in running waters. Therefore, disturbance (mainly in the form of floods) is discussed to be the dominant organizing factor in streams and rivers. The aim of my thesis was to investigate the interplay between flood disturbances and biotic interactions in determining the small-scale distribution of benthic invertebrate communities in streams.

Especially during small and mid-sized floods, the high shear forces that move and rearrange parts of the stream bed result in a complex mosaic of small (≤ 1 m^2) bed patches that experience scour, sediment deposition or remain undisturbed (“local disturbance history”). In my thesis, I found that local disturbance history patterns caused by natural floods (Chapter 1) or created experimentally (Chapters 2, 3 and 5) played an important role for the distribution of mobile invertebrates. Further, stable bed patches seemed to act as invertebrate refugia during and shortly after floods and, in the longer term, several common invertebrate taxa preferably colonized depositional or scour patches. Various habitat parameters such as current velocity, substratum size or food resources were also partly responsible for the heterogeneous distribution of stream invertebrates (Chapters 1, 2 and 5). The combined findings of my manipulative experiments described in Chapters 2 and 5 suggest that immediate, 'direct' effects of local disturbance on the invertebrates (mostly negative, i.e. density reductions in disturbed bed patches) are often in the longer term (several weeks after a flood) replaced by 'indirect' effects mediated via disturbance-induced changes in habitat parameters such as current velocity, substratum size and resource availability.

Previous studies indicate that biotic interactions such as competition, grazing and predation can also be important determinants of the distribution of stream biota. However, although most streams are subject to considerable discharge variations, almost all of these earlier studies were performed in streams or artificial channels with permanently stable flow, or during long periods of stable flow in periodically disturbed streams. To date it is still unclear if biotic interactions are also important in frequently disturbed streams. To begin closing this knowledge gap, I conducted three experiments that examined the interactive effects of physical disturbance and interspecific competition on benthic stream invertebrates and algae. Singular (Chapter 3) and repeated (Chapter 4) local disturbances were combined with frequent manual removals of the most common invertebrate taxa. Disturbance played an important role for the microdistribution of invertebrates in all experiments. By contrast, competition was only found to be an important driver in shaping community composition in a stable stream (Chapter 4). In both experiments conducted in frequently disturbed streams, I found no evidence that competition influenced the invertebrate community (Chapters 3 and 4). Moreover, there were hardly any interactions between disturbance and competition treatments. Collectively, the results from previous research conducted in stable streams and my own experiments support the hypothesis that the importance of competition in shaping aquatic communities should decrease with increasing frequency or intensity of disturbance.

In my last experiment (Chapter 5), I examined the separate and interactive effects of patchy bed disturbance and fish predation on benthic invertebrates and algae. While experimental disturbance had strong and lasting effects on the benthic community, effects of local fish exclusion were weaker. Moreover, effects of fish predation on invertebrate and algal densities were generally present or absent regardless of the disturbance history of the studied patches of stream bed. These results emphasize the pervasive importance of patchy bed disturbances for the microdistribution of stream organisms and also indicate a notable, but less prevalent, influence of fish exclusion at the patch scale on this microdistribution.

Collectively, my findings on the interplay between disturbance and competition or predation confirm the key role of local disturbance history for the small-scale distribution of stream invertebrates both in stable and in frequently disturbed streams (Chapters 3, 4 and 5). Furthermore, local habitat parameters such as current velocity or food resources may define suitable bed patches for stream invertebrates, but several of these parameters themselves seem to be influenced by local disturbance history, as well. Finally, the frequency and/or intensity of such disturbances may determine whether populations become so dense that competition or predation can strongly influence the structure of the benthic stream community.

GENERAL INTRODUCTION

Although much theorizing in community ecology assumes an even distribution of organisms in a homogeneous environment, nature rarely satisfies this assumption. Instead, many communities form a temporally shifting patchwork of irregularly distributed organisms and the identification of factors that drive these “patch dynamics” is a central concern of ecology (Pickett & White 1985) and stream ecology in particular (Pringle *et al.* 1988, Townsend 1989). Besides many habitat-specific biotic and abiotic environmental conditions, two key drivers are shaping the structure of most communities: abiotic disturbance and biotic interactions, most notably competition and predation (Paine 1966, Menge & Sutherland 1976, Connell 1978, Huston 1979, Sousa 1979, Pickett & White 1985, Sih *et al.* 1985). A closer investigation of the separate and interactive effects of these three factors on benthic stream communities are the subject of this thesis.

Disturbance of benthic stream communities by bed-moving floods

A disturbance is a discrete event that causes an abrupt change in the existing condition of an ecological system (Townsend 1989, Begon *et al.* 2005). Disturbances frequently create open space and cause changes with time (Sousa 1979, Pickett & White 1985). Few other ecosystems possess either the frequency or intensity of environmental changes that are observed in running waters, which makes disturbance a dominant factor of community organization in streams and rivers worldwide (e.g. Fisher *et al.* 1982, Power & Stewart 1987, Resh *et al.* 1988, Lake 2000, Death 2008). During floods high shear forces suspend finer sediments (silt, sand), move bed materials (gravels, cobbles and boulders), and kill or displace stream biota (Lake 2000). Consequently, significant decreases in overall macroinvertebrate densities have been recorded after bed-moving floods (e.g. Grimm & Fisher 1989, Robinson *et al.* 2003, 2004). In addition, behavioural responses of invertebrates to changes in flow by actively entering the drift were observed (Hart & Finelli 1999, Holomuziki & Biggs 1999, Lancaster 1999).

Droughts, as another important type of disturbance in streams, have been greatly neglected by stream ecologists (Resh *et al.* 1988, Lake 2000), and thus the information on the ecology of droughts in flowing waters is both limited and scattered

(Lake 2003). However, it is clear in the meantime that droughts can have direct and indirect effects on stream biota. Decreases in discharge usually cause decreased water velocity, water depth, and wetted channel width, increased sedimentation, and changes in thermal regime and water chemistry (Dewson *et al.* 2007b). As a consequence, biota become stranded, are trapped without refugia in dried-up habitats or are threathened by deoxygenation (Lake 2003). Invertebrate abundance can increase or decrease in response to decreased flow, whereas invertebrate richness commonly decreases because habitat diversity decreases (Dewson *et al.* 2007a, 2007b). Although droughts can play a very important role in certain stream types and in certain areas of the world (e.g. Australia, Western USA, Africa), overall, floods are the most frequent and dominant disturbances in streams (Poff & Ward 1989, Poff 1996).

Recent research has shown that mid-sized floods may frequently cause a complex mosaic of small (≤ 1 m^2) stream bed patches that have experienced scour, sediment deposition (fill) or remained undisturbed during the flood (Matthaei *et al.* 1999, 2003). Following a flood, this 'local disturbance history' can have relatively long-lasting (up to three months) and temporally changing effects on the microdistribution of benthic organisms (Matthaei & Townsend 2000, Matthaei *et al.* 2003). For example, Matthaei *et al.* (2000) and Matthaei & Townsend (2000) found that, while stable surface stones acted as refugia for benthic invertebrates during a bed-moving flood, invertebrate densities were higher two months later in stream bed patches that had experienced sediment deposition or scour during the same flood. These long-term patterns are remarkable, because scoured, depositional, and stable bed patches were separated by just a few meters and the most common invertebrates in the investigated stream were highly mobile larvae of mayflies and black flies, which could have easily dispersed between the different patch types within a few days or less (Mackay 1992).

While clearly showing that disturbance history can affect benthic organisms, these early studies had certain limitations. For instance, invertebrates were sampled only once after a single flood by Matthaei & Townsend (2000), and neither physical habitat parameters nor invertebrate food resources were quantified. Consequently, these studies did not permit detailed assessments of temporal changes in the effects of disturbance history on the distributions of the benthic organisms, and they also did not quantify the association of benthic invertebrates with physical microhabitat parameters such as current speed and substratum size. Moreover, the mechanisms underlying the observed density patterns remained largely unclear, partly due to the correlative nature of these studies. Clearly, this research needed to be complemented by more detailed observations and by manipulative experiments.

In Chapters 1 and 2 of my thesis, I have started to address these two research needs. In Chapter 1, I investigated the short-term (less than a week) and long-term (up to five weeks) effects of natural floods on the small-scale distribution of stream invertebrates in two streams located in different hemispheres, one in Bavaria and the other in New Zealand. I sampled the invertebrate communities in patches that were scoured, experienced sediment deposition or remained stable during several natural floods. In contrast to earlier studies, I collected samples repeatedly over an extended period of time in order to document the temporal development of the community in response to small-scale bed disturbances. Furthermore, I simultaneously measured several abiotic and biotic habitat parameters that had been affected by bed movements during the floods. In the second study (Chapter 2), I took a closer look at the mechanisms that might be driving the longer-term effects of bed movements on the microdistribution of benthic invertebrates. To help identify these mechanisms I imitated some of the key consequences of a moderate bed-moving flood for stream habitats by experimentally creating a patchwork of scoured, filled and stable bed patches in a flood-prone Bavarian stream. Similar to the previous study (Chapter 1), I sampled the benthic invertebrate fauna repeatedly over an extended post-disturbance period and measured influential microhabitat parameters (current velocity, substratum size and particulate organic matter) that were likely to be affected by bed movement. I then related the local abundances of the most common invertebrate taxa to the three disturbance history treatments and the three measured habitat parameters.

Biotic interactions in benthic stream communities

The study of interspecific competition has long been one of ecology´s most intensely researched topics. Since the first formulations of competition theory (Lotka 1932, Volterra 1926, Gause 1934), a vast amount of data (mostly observational or from laboratory studies) have been collected on resource partitioning between different organisms. In a review using a simple “vote counting” technique, Schoener (1983) found that competition was seen by the authors to be of essential importance for the investigated ecosystem in 90% of 164 analyzed studies. By contrast, another review of experimental research by Connell (1983) revealed an important effect of competition only in about two-fifths of the 527 examined experiments, a much lower percentage. At this time, few studies had investigated competition among freshwater species, especially in running waters. About ten years later, a fair amount of evidence of resource and habitat partitioning among ecologically similar species in stream environments had accumulated. Nevertheless, competitive interactions between stream organisms have been documented convincingly in only a relatively small number of studies (Allan & Castillo 2008).

In those studies that found convincing evidence of competition, the structure of benthic communities was often strongly influenced by a dominant taxon through exploitative competition for a limiting resource (e.g. Hart 1987, McAuliffe 1984) and/or aggressive interference competition, in which individuals directly harmed or displaced one another (e.g. Hemphill & Cooper 1983, Hemphill 1988, 1991, Englund 1991, Kohler 1992). In addition to competition between different species, (exploitative) intraspecific competition has also been found in stream communities (e.g. Wiley 1981, Kohler 1985, Feminella & Resh 1990). Moreover, there is a growing awareness of the importance of non-competitive interactions among species, such as mutualism or commensalisms, as factors that may influence abundance and distribution patterns of organisms in stream communities (Englund & Evander 1999). For example, Feminella & Resh (1990) found indirect positive effects (mediated through algal food) of one caddisfly species on another.

The influence of predation on communities initially received less attention by ecologists than interspecific competition and was first reviewed by Sih *et al.* (1985). Their synthesis included 139 papers of the previous 20 years from five different ecosystems (intertidal: 34 studies, other marine: 24, lotic: 8, lentic: 31 and terrestrial: 42), with most studies stemming from the early 1980s. Although many experiments showed some lack of replication, the authors found significant effects of predation on different prey species in 95% of all experimental field studies, and the great majority of these studies even showed some strong effects of predation. At this time, the importance of predation in streams had still been largely unknown. In streams, some of the first experimental studies of predator impacts did not detect significant effects on prey (Reice 1983, Flecker & Allan 1984, Culp 1986). However, other experiments found negative effects of predation on prey population sizes via direct consumption (e.g. Peckarsky & Dodson 1980, Lancaster 1990, Woodward & Hildrew 2002) or predator-induced changes in prey behaviour (e.g. Hildrew *et al.* 1984, Peckarsky 1985, Holomuzki & Hoyle 1990, Bechara *et al.* 1993).

Several authors explained these contrasting results by a “swamping” effect of prey exchange, meaning that rapid prey immigration into a patch can overwhelm local predator impacts (e.g. Peckarsky 1985, Lancaster *et al.* 1990, 1991, Cooper *et al.* 1990). Encounters with predators, their chemical or hydrodynamic cues (see Scrimgeour *et al.* 1994) often also result in changes of prey drift density or periodicity, regardless if the predator is a large invertebrate (e.g. Peckarsky 1980, Lancaster 1990, Sih & Wooster 1995) or a fish (e.g. McIntosh & Townsend 1994, McIntosh *et al.* 1999, 2002). In the first such meta-analysis of stream data, Wooster (1994) found a consistent, significant negative effect of predators on the density of their prey, with invertebrate predators (mainly stoneflies) having a significantly stronger impact than vertebrate predators (mainly fish). Both patterns were confirmed in another review by Sih & Wooster (1995). The second finding is somewhat surprising at first sight, because fish appear to be much more voracious predators than stoneflies. Sih & Wooster argued that this pattern may be partly explained by different prey emigration responses (increased prey emigration in the presence of vertebrate predators but reduced prey activity in the presence of invertebrate predators).

A number of studies (e.g. Oberndorfer *et al.* 1984, Power *et al.* 1985, Power 1990, 1992, Short & Holomuzki 1992) have shown that predators in streams may not only influence their immediate prey populations, but that predation-induced effects can cascade through the entire food web to alter primary production or leaf litter breakdown. For example, Dahl (1998) described a cascading effect of predatory trout and leeches on periphyton biomass, whereas Oberndorfer *et al.* (1984) found a similar cascading effect of predatory invertebrates on leaf litter breakdown. Interestingly, such trophic cascades do not have to be the consequence of direct consumption of herbivores by predators. In several studies (e.g. McIntosh & Townsend 1996, Peckarsky & McIntosh 1998, Diehl *et al.* 2000), changes in the biomass of primary producers could be at least partly attributed to effects of predators on prey behaviour (e.g. reduced grazing activity and/or increased emigration rates from the experimental units).

Relative importance of disturbance and biotic interactions in structuring living communities

On the whole, streams and rivers provide a highly changeable and often harsh environment characterized by variable flows and frequent disturbances by bed moving floods (Poff & Ward 1989, Poff 1996). This fact had led a number of leading stream ecologists to argue that abiotic factors, and especially physical disturbance by floods, have pre-eminence as structuring forces of communities in running waters (e.g. Resh *et al.* 1988, Townsend 1989, Lake 2000, Death 2008). Hence, the relative importance of competition or predation as a driver of community structure should be inversely related to the level of stress or disturbance (e.g. Grime 1974, Huston 1979), in this case the frequency and/or intensity of bed-moving floods (see Poff 1992). On the other hand, some ecologists have argued that the level of competition in a community should be independent of stress or disturbance and that the intensity of competition is mainly determined by how close the community is to the carrying capacity (e.g. Tilmann 1982, Taylor *et al.* 1990). How the interaction between abiotic and biotic forces influences ecological communities has been formulated into several similar, but subtly different, conceptual frameworks. These include the intermediate disturbance hypothesis (Connell 1978, Yodzis 1986), the dynamic equilibrium model (Huston 1979), the harsh-benign-hypothesis (Menge 1976, Peckarsky 1983), environmental stress models (Menge & Olson 1990), the habitat templet model (Southwood 1977, 1988) and the patch dynamics concept (Clements 1916, Pickett & White 1985, Sousa 1985, Townsend 1989). I will summarise the most widely discussed and tested of these concepts in the following paragraphs.

The intermediate disturbance hypothesis (Connell 1978) presumes a competitive hierarchy of species. In the absence of disturbance, superior competitors will eliminate inferior ones. If disturbances are too frequent and/or too intense, the resident competitors will be eliminated. Finally, under an intermediate disturbance regime both types of competitors will persist, resulting in maximum species richness. According to Wootton (1998), basal species in food webs are likely to follow the intermediate disturbance hypothesis, whereas top consumers are not. Hence, this hypothesis should be applied with caution to real multi-trophic communities, because in many situations disturbance either had no effect on coexistence or caused a monotonic decline in diversity (e.g. Resh *et al.* 1988, Lake *et al.* 1989, Death & Winterbourn 1995, Collins *et al.* 1995, Mackey & Currie 2001, Death 2002). Likewise, Ohsawa *et al.* (2003) found in a model simulation that there was no general tendency for species diversity to peak at an intermediate disturbance frequency and concluded that differences in species interactions (intraspecific versus interspecific) in local populations dynamics affected diversity in addition to disturbance. Nevertheless, Townsend *et al.* (1997a) surveyed 54 stream sites and found that bed disturbance accounted for the largest proportion of variation in invertebrate taxonomic richness. Further, both mobile and sedentary invertebrate taxa showed the predicted bell-shaped curve. In a review of 250 studies testing the intermediate disturbance hypothesis, Shea *et al.* (2004) found several studies (17 observational, 16 experimental, 12 theoretical) from a huge range of community types (from aquatic to terrestrial) at scales ranging from microcosms to the entire landscape that showed the expected hump-shaped relationship between diversity and disturbance.

In the dynamic equilibrium model, Huston (1979, 1994) offered a broader range of predictions than the classic intermediate disturbance hypothesis and regarded community structure as the result of a trade-off between growth rates, rates of competitive exclusion, and frequency of population reductions. He argued that diversity is determined not as much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of species interactions. Consequently, diversity can peak at low, high, or intermediate levels of disturbance. The applicability of this model to streams has found some support in two review articles (Resh *et al.* 1988, Reice *et al.* 1990) and one experimental study (McCabe & Gotelli 2000; but see also Lake 1990).

The harsh-benign-hypothesis (Connell 1975, Menge 1976, Peckarsky 1983), which was initially developed for marine intertidal communities, proposes that predation is the principal process organizing community structure in physically benign environments. As the environment becomes harsher, the abundance and/or efficiency of predators is reduced and competition among prey species becomes more important as their densities increase. In extreme environmental conditions, biotic processes become relatively unimportant and abiotic factors shape communities.

According to environmental stress models (Menge & Olson 1990) the outcome of consumer-prey interactions is dependent on the relative tolerance of consumers and prey to abiotic conditions. Thus, either the importance of predation decreases with increasing environmental stress (consumer stress models; see Hairston *et al.* 1960, Connell 1975, Menge & Sutherland 1976, 1987, Peckarsky 1983) or prey will be more adversely affected and consequently predator impacts will increase in disturbed habitats (prey stress models; see Menge & Olsen 1990, Chesson & Huntly 1997). According to consumer stress models, diversity in harsh environments is low because of the intolerance of most species to such conditions. With increasing environmental moderation, diversity is expected to be affected by a number of processes that cause it to change in contrasting directions as the environment becomes more and more benign. Along this gradient of environmental moderation, diversity should first increase because of the intermediate-disturbance effect, then decrease because of the competitive-exclusion effect, increase again because of the prevention of competitive exclusion by moderate predation, and finally decrease once more because of the local extinction of prey by severe predation. Further, mobile organisms should be more strongly affected by environmental stress than sessile (Menge & Sutherland 1987). This generalization assumes that stress reduces average predation rates per prey more than it reduces average growth rates of the prey population, which could possibly be true for most stream systems. Here, predators are usually larger and thus more susceptible to flood disturbances, because they offer more resistance to the current and cannot take shelter in the small interstitial spaces inside the stream bed..

The habitat templet model (Southwood 1977, 1988) defines a habitat along two axes regarding stability and productivity. The long-term regime of natural environmental heterogeneity and disturbance may be considered to establish a physical habitat template that influences which combinations of behavioural, physiological and life history characteristics constitute appropriate ecological strategies for local persistence. Thus spatial and temporal characteristics of the physical environment may predetermine the range of ecological response mechanisms available following natural and anthropogenic disturbances. The model was also applied to stream algae and invertebrates and its predictions were generally supported (e.g. Scarsbrook & Townsend 1993, Townsend & Hildrew 1994, Biggs 1995, Townsend *et al*. 1997b).

The patch dynamics concept views communities as an aggregation of patches with identical environmental conditions and identical ressource availability, which are randomly colonized by individuals of different species (Clements 1916, Pickett & White 1985, Sousa 1985, Townsend 1989). These communities are usually open systems – with dispersal between patches and varying dynamics within patches - and a combination of patchiness and movement between patches can give rise to community dynamics quite different from those that would be observed if there was just one, homogeneous patch. Disturbance plays a fundamental role in the patch dynamics concept because it creates open space and causes changes with time (Pickett & White 1985). Frid & Townsend (1989) and Townsend (1989) argued that the patch dynamics perspective was well suited for the explanation of processes and patterns in lotic ecosystems. In contrast, Downes (1990) contended that, while stream studies could benefit from examining patch dynamics models in a general way, most of these models were constructed primarily for sessile communities and were therefore unsuitable for mobile stream animals. Nevertheless, the evidence from recent studies that tested the applicability of the patch dynamics concept to running waters (Matthaei & Townsend 2000, Matthaei *et al.* 2003) suggests that this concept can be applied to lotic communities in spite of the dominance of mobile animal species in these communities.

Theoretical and empirical studies suggest that the trajectory of community recovery after a flood depends on the severity of the disturbance, the productivity of the system, and the intensity of biotic interactions during the recovery phase (Power 1992, Nisbet *et al.* 1997, Marks *et al.* 2000, Roll *et al.* 2005). This view is supported by work in other systems exposed to periodic disturbances, such as rocky intertidal communities (Lubchenco 1983, Menge & Sutherland 1987, Worm *et al.* 2002) and temporarily drying pond systems (Wellborn *et al.* 1996, Kneitel & Chase 2004). Furthermore, in all of these systems, the possibility of alternative states (depending on initial conditions immediately after the disturbance) has been discussed. For example, it has been suggested for benthic primary producers in streams that succession after disturbance may lead to dominance of either microalgae (most of which are permanently vulnerable to invertebrate grazing) or filamentous algae and macrophytes (which are which tend to be vulnerable to grazing only during early developmental stages) depending on the initial density of grazers (Power 1992, Lotze *et al.* 2000, Chase 2003a, 2003b, Roll *et al.* 2005).

It is useful to point out conceptual similarities between disturbance and predation/grazing (Chesson & Huntly 1997, Chase *et al.* 2002). From the perspective of the victims, all of these processes cause increased mortality. Within patches of sessile organisms, predation/grazing by mobile consumers may furthermore come as an almost discrete 'disturbance' event between periods of undisturbed growth. Both disturbance and consumption are rarely unselective, because victims vary in their susceptibility to both processes. Defenses that are effective against predators may frequently not be effective against abiotic disturbance and vice versa, and may furthermore come at the cost of reduced competitive ability. Because of the potential for such a 3-way trade off, the interaction among disturbance, predation and competition is likely to be complex. Attempts to integrate these processes into a common framework have only recently begun, but promise to yield deeper insights into the mechanisms that regulate population abundance and community composition (Worm *et al.* 2002, Chase *et al.* 2002, Chase 2003a, Kneitel & Chase 2004, Sih *et al.* 2004).

Disturbance versus biotic interactions in running waters

Even though most streams and rivers are subject to considerable discharge variations and frequent flooding (Poff & Ward 1989, Poff 1996), most of the field experiments investigating biotic interactions in running waters have been performed either in systems with relatively stable flow (e.g. lake outlet streams or small streams in low-gradient catchments with moderate rainfall; McAuliffe 1984, Kohler 1992, Lancaster 1996, Kohler & Wiley 1997), in periodically disturbed systems during periods of stable flow (Hemphill & Cooper 1983, Hemphill 1991), or in experimental stream channels (e.g. Flecker & Townsend 1994, McIntosh & Townsend 1996, Diehl *et al.* 2000, Thomson *et al.* 2002). While biotic interactions are likely to be important in stable streams, Poff & Ward (1989) and Townsend (1989) predicted that their importance should decrease with increasing frequency or intensity of disturbance. This prediction for running waters was in agreement with the more general ones of the habitat templet model (Southwood 1977, 1988), the harsh-benign-hypothesis (Connell 1975, Menge 1976, Peckarsky 1983) and the consumer stress models (Hairston et al. 1960, Menge & Sutherland 1976, 1987) mentioned in the previous section of my Introduction. On the other hand, Chesson & Huntly (1997) argued that biotic interactions may still play an important role in frequently disturbed ecosystems, because a relatively minor stress caused by competition or predation could be enough to "push over the edge" a population already weakened by abiotic disturbance. Finally, according to predictions of the prey stress models (Menge & Olsen 1990, Chesson & Huntly 1997), biotic interactions might even become more important in frequently disturbed ecosystems.

As pointed out above, this wealth of existing ecological theory contrasts sharply with a limited amount of empirical data from running water ecosystems, especially from frequently disturbed streams and rivers. Manipulative experiments in such systems are particularly rare. To help close this knowledge gap, I conducted three experiments that examined the interactive effects of physical disturbance and interspecific competition (Chapters 3 and 4) or disturbance and predation (Chapter 5) on benthic stream invertebrates and algae. In Chapter 3, I created a patchwork of scoured, depositional and stable bed patches (see Chapter 2) and manipulated competition among invertebrates, by twice-weekly manual removal of the most common invertebrate taxon, in a flood-prone Bavarian stream. Benthic invertebrates on surface substrata were sampled repeatedly over a 50-day period after disturbance. In the next step (Chapter 4), I examined the interactive effects of a repeated abiotic disturbance (every two weeks; three times in total) and removal of the two most common invertebrate taxa on the remaining invertebrate fauna in two Bavarian streams with contrasting flow regimes. Here the disturbance manipulation consisted of repeated scrubbing and stirring of the stream bed and the sampling substrata, and invertebrates and algae were sampled two weeks after each disturbance. In my final experiment (Chapter 5), I used electrified exclusion devices to remove fish predators from stream bed patches with contrasting, experimentally created disturbance histories (scour, fill, and stable patches). In this experiment, benthic invertebrates and algae were sampled repeatedly until 57 days after the disturbance. The section "Conclusions, limitations and research outlook" at the end of my thesis provides a concluding discussion and an outlook on possible future research directions. In this section, the findings of my main experiments are compared, focusing on identifying general patterns and on how my research could form the basis of related future studies.

1

LOCAL DISTURBANCE HISTORY AND HABITAT PARAMETERS INFLUENCE THE MICRODISTRIBUTION OF STREAM INVERTEBRATES

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Local disturbance history and habitat parameters influence the microdistribution of stream invertebrates

Michael Effenberger[1], Gabriele Sailer[1],
Colin R. Townsend[2] & Christoph D. Matthaei[1,2]

[1]Department Biology II, Aquatic Ecology, University of Munich (LMU),
Großhaderner Straße 2, 82152 Planegg-Martinsried, Germany

[2]Department of Zoology, University of Otago, P.O. Box 56,
Dunedin, New Zealand

Corresponding author
E-mail: effenberger@zi.biologie.uni-muenchen.de
Fax: 0049-89-2180-74211

Abstract

We investigated the effects of local disturbance history and habitat parameters (abiotic and biotic) on the microdistribution of benthic invertebrates during several floods in two streams, the Schmiedlaine in Germany (four events) and the Kye Burn in New Zealand (two events). Bed movement patterns were quantified using metal-link scour chains. Before and after each flood, quantitative invertebrate samples were taken from replicate bed patches that had experienced sediment scour, fill or remained stable. Patterns of invertebrate density in the different bed stability types (i.e. scour, fill, stable) varied between floods, sampling dates and streams, but invertebrate density was highest in stable patches in >50% of all detected patch type effects and lowest in fill patches in 75% of all detected effects. Stable bed patches acted as a refugium for *Liponeura* spp. and *Leuctra* spp. in the Schmiedlaine and for Hydracarina and *Deleatidium* spp. in the Kye Burn. Averaged across both streams, only near-bed current velocity was correlated with invertebrate distribution on the stream bed more often than disturbance history. In the Kye Burn, disturbance history and water depth were the most influential habitat parameters. Our results suggest that a thorough understanding of the microdistribution of benthic invertebrates requires knowledge of disturbance history, as well as more readily measured habitat parameters such as current velocity or water depth.

Keywords: disturbance, patch dynamics, streams, microhabitat, macroinvertebrates

Introduction

The patch dynamics concept, which pervades most fields of ecology, views ecosystems as dynamic in four dimensions: the three spatial dimensions and time (Minshall 1988, Ward 1989). Disturbance plays a fundamental role in the patch dynamics concept because it creates open space and causes changes with time (Pickett & White 1985). Frid & Townsend (1989) and Townsend (1989) argued that the patch dynamics perspective was well suited for the explanation of processes and patterns in lotic ecosystems. In contrast, Downes (1990) contended that, while stream studies could benefit from examining patch dynamics models in a general way, most of these models were constructed primarily for sessile communities and were therefore unsuitable for mobile stream animals.

It is well known that the microdistributions of both benthic macroinvertebrates and algae in streams are correlated with abiotic factors, including near-bottom current velocity or shear stress, water depth and substratum grain size, and with biotic factors such as predation, competition and food (see e.g. Ulfstrand 1967, Hearnden & Pearson 1991, Kohler 1992, Holomuzki & Messier 1993, Stevenson 1996, Biggs *et al.* 1998). By contrast, the importance of hydrological disturbance in generating patchy distributions of stream biota has received less attention and rigorous research in this area began only fairly recently, especially on benthic invertebrates (e.g. Palmer *et al.* 1992, Lancaster & Hildrew 1993, Robertson *et al.* 1995, Palmer *et al.* 1996, Winterbottom *et al.* 1997). To address this deficiency further, Matthaei *et al.* (1999a) used arrays of buried, metal-link scour chains to investigate the three-dimensional disturbance history of the bed in the Kye Burn, a New Zealand stream, and found that most spates and floods caused a complex mosaic of small (≤ 1 m^2) bed patches that had experienced scour (sediment removal), fill (sediment deposition) or remained stable (≤ 1 cm change in sediment depth). This “local disturbance history” (the specific stability or instability of bed patches during high-flow events) had long-term effects on the microdistribution of invertebrates, with higher densities in fill or scour patches 2 months after a disturbance (Matthaei & Townsend 2000), even though a large proportion of invertebrates in the Kye Burn is highly mobile (Mackay 1992) and could have easily dispersed between the different patch types, which were separated by only a few metres, within a few days or less. The effect of disturbance history on these mobile stream animals contrasts with the expectations of Downes (1990) and suggests that patch dynamics models may be appropriate for many streams. Matthaei *et al.* (2003) also found a strong influence of disturbance history on algal distribution in a German river, with highest densities in stable bed patches six days after, and in scour patches four weeks after, one flood. In fill patches, however, greatest density was achieved three months after another flood.

While clearly showing that disturbance history can affect benthic organisms, these early studies had certain limitations. For instance, invertebrates were sampled only once after a single spate by Matthaei & Townsend (2000), and neither physical habitat parameters nor invertebrate food resources were quantified. In Matthaei *et al.* (2003), algae were collected at lengthy intervals (up to two months) and only a few habitat parameters were measured. Consequently, these studies did not permit detailed assessments of temporal changes in the effects of disturbance history or the relative contributions of history and other habitat parameters in determining the distributions of the benthic organisms. Thus, our objectives were to investigate for stream invertebates (1) short-term effects (2-7 days after disturbance) and longer-term effects (3-5 weeks after) of disturbance history on the microdistributions of the invertebrates, (2) the relative contributions of disturbance history, physical habitat parameters and food resources to invertebrate distribution, (3) effects of disturbance history on the habitat parameters themselves (which could lead to indirect effects of disturbance history on invertebrate distribution, see below).

Based on the results of our previous research (see above), we expected local disturbance history to play an important role for invertebrate distribution. While stable patches should act as refugia for invertebrates during the floods, invertebrate density may become highest in scour or fill patches with increasing time since disturbance. One of the reasons for such long-term differences in densities between patch history types could be indirect effects of disturbance history on physical habitat parameters and food resources of benthic organisms.

Methods

Study sites

We conducted the study in two streams, the Schmiedlaine in southern Germany (47°40´N, 11°28´E) and the Kye Burn in New Zealand (in the Otago province of the South Island; 45°58´S, 170°18´E), and selected a single reach of about 40 m length in each stream.

The studied reach of the Schmiedlaine runs through a narrow, v-shaped valley and has a steep, mostly forested catchment (750-1800 m a.s.l.) in a high rainfall zone at the northern edge of the Alps (annual rainfall 1500-2150 mm; Felix *et al.* 1988). Floods occur frequently and are often quite severe (Ergenzinger & de Jong 1997, Matthaei & Huber 2002). Mean flow at the study reach is about 0.54 m^3 s^{-1} and baseflow about 0.12 m^3 s^{-1} (Wagner 1987). The stream bed consists mainly of cobbles (particles with a b-diameter width of 64-256 mm) interspersed with boulders (256-1024 mm).

The studied reach of the Kye Burn is located in a small, steep canyon and the relief is less steep than that of the Schmiedlaine catchment. Annual rainfall in the tussock grassland catchment (600-1600 m a.s.l.) is 600-1000 mm (Otago Catchment Board 1983), The Kye Burn has a more moderate flow regime (in terms of frequency and severity of floods; Matthaei *et al.* 1999a, 1999b) than the Schmiedlaine. Mean flow is 1.1 m^3 s^{-1} and baseflow about 0.4 m^3 s^{-1} (National Institute of Water and Atmospheric Research, Dunedin). The stream bed consists mainly of cobbles and gravels (2-64 mm). Both streams are 5-10 m wide at baseflow, and their flow regimes and stream channels are natural. Water temperature is low, <13°C in summer in the Schmiedlaine and <15°C in the Kye Burn (G. Sailer, unpublished data). Both systems are nutrient-poor (Water Management Authority Weilheim, unpublished data; Niyogi *et al.* 2003). Sediment supply to the two streams is high because of several steep, unstable scree slopes, resulting in unstable stream beds that are easily moved by floods.

Quantification of bed movement

Bed movement was quantified in each stream using metal-link scour chains (for details of the method see Matthaei *et al.* 1999a). Chains (each 0.5 m long) were installed vertically in the bed (using a hollow steel standpipe and a metal fencepost driver), with only the top one or two chain links exposed. Scour during a flood exposes additional links, whereas fill can be measured by the thickness of the sediment layer deposited on top of the originally exposed links. The chains can also detect and quantify scour-before-fill, when a bed patch is scoured during some stage of a flood (exposing some links that come to lie horizontally), but where this is followed by sediment deposition during a later stage of the same event, so the net result is fill or no change. However, this type of bed disturbance occurred extremely rarely in our previous research (Matthaei *et al*. 1999a).

From 26 April to 5 May 2001, we installed 200 chains in a systematic grid in the Schmiedlaine. Three to six chains were buried across each of 40 transects, with ~1 m between chains and transects. Most transects contained five chains. The exact horizontal location of each chain in the stream bed was determined by measuring distances to three pairs of permanently-marked points on the stream banks situated at least 1.5 m above the water line (at base flow). All chains were equipped with magnetic tracers (Ergenzinger & Conrady 1982) to facilitate re-location after floods using a magnetic locator (model GA-52B, Schonstedt, Virginia, USA). In addition, we used a theodolite (Tachymeter SET 3, Sokkisha/SOKKIA, Tokio; levelling unit Ni 2, Zeiss, Jena, Germany) to measure the positions of all chains relative to another permanently marked point on the true left bank (2 m above the water line at base flow) on 16 May. These measurements ensured that, in case of large floods, we could determine the net change for chain locations experiencing substantial fill, without disturbing the stream bed by digging for deeply buried chains. Theodolite measurements were repeated on 26 July, five weeks after a large flood in late June (Table 1), and on 16 October, after taking our last set of biological samples.

In the Kye Burn, we installed 208 chains (as described above) from 7 to 9 November 2001 (Austral spring). We did not equip these chains with magnetic tracers or conduct theodolite measurements because previous work indicated that relocation would not require these measures (Matthaei *et al*. 1999a, Matthaei & Townsend 2000).

Studied floods and biological sampling

Schmiedlaine. We investigated all bed-moving floods (events causing enough bed movement to be detected with our scour chains) that occurred during a six-month period in each stream. In the flood-prone Schmiedlaine, we studied four floods. Whenever possible, samples were taken before and three times after each flood (for exact dates see Table 1). Each sampled bed patch was sampled only once during each pre- or post-flood sampling series.

On each post-flood sampling date, five samples were collected randomly from patches that in relation to an adjacent scour chain, had experienced □5 cm of scour, five from patches that had experienced □5 cm of fill, and five from stable patches (≤1 cm change). In each bed patch, a Surber sample (25 cm × 25 cm, 200µm mesh size) was taken as near as possible to the focal chain (either one side of the sampler frame touched the chain or the chain was entirely inside the area covered by the sampler). A marked screwdriver fixed a sampling depth of 10 cm. The criterion of □5 cm change in the disturbed bed patches was chosen to ensure that at least half the sampled invertebrate habitat had been affected by the floods. Samples were preserved with 70% ethanol in the field. Invertebrates in all 245 samples (Schmiedlaine 167, Kye Burn 78) were sorted, identified to the lowest practical taxonomic level and counted using a stereomicroscope (WILD, Heerbrugg, Germany; magnification 6.5–40×).

A parallel study (G. Sailer, unpublished data) investigated epilithic algal biomass and total density of epilithic bacteria, which were used as additional covariates in this study. These two parameters were determined from a single stone chosen at random from the surface stones in the area framed by the Surber sampler. All invertebrates on this stone were washed off gently into the sampler. Epilithic bacteria and algae were sampled by scraping the entire surface area of each stone with a tooth brush with shortened bristles. Samples were preserved immediately with formaldehyde solution (final concentration 4%) and stored on ice in the dark (G. Sailer, unpublished data). Epilithic algal biomass was determined as chlorophyll a, and total density of epilithic bacteria was estimated using epifluorescence microscopy. The surface area of each stone was determined by wrapping it in aluminium foil and weighing the foil (Townsend *et al.* 1997), and algal biomass and bacterial counts were converted to values per cm^2 of stone surface area.

For each sample, we measured water depth and near-bed current velocity with a Hoentzsch flow meter (Waiblingen, Germany; propeller diameter 2 cm). We also determined substratum composition by eye as the averaged particle widths of the first- to third-most common substratum grain size classes inside the Surber sampler. These size classes were identified using a modified Wentworth scale (Harrelson et *al.* 1994) with a half-phi scale (e.g. 16-22 mm, 22-32 mm etc.). All particles smaller than 8 mm were combined as a single category. Depth, current velocity and substratum composition were used as covariates in the analyses.

Sampling started on 9 May 2001, four days after completing chain installation. Chain installation causes little damage to the sediment structure within the stream bed (Matthaei *et al*. 1999a), and vibrations during insertion were comparable to those caused by installing metal standpipes when taking freeze core samples of the hyporheic fauna (Fraser & Williams 1997). Because invertebrate disturbance due to standpipe installation lasted <2 days during a freeze core study in the Kye Burn (Olsen *et al.* 2002), we expected invertebrates to recover quickly from the disturbance caused by chain installation.

On 9 and 15 May, we collected eight random pre-flood samples in our study reach, because we did not know the local disturbance history patterns caused by the previous (unstudied) flood. In the evening and night of 15 May, a brief spate with moderate peak flow caused a patchy mosaic of disturbance history categories in our study reach (Event 1; Tables 1 & 2). Post-flood sampling started seven days after Event 1 and continued another 14 days later on 5 June, when we took five random samples in addition to samples from fill and stable patches because no patches with □5 cm of scour were left. Five days later, another moderate spate happened (Event 2; Tables 1 & 2).

Event 3, the largest flood recorded during our field work in the Schmiedlaine, occurred seven days later (Tables 1 & 2). For Event 3, we conducted a complete series of one pre- and three post-flood sampling dates. Between the second and third post-flood dates, a minor spate on 20-21 July (peak flow 6 m^3 s^{-1}) caused shallow scour or fill at a few chain locations, which we carefully avoided on the third sampling date.

After completing the post-flood series for Event 3, we ran out of stable bed patches to sample. Therefore, we took random samples on 14 and 30 August. On 5-

6 and 8-9 September, a sizeable flood with two flow peaks occurred (Table 1). Post-flood sampling started two days after Event 4 and continued on 26 September. Another brief flow peak of 6.5 $m^3 s^{-1}$ occurred on 15 September, but data from 30 randomly chosen chains measured on 26 September showed that this flood caused little bed movement. On 9 October, we completed a second series of two pre- and three post-flood sampling dates.

Kye Burn. A moderate spate occurred on 5-6 December 2001, about four weeks after chain installation (Tables 1 & 2). Before Event 1, we had taken two weekly sets of random pre-flood samples. After the event, we collected two sets of post-flood samples.

On the day we intended to take our next set of samples, a major flood (return period ≈5 years) began that lasted from 9-21 January 2002 and had four distinct flow peaks (Table 2). Because we expected invertebrate recovery to be slow after this flood, we monitored recovery by taking four sets of eight random post-flood samples from fill patches (Table 1). No further bed-moving floods occurred until the end of this second sampling series.

Data analysis

To determine the overall initial effect of each flood on invertebrate density, taxon richness and densities of the most common invertebrate taxa (10 in the Schmiedlaine, and nine in the Kye Burn), we compared each respective pre-flood sampling date with each first post-flood date, using one-way ANOVAs. For this analysis, all three disturbance history categories for the first post-flood date were combined. Comparisons between disturbance history categories were conducted using one-way ANOVAs and one-way analysis of covariance (ANCOVA), with “disturbance history type” as factor and the five habitat parameters as covariates. Exploratory correlation matrices for both streams (all samples combined in each stream) revealed that the five covariates were correlated weakly with each other (r_p-values < 0.40 in all cases).

Direct effects of disturbance history on habitat parameters themselves were also assessed using one-way ANOVAs. After exploratory analysis, data were log-transformed where necessary to improve normality and homoscedasticity. Based on our previous results for stream invertebrates (Matthaei *et al.* 2000, Matthaei & Townsend 2000), we expected the effects of disturbance history to change with time since the last previous flood. Consequently, we analysed each history-specific sampling date separately (nine in the Schmiedlaine, and two in the Kye Burn). We also calculated separate ANCOVAs for each covariate to avoid collinearity problems (Quinn & Keough 2002, Matthaei *et al.* 2003). If a significant factor × covariate interaction was found, we verified the reliability of the estimated marginal means for each patch type using the technique described in Matthaei & Huber (2002). This test was performed by determining the actual adjusted means for each patch type (using the three individual regression lines of the dependent variable against the covariate). These adjusted means were compared with the estimated marginal means calculated by the ANCOVA (which uses a single regression line, the slope of which is calculated using the combined data for the covariate from all three patch types). Reliability was then expressed as the percentage difference between the patch-type-specific means and those calculated by the ANCOVA.

Only covariates with significant effects on the dependent variable are discussed, and an effect of disturbance history was only considered valid if it was detected in at least 50% of all ANCOVAs with significant covariate effects. In cases where no covariate had a significant effect, all covariates were dropped from the analysis and a simple one-way ANOVA was calculated.

The type-I error rate of the main analysis was controlled for each sampling date, dependent variable and covariate. Because each analysis represented a separate hypothesis, there was no need to adjust α for multiple testing (Perneger 1998, Quinn & Keough 2002). Due to the relatively small number of replicates on dates with disturbance-history-specific sampling ($n = 5$) compared to our earlier studies (Matthaei *et al.* 2000, Matthaei & Townsend 2000; $n = 8$-15), we set α at 0.1 in all patch-specific analyses. This deviation from the conventional significance level of 0.05 follows the recommendation of Fisher (1956) that fixed significance levels are too restrictive and that a researcher's chosen significance level should depend on the specific circumstances (see also Quinn & Keough 2002). Comparisons between sampling dates (in which all samples collected on each date were combined) were conducted with α set at 0.05.

If the main effects of the analysis were significant, we conducted pairwise comparisons with *post-hoc* tests. For the ANCOVAs, these were *t*-tests on estimated marginal means (adjusted with the Sidak procedure; Day & Quinn 1989). With the ANOVAs, we used Tukey-HSD tests, except in cases of persisting heteroscedasticity, where we performed Games-Howell tests (Quinn & Keough 2002). In a few cases, more than one analysis (ANOVAs and/or ANCOVAs) produced significant results for a dependent variable and rankings of post-hoc tests differed between these analyses (see Tables 3 & 5 below). Here we selected the ranking that had been determined in the majority of these tests. All analyses were performed using SPSS® version 11.0 (SPSS Inc., Chicago).

Results

Initial impact of the floods on the invertebrates

In the Schmiedlaine, only Events 3 and 4 reduced total invertebrate density and taxon richness ($P \leq 0.02$). Densities of seven of the ten common taxa decreased after both (*Baetis alpinus* Pictet) or one of these floods (Event 3: Chironomidae and *Thienemanniella/ Corynoneura* spp.; Event 4: *Simulium* spp., *Leuctra* spp., *Rhithrogena* spp. and *Protonemura* spp.; $P \leq 0.03$).

In the Kye Burn, both floods reduced total invertebrate density ($P = 0.05$ and $P < 0.001$, respectively), whereas taxon richness decreased only after Event 2 ($P < 0.001$). While invertebrate density recovered to pre-flood levels within 3 weeks of Event 1 ($P = 0.74$), it remained low six weeks after Event 2 ($P = 0.02$). The density of *Deleatidium* spp. decreased after both events ($P \leq 0.001$), and that of another six common taxa decreased after Event 2 (*Pseudotryssaturus* spp., Hydracarina, Chironomidae, Oligochaeta, *Hydora* spp. and *Eriopterini* spp.; $P \leq 0.04$).

Summary of effects of disturbance history and habitat parameter on invertebrates

In the Schmiedlaine, we analysed disturbance-history-specific patterns of total invertebrate density, taxon richness and densities of the ten most common taxa for all nine post-flood sampling dates (note that *Liponeura* spp. was only recorded on six and *Protonemura* spp. on eight dates). Hence, a total of 104 cases was analysed for each of the five covariates. Near-bed current velocity was related to invertebrate distributions most often (in 31% of all analysed cases), followed by substratum grain size (25%), local disturbance history (20%), epilithic algal biomass (17%), water depth (15%) and total epilithic bacteria (11%). In the Kye Burn, 22 analyses of patch-specific patterns of invertebrate density and richness were possible only after Event 1. The most influential parameters were disturbance history and water depth (both 36% of all cases), followed by near-bed velocity (32%), algal biomass (27%), substratum grain size (5%) and epilithic bacteria (0%).

Patch effects of disturbance history and habitat parameters

Schmiedlaine. The majority of all differences in density or richness between patch types (57%) occurred 5 weeks after the two largest floods (on 24 July and 9 October). Invertebrate taxon richness was higher in scour than fill patches on 13 June, and higher in scour and stable than in fill patches on 25 June and 24 July. Total invertebrate density was also higher in scour and stable than in fill patches on 24 July (Fig. 1; Table 3). Total density and taxon richness were correlated with most covariates (except for water depth and/or epilithic bacteria) on at least one sampling date each (Table 4).

Densities of the stonefly *Leuctra* spp. and the black fly *Simulium* spp. (Fig. 1) each differed between bed stability types on three of the nine sampling dates. *Leuctra* spp. was more abundant in scour and stable than in fill patches on 13 June, in stable than in scour patches on 11 September, and in fill than in stable patches on 9 October (Table 3). *Simulium* spp. was more common in stable than in fill patches on 11 July, in scour and stable patches than in fill patches on 24 July, and in fill than in scour patches on 9 October. *Leuctra* spp. density was correlated with near-bed velocity, substratum grain size and epilithic bacteria, and *Simulium* spp. density by all covariates, on at least one sampling date each (Table 4).

Densities of the dipterans *Liponeura* spp., *Thienemanniella/ Corynoneura* spp., Chironomidae (excluding *Thienemanniella/ Corynoneura* spp. and Tanypodinae) and *Dicranota* spp. (Fig. 2) differed between bed stability types on two sampling dates each. *Liponeura* spp. was more abundant in stable than in fill patches on 25 June and on 24 July (Table 3). *Thienemanniella/ Corynoneura* spp. was more abundant in scour than in stable patches on 24 July and in stable than in fill patches on 26 September (Table 3). Density of Chironomidae was higher in scour and stable than in fill patches on 24 July, and higher in fill than the other patch types on 9 October (Table 3). *Dicranota* spp. density was higher in fill than in stable patches on 5 June, but lowest in fill patches on 9 October (Table 3). All four taxa were related to all covariates on at least one sampling date (Table 4).

Densities of the mayflies *Rhithrogena* spp. and *Baetis alpinus* and the stonefly *Chloroperla* spp. (Fig. 3) differed between bed stability types on one sampling date each. *Rhithrogena* spp. was more common in stable than in fill patches on 24 July, *B. alpinus* in stable than in scour or fill patches on 26 September, and *Chloroperla* spp.

in scour than in fill or stable patches on 9 October. Densities of the two mayflies were correlated with most of the covariates (except for epilithic bacteria and/or algal biomass), and *Chloroperla* spp. density with all covariates, on at least one sampling date each (Table 4).

The stonefly *Protonemura* spp. (Fig. 3) was equally abundant across bed stability types on all sampling dates. *Protonemura* spp. density was related to substratum grain size, epilithic bacteria and algal biomass on at least one date each (Table 4).

Kye Burn. The majority of all differences in density or richness between patch types (63%) occurred 7 days after the first flood (on 11 December). Total invertebrate density and taxon richness were both higher in stable than in fill patches on 11 December (Fig. 4; Table 5). Total density was correlated with near-bed current velocity, algal biomass and water depth on one sampling date each (Table 6) while taxon richness was correlated with algal biomass on 11 December (Table 6).

Density of the water mite *Pseudotryssaturus* spp. (Fig. 4) differed between bed stability types on both disturbance-history-specific sampling dates. This taxon was more abundant in scour than in fill patches on 11 December, and in stable than in fill patches on 27 December (Table 5). Current velocity influenced the distribution of this taxon on 27 December (Table 6).

Densities of Hydracarina (excluding *Pseudotryssaturus* spp.; Fig. 4) and the mayfly *Deleatidium* spp. (Fig. 5) differed between bed stability types on 11 December, and densities of Chironomidae (excluding Tanypodinae) and Oligochaeta differed between bed stability types on 27 December. Hydracarina were more common in stable than in fill patches, and *Deleatidium* spp. was more abundant in stable and scour patches than in fill patches (Table 5). Chironomidae density was higher in scour than in fill patches, whereas Oligochaeta density showed the opposite pattern. Hydracarina and *Deleatidium* spp. densities were both correlated positively with current velocity on 11 December (Table 6). Midge and worm densities were correlated with water depth, and worm densities also with algal biomass, on both sampling dates.

Densities of beetle larva *Hydora* spp., dipterans *Eriopterini* spp. and Tanypodinae and Isopoda were similar across bed stability types on both sampling dates. *Hydora* spp. was correlated with water depth, Tanypodinae with near-bed velocity, Isopoda with both, and *Eriopterini* spp. with depth, near-bed velocity and algal biomass on at least one sampling date each (Table 6).

Interactions between disturbance history effects and habitat parameter effects

In all cases where a disturbance history effect in the ANOVA occurred simultaneously with a habitat parameter effect in the ANCOVAs, the disturbance history effect was detected in at least 50% of all ANCOVAs with significant covariate effects and, therefore, remained valid (see Methods). Further, there were several cases when significant habitat parameter effects revealed significant differences between the three bed stability types that had not been found in the ANOVAs without covariates (12 in the Schmiedlaine and 3 in the Kye Burn; see Tables 3 & 5).

Effects of disturbance history on habitat parameters and indirect effects on stream biota

Disturbance history influenced the five measured habitat parameters in five of 45 possible cases (11%) in the Schmiedlaine, and in four of 10 cases (40%) in the Kye Burn.

In the Schmiedlaine, the water was deeper in scour than in fill patches on 22 May (25 ± 2 [SE] versus 16 ± 3 cm; $P = 0.06$) and on 11 July (21 ± 0.4 versus 13 ± 1 cm; $P = 0.08$). Substratum grain size was twice as large in stable than in scour patches on 25 June (95 ± 20 versus 42 ± 7 mm; $P = 0.06$), and three times larger in stable than in fill patches on 24 July (130 ± 38 versus 41 ± 13 mm; $P = 0.09$). Densities of epilithic bacteria were higher in fill ($1.3 \times 10^7 \pm 3.5 \times 10^6$ cells cm^{-2}) than in scour patches ($4.0 \times 10^6 \pm 6.7 \times 10^5$ cells cm^{-2}) on 13 June ($P = 0.07$).

One or more of these three parameters, in turn, influenced the distributions of total invertebrates (substratum grain size on 11 July), taxon richness (substratum grain size, 25 June), *Leuctra* spp. (epilithic bacteria, 13 June), *Liponeura* spp. (substratum grain size, 25 June; bacteria, 13 June), *Dicranota* spp. (water depth, 11 July), *Rhithrogena* spp. (depth, 22 May), *Chloroperla* spp. (depth, 11 July) and *Protonemura* spp. (substratum grain size, 25 June). Consequently, the habitat parameter effects on invertebrates in these nine cases can be seen as indirect effects of local disturbance history on these stream biota.

In the Kye Burn, the water was deeper in fill than in stable patches on 11 December (40 ± 2 versus 28 ± 4 cm; $P = 0.09$), near-bed current velocity was three times faster in fill than in scour patches on 27 December (11 ± 5 versus 33 ± 7 cm·s^{-1}; $P = 0.04$) and the substratum was twice as coarse in stable than in scour patches on 11 December (63 ± 13 versus 34 ± 7 mm; $P = 0.06$). Density of epilithic bacteria was higher in fill ($1.0 \times 10^8 \pm 2.3 \times 10^7$ cells cm^{-2}) than in stable patches ($2.5 \times 10^7 \pm 1.1 \times 10^7$ cells cm^{-2}) on 11 December ($P = 0.04$).

At least one of these parameters, in turn, influenced the distributions of total invertebrates (water depth, 11 December; near-bed velocity, 27 December), *Pseudotryssaturus* spp., Hydracarina, *Deleatidium* spp. and Tanypodinae (velocity, 27 December), Chironomidae (depth and substratum grain size, 11 December), Oligochaeta and *Hydora* spp. (depth, 11 December), and Isopoda and *Eriopterini* spp. (depth, 11 December; velocity, 27 December), resulting in another 13 indirect effects of local disturbance history on the invertebrates.

Discussion

Relative importance of disturbance history, physical habitat and food

Disturbance history clearly played an important role influencing invertebrate distribution in the present study, supporting conclusions from our previous research (Matthaei *et al*. 2000, Matthaei & Townsend 2000). Averaged across both study streams, only near-bed current velocity was related to invertebrate distribution more often than disturbance history. In the Kye Burn, disturbance history and water depth were the most influential habitat parameters. Further important parameters were substratum grain size and epilithic algal biomass, in accordance with previous microhabitat studies (Ulfstrand 1967, Barmuta 1989, Holomuzki & Messier 1993, Hearnden & Pearson 1991). Patterns in invertebrate density in the different bed stability types varied between individual floods, sampling dates and streams. However, density was highest in stable patches in more than 50% of all detected patch type effects and lowest in fill patches in 75% of all detected effects.

Effects of disturbance history on habitat parameters: direct or indirect effects of disturbance history?

Disturbance history affected invertebrate distributions both directly and indirectly, via history effects on habitat parameters. In addition, significant habitat parameter effects revealed previously undetected history effects in several cases. Consequently, habitat parameter effects and disturbance history effects interacted strongly with each other. In contrast, in our study of benthic river algae (Matthaei *et al*. 2003), disturbance history effects were largely independent of habitat parameter effects.

Matthaei & Townsend (2000) speculated that indirect effects of disturbance history on physical habitat parameters and food resources of benthic organisms were more likely to be responsible for long-term differences (several weeks after disturbance) in density between patch history types. Our present results provide little support for this idea, at least for invertebrates and the five studied habitat parameters, because the majority of indirect effects of disturbance history (12 of 22, data from both streams combined) were found within 7 days after disturbance.

One might argue that our chosen analysis caused inflated effect frequencies for disturbance history relative to those for habitat parameters, because five ANCOVAs that included the factor disturbance history were calculated for each dependent variable on each date, whereas only a single ANCOVA was calculated for each of the five covariates. However, we included these covariates in our analysis to find out if "apparent" effects of disturbance history on invertebrate distributions were actually caused by effects of certain habitat parameters (see Matthaei *et al*. 2003). Consequently, the likelihood that a disturbance history effect remained valid (because it could not be explained by a habitat parameter effect) decreased linearly with each habitat parameter that was included in our analysis. This decrease should counterbalance the increased probability of spurious disturbance history effects caused by conducting several "non-independent" tests for a single factor. As a further safeguard, we only considered disturbance history effects as valid that were detected in at least 50% of all ANCOVAs with significant covariate effects. Therefore, we believe that the above interpretation of our results is justified (see also discussions on "non-independent" tests in Perneger 1998 and Quinn & Keough 2002).

Refugium and habitat roles of bed patches with different disturbance histories

Based on our previous research (Matthaei *et al.* 2000, Matthaei & Townsend 2000, Matthaei *et al*. 2003), we had expected stable bed patches to act as refugia for benthic invertebrates during the floods. Our data partly support this expectation. In the Kye Burn, stable bed patches appear to have acted as an invertebrate refugium during Event 1 (similar in function to stable surface stones in an earlier study in this stream; see Matthaei *et al*. 2000). Total invertebrate density, taxon richness and densities of *Deleatidium* spp. and Hydracarina were highest in stable patches shortly after this spate. In the Schmiedlaine, similar patterns were observed for taxon richness and *Liponeura* spp. after Event 3 and *Leuctra* spp. after Event 4. These results support findings of earlier research (Lancaster & Hildrew 1993, Robertson *et al*. 1995, Palmer *et al*. 1996, Winterbottom *et al*. 1997) that undisturbed patches of stream bed (in these cases hydraulic "dead zones" or areas sheltered by debris dams) can play an important role as invertebrate refugia during floods.

In some cases in the present study, invertebrate density was also higher in stable patches than in one or both of the other patch types several weeks after disturbance. This occurred 3 weeks after Event 1 in the Kye Burn (*Pseudotryssaturus* spp. and Oligochaeta on 27 December) and 5 weeks after Event 3 in the Schmiedlaine (total invertebrate density, taxon richness, and four of the 10 common taxa on 24 July). These results imply that invertebrates may also ‘prefer’ stable bed patches for reasons other than a short-term refugium role during floods, presumably because they provide some advantage in terms of physical habitat, food availability or lack of enemies.

Five weeks after Event 4 in the Schmiedlaine, three of the common taxa were more abundant in scour or fill patches than in stable patches. This result parallels those of Matthaei & Townsend (2000) for certain invertebrate taxa in the Kye Burn and Matthaei *et al.* (2003) for benthic algae in a somewhat larger German river. Again, this is probably related to the relative favourability of conditions and resources in different patch types with time since a disturbance. Matthaei & Townsend (2000) also found certain invertebrate taxa were most abundant in fill patches two months after an earlier spate in the Kye Burn.

Overall, long-term effects of disturbance history (4-5 weeks after disturbance) dominated in the Schmiedlaine (63% of all observed effects). In the Kye Burn, short-term effects (5 days after disturbance) were more common (63% of all effects), but note that we were unable to sample this stream 5 weeks after disturbance (see Methods). These results also agree with findings of our previous research on invertebrates and river algae.

Differences between streams

We had expected local disturbance history to be relatively more important for invertebrate microdistributions in the Schmiedlaine than in the Kye Burn because of the higher frequency of bed-moving floods (which have the potential to cause a redistribution of the benthic fauna; Townsend & Hildrew 1976). However, our results suggest the opposite. Further, the two smaller spates in the Schmiedlaine did not affect invertebrate density, whereas the similarly moderate Event 1 in the Kye Burn caused a significant density reduction. Moreover, even the two large floods in the Schmiedlaine reduced invertebrate density by little more than 50%, while the large flood in the Kye Burn caused a reduction of almost 90% (compare Figs. 1 & 4).

These differences may be partly caused by the coarser and more heterogeneous substratum in the Schmiedlaine, where smaller spates may move mainly fine sediment and leave the larger particles in the surface layer mostly intact.

Alternatively, the fauna may be so well adapted (e.g. through a higher genetic variability) to the frequent disturbances in the harsh environment of the Schmiedlaine that invertebrates there are able to survive individual floods better than those in the more benign environment of the Kye Burn (see Hedrick 1986, Robinson *et al.* 1992, Lytle & Poff 2004). At the same time, the high frequency and intensity of disturbance in the Schmiedlaine may keep total invertebrate density permanently at fairly low levels, whereas total density can reach much higher values in the more benign Kye Burn (compare Figs. 1 & 4; see also Scarsbrook & Townsend 1993). Recall that both streams are nutrient-poor, with slow algal growth and low algal biomass on surface stones (see Methods). Therefore, the observed differences between the streams in invertebrate densities are unlikely to be caused by differences in food availability.

Invertebrate recovery after a rare depositional flood

We had expected invertebrate recovery to be very slow after Event 2 in the Kye Burn, because of its magnitude, the lack of surface refugia, and the fact that the uppermost 15-40 cm of the stream bed consisted entirely of newly deposited sediment. Of 14 floods investigated using scour chains in three different rivers (Matthaei *et al*. 1999a, Matthaei *et al*. 2003, present study), this was the only one to produce such a uniform pattern of bed disturbance. Our expectation was supported, because total invertebrate density and the densities of five of the nine common taxa had reached only 50% of pre-flood values by our final sampling date in March, more than six weeks after the flood. By contrast, invertebrate recovery in the Kye Burn after the smaller Event 1, and also in a previous bed-moving spate investigated by Matthaei *et al.* (2000), was much faster (within three weeks in both cases). Consequently, large and purely depositional floods may represent particularly harsh disturbances for stream invertebrates. In this respect, they may resemble catastrophic debris flows, although these large-scale disturbances have been shown to have even more drastic and longer-lasting negative effects on the benthic fauna (e.g. Lamberti *et al*. 1991).

Our results suggest that a thorough understanding of the microdistribution of benthic invertebrates requires knowledge of disturbance history, as well as more readily measured habitat parameters such as current velocity or water depth. Future research should include investigating how the disturbance history of individual bed patches changes with time and how this temporal change influences the stream biota in these patches. It is also possible that invertebrates are differently affected by local disturbance history patterns depending on the time of year and their actual life stages. Finally, researchers should aim to identify invertebrate taxa to the level of individual species, especially in speciose genera, because congeneric species may have different susceptibilities to disturbance history.

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Table 1. Floods and sampling series in the Schmiedlaine (May to October 2001) and in the Kye Burn (November 2001 to March 2002).

Stream	Event	Sampling date	Sampling series	Sample type	n
Schmiedlaine		9 May	Before Event 1	Random	8
		15 May	Before Event 1	Random	8
	Event 1 (15 May)				
		22 May	After Event 1	Scour, Fill, Stable	5 each
		5 June	After Event 1 *(=Before Event 2)*	Fill, Stable, Random	5 each
	Event 2 (10-11 June)				
		13 June	After Event 2 *(=Before Event 3)*	Scour, Fill, Stable	5 each
	Event 3 (18-20 June)				
		25 June	After Event 3	Scour, Fill, Stable	5 each
		11 July	After Event 3	Scour, Fill, Stable	5 each
		24 July	After Event 3	Scour, Fill, Stable	5 each
		14 August	Before Event 4	Random	8
		30 August	Before Event 4	Random	8
	Event 4 (5-9 September)				
		11 September	After Event 4	Scour, Fill, Stable	5 each
		26 September	After Event 4	Scour, Fill, Stable	5 each
		9 October	After Event 4	Scour, Fill, Stable	5 each
Kye Burn		28 November	Before Event 1	Random	8
		4 December	Before Event 1	Random	8
	Event 1 (5-6 December)				
		11 December	After Event 1	Scour, Fill, Stable	5 each
		27 December	After Event 1 *(=Before Event 2)*	Scour, Fill, Stable	5 each
	Event 2 (9-21 January)				
		25 January	After Event 2	Fill	8
		7 February	After Event 2	Fill	8
		20 February	After Event 2	Fill	8
		7 March	After Event 2	Fill	8

Table 2. Flood magnitudes and percentages of scour, fill and stable bed patches caused by each flood in the Schmiedlaine and the Kye Burn.

Schmiedlaine

Date	**15 May**	**10-11 June**	**18-20 June**	**5-9 September**
Peak flow ($m^3 s^{-1}$)	7.5	9.5	25	14.5
Duration (days)	< 1	1-2	2-3	3-4
Return period (years)	≤ 0.5	0.5-0.75	2-3	1
Bed movements				
fill	63% (2-15 cm)	19% (2-9 cm)	61% (2-40 cm)	28% (2-22 cm)
scour	7% (2-10 cm)	31% (2-16 cm)	28% (2-30 cm)	38% (2-45 cm)
stable	30%	51%	11%	34%

Kye Burn

Date	**5-6 December**	**9-21 January**
Peak flow ($m^3 s^{-1}$)	4.7	20.7
Duration (days)	≈ 1	≈ 12
Return period (years)	≈ 0.4	≈ 5
Bed movements		
fill	62% (2-20 cm)	100% (2-39 cm)
scour	12% (2-11 cm)	
stable	26%	

Table 3. Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing the invertebrate communities between scour, fill and stable patches in the Schmiedlaine. Factor × covariate interactions were explored prior to final analysis (see column 4). For each dependent variable, the results of ANOVAs resulting in significant factor effects are listed first, followed by the results of the corresponding ANCOVAs. Only covariates with significant effects on the dependent variables are included, and only ANCOVAs resulting in significant factor effects are shown (for a complete list of all significant covariate effects see Table 4). $\alpha = 0.10$.

Date & dependent variable	**Covariate in ANCOVA**	**Covariate**	**Interaction**	**Factor**	**Ranking**
5 June					
Dicranota spp.	-	-	-	0.004	Fill > (stable = random)
	Water depth	0.09	0.57	0.004	Fill > stable
	Substratum size	0.04	0.51	0.004	Fill > stable
13 June					
Taxon richness	-	-	-	0.06	Scour > fill
Leuctra spp.	Epilithic algal biomass	0.02	0.11	0.03	(Scour = stable) > fill
25 June					
Taxon richness	Near-bed velocity	0.002	0.14	0.04	(Scour = stable) > fill
Liponeura spp.	-	-	-	0.08	Stable > fill
	Near-bed velocity	0.02	0.33	0.04	Stable > fill
11 July					
Simulium spp.	Near-bed velocity	0.008	0.57	0.08	Stable > fill
24 July					
Total invertebrates	Near-bed velocity	0.005	0.27	0.03	Stable > fill
	Substratum size	0.05	0.25	0.09	Stable > fill
Taxon richness	-	-	-	0.006	(Scour = stable) > fill
Chironomidae	-	-	-	0.03	(Scour = stable) > fill
	Total epilithic bacteria	0.04	0.06	0.008	(Scour = stable) > fill
Rhithrogena spp.	Near-bed velocity	< 0.001	0.78	0.04	Stable > fill
Simulium spp.	-	-	-	0.07	Stable > fill
	Near-bed velocity	0.03	0.61	0.009	(Scour = stable) > fill
	Total epilithic bacteria	0.08	0.56	0.08	Scour > fill
	Epilithic algal biomass	0.07	0.18	0.02	(Scour = stable) > fill

Table 3 (continued)

Date & dependent variable	**Covariate in ANCOVA**	**Covariate**	**Interaction**	**Factor**	**Ranking**
24 July (contin.)					
Liponeura spp.	-	-	-	0.09	Stable > fill
	Near-bed velocity	0.07	0.87	0.02	(Scour = stable) > fill
	Epilithic algal biomass	0.05	0.32	0.02	Stable > fill
Thienem./ Corynon.	Epilithic algal biomass	0.07	0.26	0.07	Scour > stable
11 September					
Leuctra spp.	-	-	-	0.07	Stable > scour
26 September					
Thienem./ Corynon.	Near-bed velocity	0.005	0.10	0.08	Stable > fill
Baetis alpinus	Near-bed velocity	0.04	0.35	0.02	Stable > (fill = scour)
9 October					
Leuctra spp.	Substratum size	0.002	0.83	0.06	Fill > stable
Chironomidae	Total epilithic bacteria	0.05	0.80	0.03	Fill > (scour = stable)
Dicranota spp.	Water depth	0.07	0.63	0.09	Stable > fill
	Total epilithic bacteria	0.05	0.04	0.01	(Scour = stable) > fill
Chloroperla spp.	-	-	-	0.05	Scour > stable
	Water depth	0.02	0.41	0.008	Scour > (stable = fill)
	Substratum size	0.09	0.81	0.03	Scour > (stable = fill)
Simulium spp.	Substratum size	0.03	0.12	0.08	Fill > scour

Table 4. Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing the invertebrate communities between scour, fill and stable patches in the **Schmiedlaine** (for factor effects see Table 3). Only significant results are shown; omitted dependent variables or blanks indicate non-significant results. * $P < 0.10$; ** $P < 0.01$; *** $P < 0.001$; + positive correlation; - negative correlation.

Covariate & dependent variable	**22 May**	**5 June**	**13 June**	**25 June**	**11 July**	**24 July**	**11 Sept**	**26 Sept**	**9 Oct**
Water depth									
Taxon richness				* (+)					
Simulium spp.		* (-)	* (+)					* (+)	
Liponeura spp.			* (-)				no data	no data	
Thienem./ Corynon. spp.				* (+)					
Chironomidae				* (+)			* (+)		
Dicranota spp.		* (-)			* (+)				* (+)
Rhithrogena spp.	* (+)								
Baetis alpinus			* (+)						
Chloroperla spp.				* (+)	* (+)				* (-)
Near-bed velocity									
Total invertebrates				* (+)	* (+)	** (+)		* (+)	** (+)
Taxon richness				** (+)					
Leuctra spp.					* (+)			** (+)	
Simulium spp.				* (+)	** (+)	* (+)		* (+)	* (+)
Liponeura spp.	* (+)		* (+)	* (+)	* (+)	* (+)	no data	no data	
Thienem./ Corynon. spp.	* (-)							** (+)	
Chironomidae								* (+)	
Dicranota spp.					* (+)			** (+)	
Rhithrogena spp.					* (+)	*** (+)		* (+)	** (+)
Baetis alpinus	* * (+)					* * (+)		* (+)	* (+)
Chloroperla spp.								*** (+)	
Substratum size									
Total invertebrates						* (-)	* (+)	* (+)	* (+)
Taxon richness				* (+)			* (+)		* (+)
Leuctra spp.		* (-)							** (+)
Simulium spp.	* (+)	* (-)							* (+)
Liponeura spp.			* (+)	* (+)			no data	no data	
Thienem./ Corynon. spp.			* (-)				* (+)		
Chironomidae							* (+)		* (+)
Dicranota spp.		* (-)			* (+)				
Rhithrogena spp.								* (+)	
Baetis alpinus	* (+)								* (+)

Table 4 (continued)

Covariate & dependent variable	**22 May**	**5 June**	**13 June**	**25 June**	**11 July**	**24 July**	**11 Sept**	**26 Sept**	**9 Oct**
Substratum size (contin.)									
Chloroperla spp.			* (-)						
Protonemura spp.				* (+)			* (+)	no data	
Total epilithic bacteria									
Leuctra spp.			* (+)					* (-)	
Simulium spp.						* (+)			
Liponeura spp.			* (+)				no data	no data	
Thienem./ Corynon. spp.	* (-)								
Chironomidae						* (+)			* (-)
Dicranota spp.									* (+)
Rhithrogena spp.				* (-)					
Chloroperla spp.	* (-)							* (-)	
Protonemura spp.	* (+)							no data	
Epilithic algal biomass									
Total invertebrates							* (+)		
Taxon richness							* (+)		
Simulium spp.				*** (+)		* (-)			
Liponeura spp.	* (-)			*** (+)		* (-)	no data	no data	* (+)
Thienem./ Corynon. spp.						* (+)	* (+)		
Chironomidae							** (+)		
Dicranota spp.					** (-)				
Chloroperla spp.		* (+)				* (+)	* (+)		
Protonemura spp.				* (+)			* (+)	no data	*** (+)

Table 5. Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing the invertebrate communities between scour, fill and stable patches in the Kye Burn. See Table 3 for further details. For a complete list of all significant covariate effects see Table 6.

Date & dependent variable	**Covariate in ANCOVA**	**Covariate**	**Interaction**	**Factor**	**Ranking**
11 December					
Total invertebrates	-	-	-	0.04	Stable > fill
	Epilithic algal biomass	0.01	0.69	0.07	Stable > fill
Taxon richness	-	-	-	0.003	Stable > fill
	Epilithic algal biomass	0.008	0.24	0.004	(Stable = scour) > fill
Pseudotryssaturus spp.	-	-	-	0.02	Scour > fill
Hydracarina	-	-	-	0.09	Stable > fill
Deleatidium spp.	-	-	-	0.02	(Stable = scour) > fill
Chironomidae	-	-	-	0.02 ▪	Stable > fill
	Epilithic algal biomass	0.001	0.50	0.06 ▪	Stable > fill
27 December					
Pseudotryssaturus spp.	Near-bed velocity	0.02	0.68	0.07	Stable > fill
Chironomidae	Water depth	0.09	0.54	0.05	Scour > fill
Oligochaeta	Water depth	0.05	0.04	0.05	Fill > scour
	Epilithic algal biomass	0.03	0.91	0.05	(Stable = fill) > scour

▪ unreliable result (detected in < 50% of all ANCOVAs with significant covariate effects).

Table 6. Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing the invertebrate communities between scour, fill and stable patches in the Kye Burn (for factor effects see Table 5). See Table 4 for further details.

Covariate & dependent variable	**11 Dec**	**27 Dec**
Water depth		
Total invertebrates	** (-)	
Chironomidae	* (-)	* (-)
Oligochaeta	* (-)	* (-)
Hydora spp. (larvae)	* (-)	
Isopoda	* (-)	
Eriopterini spp.	* (-)	
Near-bed velocity		
Total invertebrates		* (+)
Pseudotryssaturus spp.		* (+)
Hydracarina		* (+)
Deleatidium spp.		** (+)
Isopoda		** (+)
Eriopterini spp.		* (+)
Tanypodinae		* (-)
Substratum size		
Chironomidae	* (+)	
Epilithic algal biomass		
Total invertebrates	* (+)	
Taxon richness	** (+)	
Chironomidae	** (+)	
Oligochaeta	* (+)	* (+)
Eriopterini spp.	** (+)	

Figure Legends

Fig. 1. Total invertebrate density, taxon richness and the densities of *Leuctra* spp. and *Simulium* spp. in fill, scour, stable and random patches in the Schmiedlaine. The arrows indicate timing and magnitude (arrow length) of each flood (for details see text). Error bars indicate standard errors (in some cases, errors are too small to be visible). Significant differences between patch types in the ANOVAs and ANCOVAs are shown by asterisks above the mean values (*$P < 0.1$; ** $P < 0.01$). See Table 3 for *P*-values of all significant differences between patch types.

Fig. 2. Densities of *Liponeura* spp., *Thienemanniella/ Corynoneura* spp., Chironomidae and *Dicranota* spp. in fill, scour, stable and random patches in the Schmiedlaine. See Fig. 1 for further details.

Fig. 3. Densities of *Rhithrogena* spp., *Baetis alpinus*, *Chloroperla* spp. and *Protonemura* spp. in fill, scour, stable and random patches in the Schmiedlaine. See Fig. 1 for further details.

Fig. 4. Total invertebrate density, taxon richness and densities of *Pseudotryssaturus* spp. and Hydracarina in fill, scour, stable and random patches in the Kye Burn. The arrows indicate timing and magnitude (arrow length) of each flood (for details see text). Error bars indicate standard errors (in some cases, errors are too small to be visible). Significant differences between patch types in the ANOVAs and ANCOVAs are shown by asterisks above the mean values (*$P < 0.1$; ** $P < 0.01$). See Table 5 for *P*-values of all significant differences between patch types.

Fig. 5. Densities of *Deleatidium* spp., Chironomidae and Oligochaeta in fill, scour, stable and random patches in the Kye Burn. See Fig. 4 for further details.

Fig. 6. Densities of *Hydora* spp , Isopoda, *Eriopterini* spp. and Tanypodinae in fill, scour, stable and random patches in the Kye Burn. See Fig. 4 for further details.

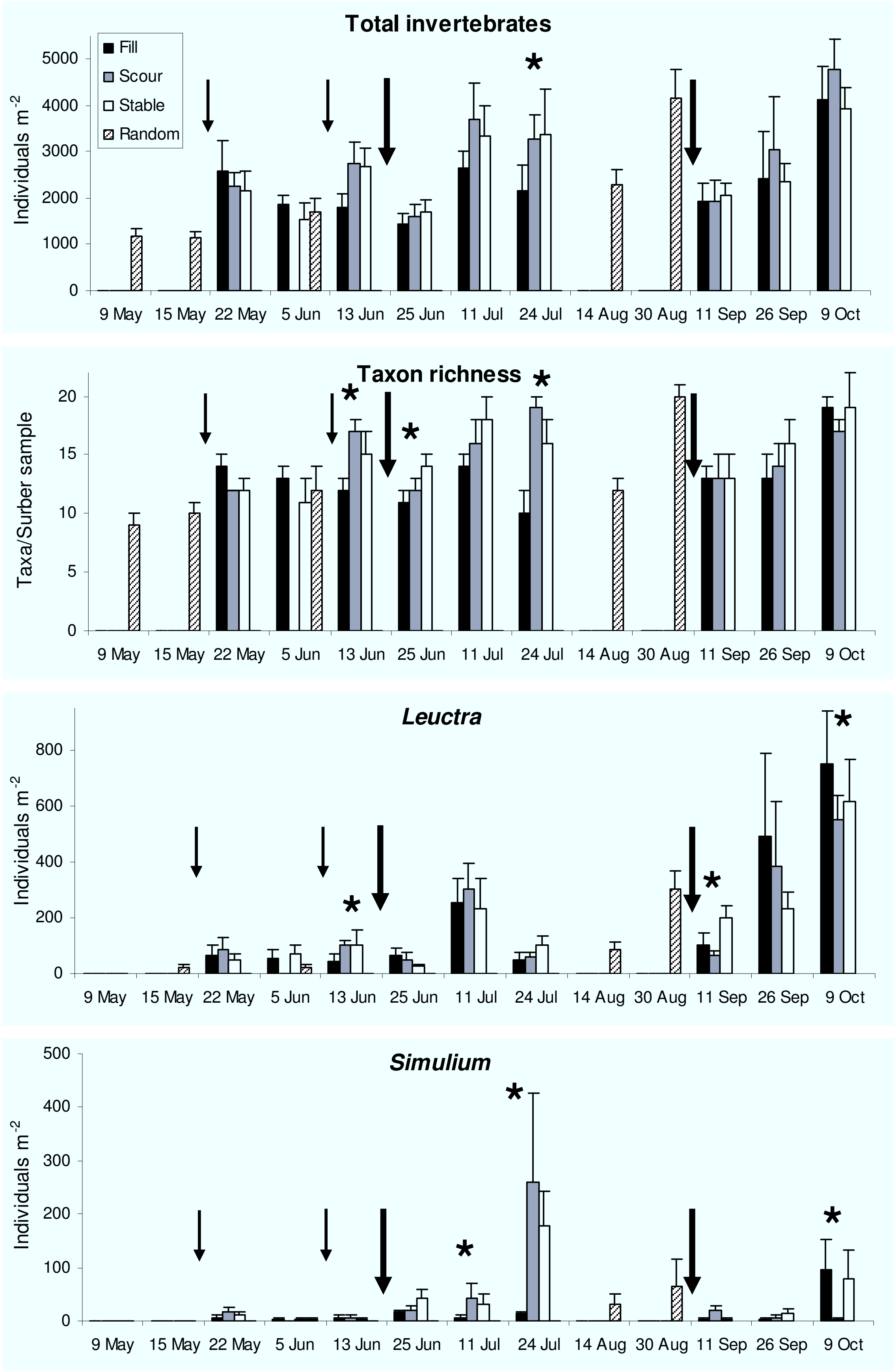
Total invertebrates
■ Fill
■ Scour
☐ Stable
▨ Random
Individuals m^{-2}
5000
4000
3000
2000
1000
0
*
9 May
15 May
22 May
5 Jun
13 Jun
25 Jun
11 Jul
24 Jul
14 Aug
30 Aug
11 Sep
26 Sep
9 Oct
Taxon richness
Taxa/Surber sample
20
15
10
5
0
*
*
*
Leuctra
Individuals m^{-2}
800
600
400
200
0
*
*
*
Simulium
Individuals m^{-2}
500
400
300
200
100
0
*
*
*

Fig. 1

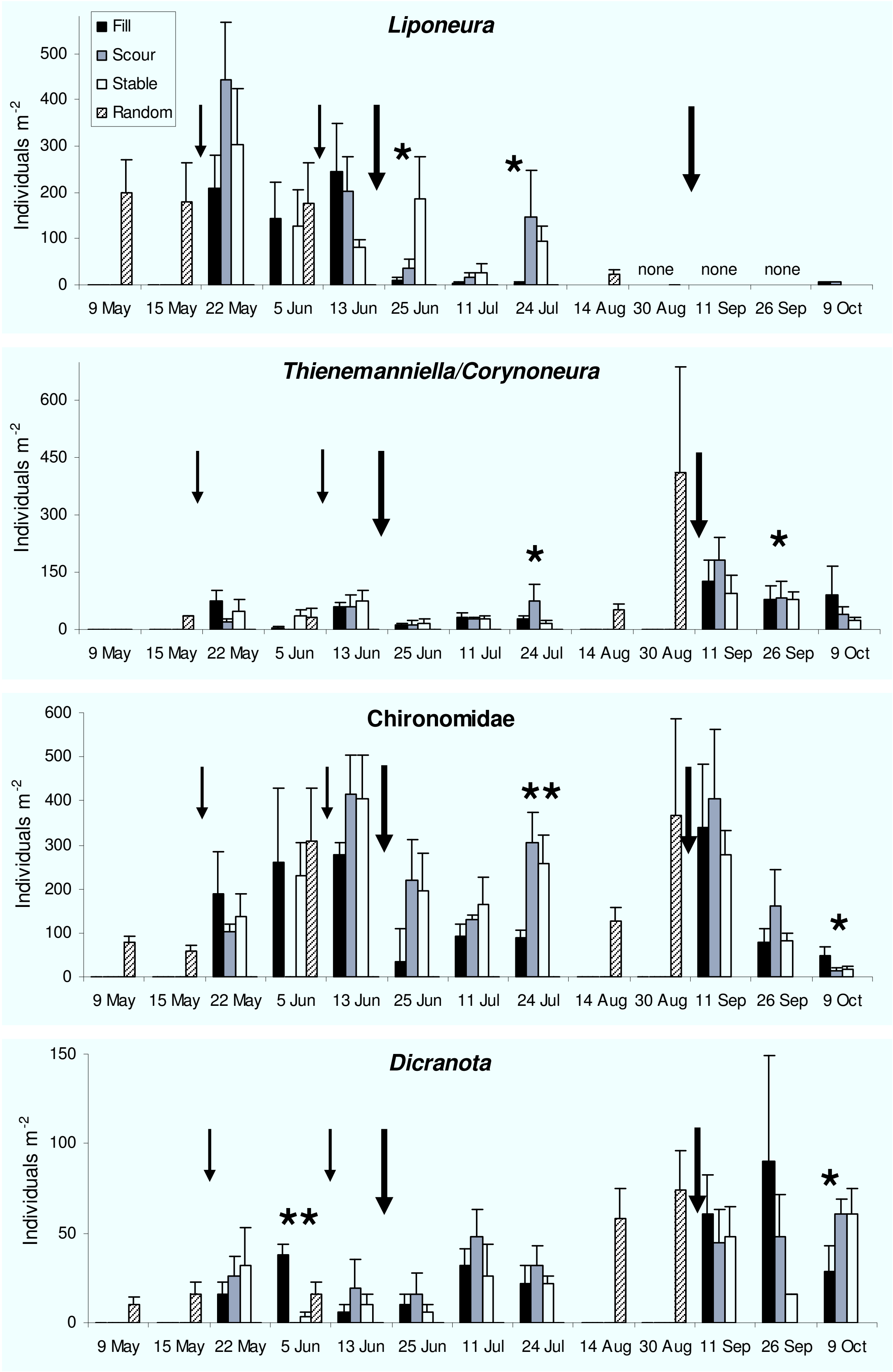
■ Fill
▨ Scour
☐ Stable
▨ Random
Liponeura
Individuals m^{-2}
0
100
200
300
400
500
*
*
none
none
none
9 May
15 May
22 May
5 Jun
13 Jun
25 Jun
11 Jul
24 Jul
14 Aug
30 Aug
11 Sep
26 Sep
9 Oct
Thienemanniella/Corynoneura
Individuals m^{-2}
0
150
300
450
600
*
*
Chironomidae
Individuals m^{-2}
0
100
200
300
400
500
600
**
*
Dicranota
Individuals m^{-2}
0
50
100
150
**
*

Fig. 2

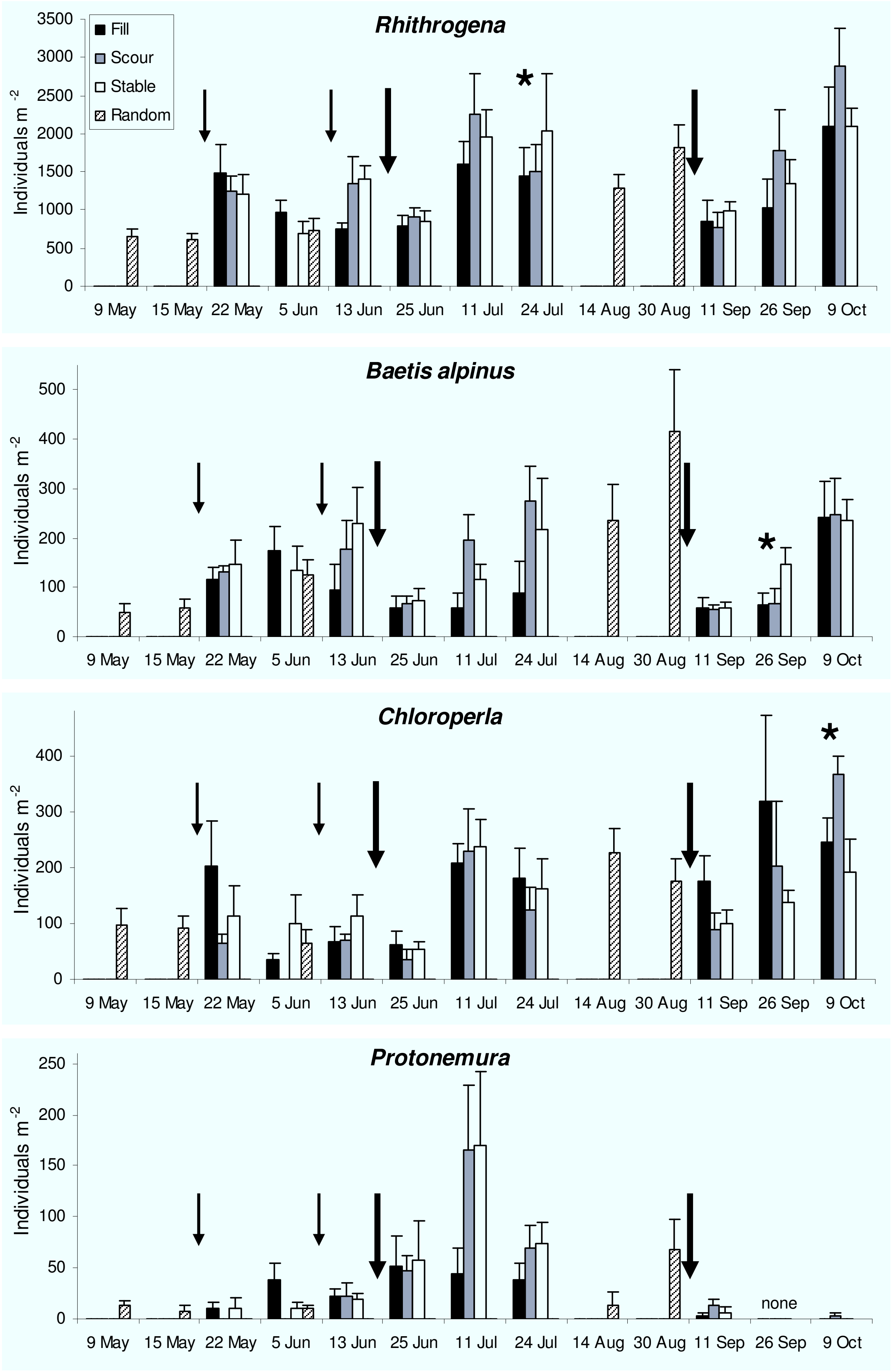
Rhithrogena
Fill
Scour
Stable
Random
Individuals m -2
3500
3000
2500
2000
1500
1000
500
0
*
9 May
15 May
22 May
5 Jun
13 Jun
25 Jun
11 Jul
24 Jul
14 Aug
30 Aug
11 Sep
26 Sep
9 Oct
Baetis alpinus
500
400
300
200
100
0
*
Chloroperla
400
300
200
100
0
*
Protonemura
250
200
150
100
50
0
none

Fig. 3

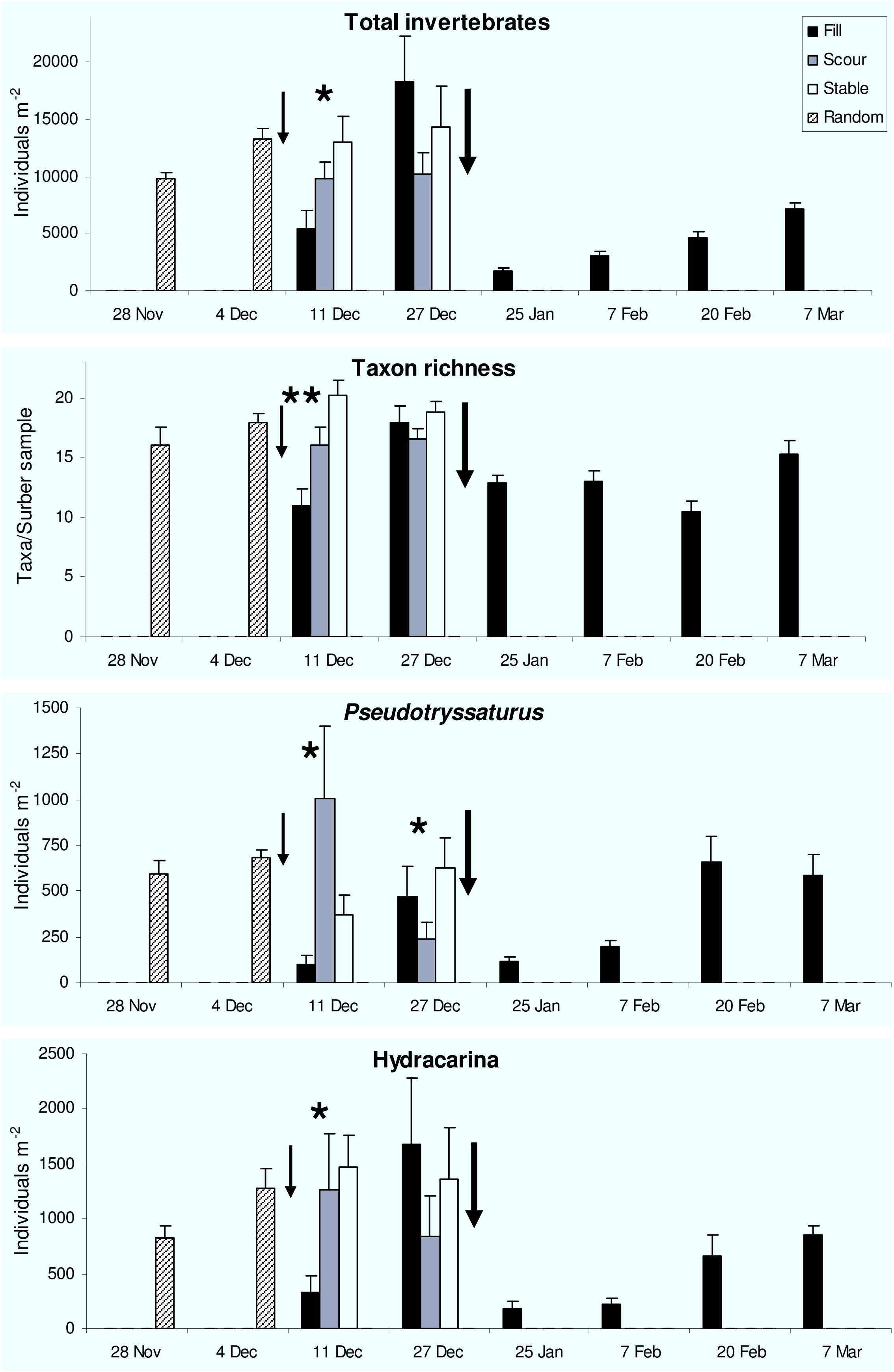
Total invertebrates
Individuals m-2
0
5000
10000
15000
20000
■ Fill
▨ Scour
□ Stable
▨ Random
*
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Taxon richness
Taxa/Surber sample
0
5
10
15
20
**
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Pseudotryssaturus
Individuals m-2
0
250
500
750
1000
1250
1500
*
*
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Hydracarina
Individuals m-2
0
500
1000
1500
2000
2500
*
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar

Fig. 4

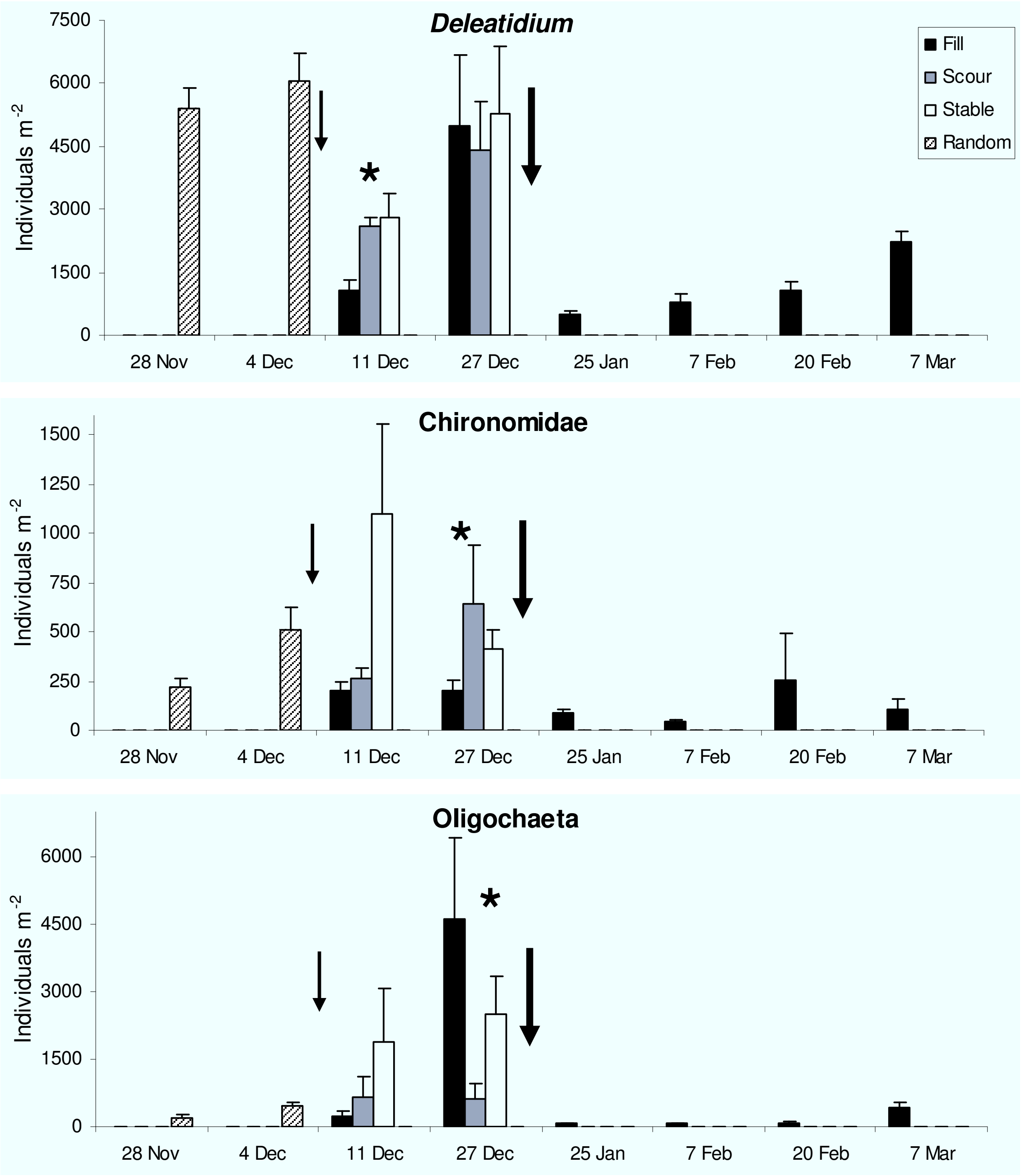
Deleatidium
Individuals m^{-2}
7500
6000
4500
3000
1500
0
■ Fill
▨ Scour
☐ Stable
▧ Random
*
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Chironomidae
Individuals m^{-2}
1500
1250
1000
750
500
250
0
*
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Oligochaeta
Individuals m^{-2}
6000
4500
3000
1500
0
*
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar

Fig. 5

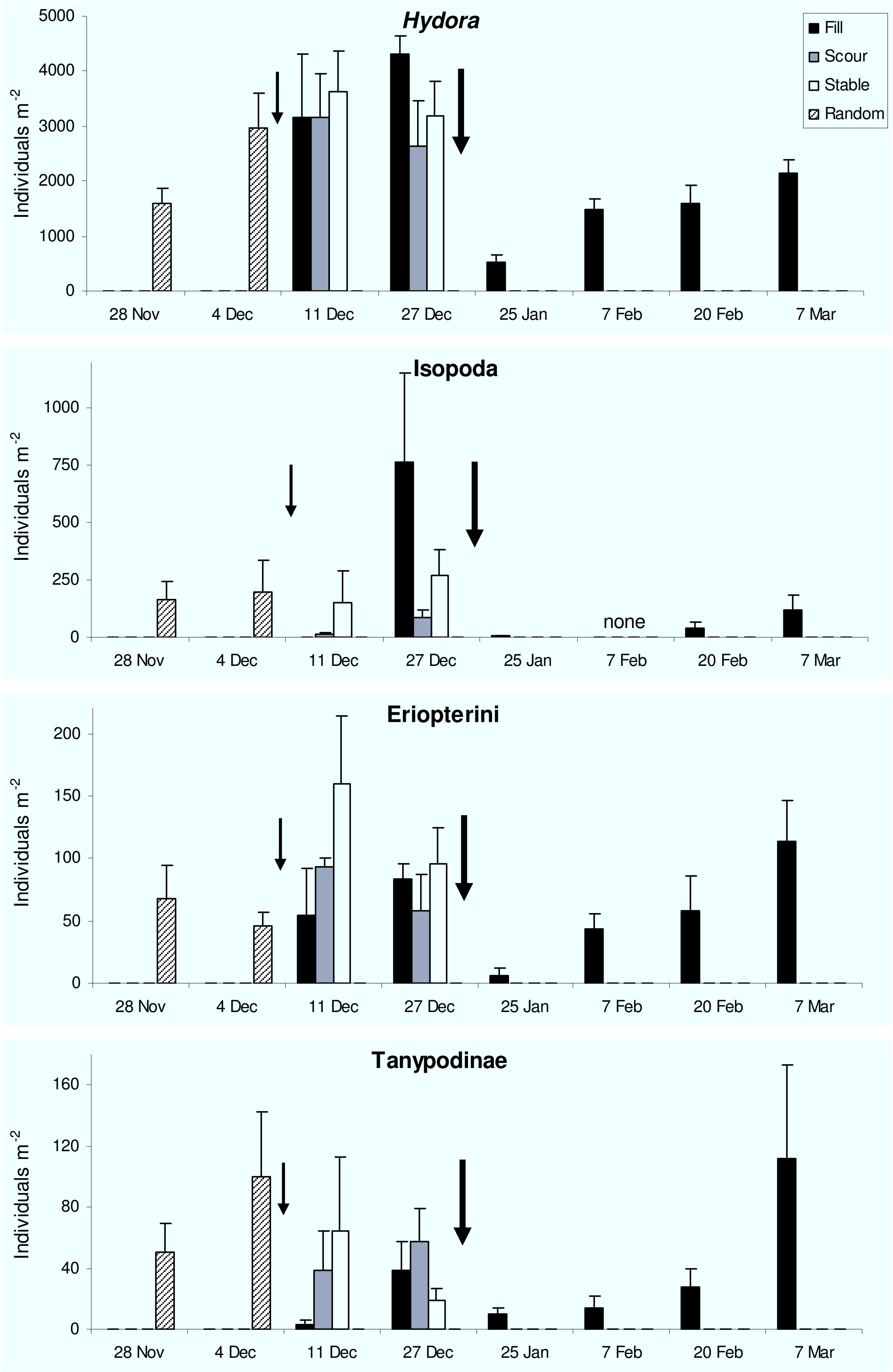
Hydora
Individuals m^{-2}
5000
4000
3000
2000
1000
0
■ Fill
▨ Scour
☐ Stable
▨ Random
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Isopoda
Individuals m^{-2}
1000
750
500
250
0
none
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Eriopterini
Individuals m^{-2}
200
150
100
50
0
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar
Tanypodinae
Individuals m^{-2}
160
120
80
40
0
28 Nov
4 Dec
11 Dec
27 Dec
25 Jan
7 Feb
20 Feb
7 Mar

Fig. 6

DISTURBANCE HISTORY INFLUENCES THE DISTRIBUTION OF STREAM INVERTEBRATES BY ALTERING MICROHABITAT PARAMETERS: A FIELD EXPERIMENT

2

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Effenberger M., Engel J., Diehl S. & Matthaei C.D.

Disturbance history influences the distribution of stream invertebrates by altering microhabitat parameters: a field experiment

Michael Effenberger[1], Johanna Engel[1], Sebastian Diehl[1]
& Christoph D. Matthaei[2]

[1]Department Biology II, Aquatic Ecology, University of Munich (LMU), Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

[2]Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Corresponding author
E-mail: effenberger@zi.biologie.uni-muenchen.de
Fax: 0049-89-2180-74211

Abstract

We investigated the effects of local disturbance history and several biotic and abiotic habitat parameters on the microdistribution of benthic invertebrates after an experimental disturbance in a flood-prone German stream. Bed movement patterns during a moderate flood were simulated by scouring and filling stream bed patches (area 0.49 m^2) to a depth of 15-20 cm. Invertebrates were investigated using ceramic tiles as standardised substrata. After 1, 8, 22, 29, 36 and 50 days, we sampled one tile from each of 16 replicates of three bed stability treatments (scour, fill and stable controls). For each tile, we also determined water depth, near-bed current velocity, the grain size of the substratum beneath the tile, epilithic algal biomass and standing stock of particulate organic matter. Shortly after disturbance, total invertebrate density, taxon richness and density of the common taxa *Baetis* spp. and Chironomidae were highest in stable patches. Several weeks after disturbance, by contrast, *Baetis* spp. and Hydropsychidae were most common in fill and *Leuctra* spp. in scour patches. The black fly *Simulium* spp. was most abundant in fill patches from the first day onwards. Community evenness was highest in scour patches during the entire study. Local disturbance history also influenced algal biomass and POM standing stock at the beginning of the experiment, and water depth, current velocity and substratum grain size throughout the experiment. Scouring mainly exposed finer substrata and caused local depressions in the stream bed characterized by slower near-bed current velocity. Algal biomass was higher in stable and scour patches and POM was highest in scour patches. In turn, all five common invertebrate taxa were frequently correlated with one or two of these habitat parameters. Our results suggest that several ‘direct’ initial effects of local disturbance history on the invertebrates were subsequently replaced by ‘indirect’ effects of disturbance history (via disturbance-induced changes in habitat parameters such as current velocity or food).

Keywords: experimental disturbance, habitat parameters, stream invertebrates, patch dynamics, flood.

Introduction

Few ecosystems experience either the frequency or intensity of disturbance observed in running waters. Hence, disturbance is regarded as one of the dominant organizing factors in streams (Fisher *et al.* 1982, Power & Stewart 1987, Resh *et al.* 1988, Lake 2000). During high flow events, high shear forces suspend sediments, move bottom materials and kill or displace stream biota (Lake 2000). Consequently, significant decreases in the mean density of benthic organisms, for instance macroinvertebrates, have been recorded after bed-moving floods (e.g. Grimm & Fisher 1989, Robinson *et al.* 2003, 2004, Effenberger *et al.* 2006). However, recent research has shown that floods can affect benthic organisms not just by killing or displacing them, but also more subtly.

It is well known that the microdistribution of benthic invertebrates and algae is influenced by abiotic habitat parameters, such as water depth, substratum grain size and current velocity (e.g. Barmuta 1989, Peckarsky *et al.* 1990, Holomuzki & Messier 1993), and also by the availability of food (e.g. Flecker 1984, Downes *et al.* 2000, Roll *et al.* 2005) and predators (Cooper *et al.* 1990, Diehl *et al.* 2000). By contrast, the possibility that hydrological disturbance can also contribute to the patchy distribution of stream biota has received less attention, and rigorous research in this area has begun only relatively recently (e.g. Palmer *et al.* 1992, Lancaster & Hildrew 1993, Robinson *et al.* 2003).

Matthaei *et al.* (1999) showed that floods can induce a patchy mosaic of bed disturbance, with some patches experiencing sediment scour and some deposition (fill) while others remain unchanged (stable). Matthaei & Townsend (2000) termed the small-scale patterns of scour, fill or no bed movement during floods "local disturbance history" and demonstrated that this disturbance history strongly influenced the small-scale distribution of benthic invertebrates in a flood-prone New Zealand stream. More than two months after a flood, larvae of the mayfly *Deleatidium*, the black fly *Austrosimulium* and the dipteran *Eriopterini* were most abundant in fill patches, whereas Isopoda were most abundant in scour patches. Subsequent research has provided further evidence that local disturbance history can affect the small-scale distributions of benthic invertebrates (Effenberger *et al.* 2006) and algae (Matthaei *et al.* 2003). Nevertheless, the mechanisms underlying the observed density patterns remain largely unclear, partly due to the correlative nature of most studies to date. Clearly, this observational research needs to be complemented by manipulative experiments.

Olsen *et al.* (2007) have begun to close this knowledge gap by investigating the effects of an experimentally created disturbance history mosaic on benthic invertebrates. Their results paralleled several of the earlier findings after natural disturbances. For instance, invertebrates were most abundant in stable patches shortly after disturbance and differences between fill and stable patches disappeared after 14 days, whereas differences between scour and stable patches persisted until the end of their 6-week study. In contrast to previous non-manipulative studies, densities in scour and fill patches never exceeded those in stable patches, and correlations between flow velocity (measured only once after 6 weeks) and invertebrate densities were weak.

Here, we report the findings of another experimental study investigating the influence of patchy local disturbances on the microdistribution of benthic invertebrates. To expand on Olsen *et al.* (2007), we included several abiotic and biotic habitat parameters (water depth, near-bed current velocity, substratum grain size, epilithic algal biomass and particulate organic matter) and measured these parameters on every sampling occasion. We also increased the number of replicates (n = 16) and thus statistical power, and extended sample collection until seven weeks after disturbance. Based on previous studies (see references above), we expected that invertebrate densities would be highest in stable patches shortly after disturbance, but should become highest in scour or fill patches with increasing time since disturbance. We predicted immediate, negative effects of scour and fill on invertebrate densities as direct consequences of increased mortality and emigration from disturbed patches (defined as ‘**direct**’ effects of disturbance history in the context of our paper). Further, we expected longer-term (positive or negative) effects of scour and/or fill on the invertebrates to occur as consequences of disturbance-mediated changes in physical habitat parameters and food resources (defined here as ‘**indirect**’ effects of disturbance history; see also Matthaei & Townsend 2000). If such ‘indirect’ effects were common, this would imply that after a flood invertebrates colonise bed patches according to their habitat preferences, but that the suitability of these patches is shaped by local disturbance history.

Methods

Study site

Our study was carried out in the Eyach, a flood-prone stream in southern Germany. The Eyach (47°46´N, 11°05´O) has a steep catchment (area ca. 27 km², altitude 570-930 m a.s.l.) that lies in a zone of fairly high rainfall at the northern edge of the Alps (mean annual rainfall in the catchment is about 1210 mm; German Weather Service, station Hohenpeissenberg). Consequently, the Eyach has a harsh discharge regime with frequent floods that are often quite severe. Mean flow is about 0.5 $m^3 s^{-1}$, baseflow about 0.05 $m^3 s^{-1}$, and water temperature is less than 17°C in summer (M. Effenberger, unpublished data). The sediment supply into the Eyach is high because of the presence of several steep, unstable scree areas in the catchment. This high sediment input results in an unstable stream bed that is easily moved by floods. The stream bed consists mainly of large pebbles and small cobbles (particle width 32-128 mm) interspersed with small- and medium-sized boulders (256-1024 mm). About 70 % of the catchment is covered by forest, and the remaining area is pasture lightly grazed by cattle. Stream width at baseflow is about 5-10 m, the flow regime and the stream channel is more or less natural, water depth at the study site is about 15-25 cm, and the water is nutrient-poor.

Experimental disturbance

Our study was conducted from June to August 2005. On 7 June, we exposed 288 unglazed white tiles (9.8 x 9.8 x 0.8 cm; surface area 223.4 cm²) across a reach of 200 m length and left them undisturbed for 12 days to allow natural colonization by stream organisms. These tiles were used as sampling units for epilithic algae and macroinvertebrates. Tiles were equipped with two silicon "feet" (1 x 1 x 0.5 cm) near their downstream edges to facilitate invertebrate colonization of tile undersides and to increase the hydraulic pressure holding the tiles on the substratum. Tiles were exposed in four blocks in riffles along the experimental reach (Fig.1), each covering an area of 5 x 5 m. Blocks were spaced at intervals of 5 to 50 m (depending on the in-stream sequence of riffles). Within each block, tiles were organized in 12 experimental patches (spaced 1.5 m from each other) containing six tiles each.

At the beginning of the experiment (on 19 June) each experimental patch (area 0.7 x 0.7 m) was subjected to one of three disturbance treatments (scour, fill and stable). Patches were randomly assigned to the three disturbance treatments, and one tile from each patch was collected on each of six successive post-disturbance sampling dates. For the disturbance treatments, the substratum in the patches was either ‘scoured’ or filled to a depth of 15-20 cm. The substratum for the fill patches was collected from dry gravel bars in the floodplain three days before the start of the experiment (see Olsen *et al.*, 2007) and stored dry in buckets on the stream bank to ensure that it contained no living stream invertebrates or algae. Scour patches were created by removing the surface sediment of the stream bed using a shovel. Additionally, tiles in scour and fill patches were scrubbed with a soft brush (see McCabe & Gotelli, 2000) to remove all invertebrates and a large proportion of the epilithic algae and were placed atop the scoured or filled stream bed, respectively. This experimental disturbance can simulate important aspects of a natural flood, such as local rearrangement of substrata and efficient removal of invertebrates (see Matthaei *et al.* 1997).

The experiment started with the creation of the bed disturbance mosaic and ended on 8 August (= day 50) with the last sampling occasion. During sampling on day 22, a moderate flow peak with increased water turbidity (peak flow about twice the annual mean flow; M. Effenberger, personal observation) occurred in the Eyach and lasted for five days. This flow peak did not move any of the experimental tiles, but may have washed some particulate organic matter out of the patches (see Discussion). Another smaller flow peak on day 50 also moved none of the tiles.

Biological sampling

One randomly selected tile from each of the 48 patches was sampled 1, 8, 22, 29, 36 and 50 days after the experimental disturbance. All invertebrates were dislodged gently from the entire surface of each tile, caught in a hand net and preserved with 70% ethanol in the field. In the laboratory, invertebrates were identified (most taxa to genus, dipterans to family) and counted under a stereomicroscope (at 6.5 – 40x magnification; WILD, Heerbrugg, Germany). All particulate organic matter (POM) washed from the tile into the hand net (mesh size 250 µm) was quantified as ash-free dry matter (AFDM; APHA 1998). Epilithic algal biomass was sampled by scraping the top surface of each tile with a tooth brush with shortened bristles. Algal samples were preserved immediately with formaldehyde solution (final concentration 4%) in the field, stored on ice in the dark and measured as chlorophyll a (using acetone for extraction; APHA, 1998) per cm^2 of tile surface area.

To test whether colonization of our experimental tiles was similar to colonization of natural substrata, we randomly selected one surface stone per block on each sampling date and sampled it in the same way as the tiles. Stone surface areas were determined by wrapping stones in aluminium foil of known mass per unit area and weighing the foil (Townsend *et al.* 1997). For graphical illustration of the results, invertebrate numbers on both stones and tiles were converted to densities (individuals per 1000 cm^2).

For each tile or stone sampled, we measured water depth and near-bed current velocity (≈3-5 cm above the substratum) with a propeller flow meter (Hoentzsch GmbH, Waiblingen, Germany; propeller diameter 2 cm). Further, a single observer (to minimise variation) estimated substratum composition by eye as the mean particle widths of the first- and second-most common substratum grain size classes (see Effenberger *et al.* 2006) in the area that had been covered by the tile removed. These size classes were identified using a modified Wentworth scale with a half-phi scale (e.g. 16-22 mm, 22-32 mm etc.; Harrelson *et al.* 1994). All particles smaller than 8 mm were combined into a single category.

Data analysis

Invertebrate community structure (including rare taxa) was compared between the three disturbance patch types on each of the six sampling occasions using analysis of similarities (ANOSIM; Clarke 1993) and non-metric multidimensional scaling (NMDS) on a Bray-Curtis similarity matrix obtained from $\log_{10}(x+1)$ transformed invertebrate density data. Differences between patch types on each sampling date were interpreted from pairwise tests in the ANOSIM. The same procedure was used to compare invertebrate community structure between stable experimental tiles and natural surface stones.

Further comparisons between disturbance history categories were conducted using two-way analysis of variance (ANOVA), multivariate analysis of variance (MANOVA) and two-way analysis of covariance (ANCOVA). Disturbance history category (scour, fill or stable) was treated as a fixed factor, block as a random factor, and four of the five habitat parameters (current velocity, substratum grain size, algal biomass and POM) as a covariate in the ANCOVAs [because water depth was significantly correlated with near-bed current velocity on all sampling dates (Pearson's correlation coefficient ranged from -0.42 to -0.62), we included only current velocity as a covariate]. We chose these four covariates because they can vary considerably at the spatial scale of our experimental patches and are well-known to influence the microdistribution of benthic invertebrates (see Introduction). Treatment effects on total invertebrate density, taxon richness and community evenness (Shannon's equitability; Krebs 1985) were investigated with separate ANOVAs and ANCOVAs. Treatment effects on the densities of the five most common invertebrate taxa were first analysed with MANOVAs, followed by separate ANOVAs and ANCOVAs for each individual taxon. To determine the influence of local disturbance history on the four habitat parameters, we conducted separate ANOVAs for each habitat parameter, with disturbance history as the fixed factor. After exploratory analysis, data were log (x) or log (x+1) transformed where necessary to improve normality and homoscedasticity. The results for the block factor are not presented because they were not relevant for our research objectives. Disturbance history x covariate interactions were significant only in a few cases and did not affect the interpretations of the results in question. Hence, these interactions are not presented either.

The use of ANCOVA in our local disturbance history research has been described in detail and justified in Effenberger *et al.* (2006). Therefore, we present only the main points of this analysis here. Due to the expected change of disturbance history effects with time, we analysed each sampling date separately. To avoid collinearity problems (see Quinn & Keough 2002), we calculated separate ANCOVAs for each covariate. Only covariates that were significantly correlated with the dependent variable are discussed. In cases where no covariate was significant, all covariates were dropped from the analysis and a simple two-way ANOVA was calculated. If a disturbance history effect was significant, we conducted pairwise *post-hoc* comparisons. After ANOVA, we used Tukey HSD tests, except in cases of persisting heteroscedasticity (results of Levene´s test still significant after transformation) when we performed Games-Howell tests, which do not assume equal variances between groups (Quinn & Keough 2002). After ANCOVA, we performed t-tests on estimated marginal means (adjusted with the Sidak procedure; Day & Quinn 1989).

We interpreted our findings as 'direct' effects of disturbance history on the invertebrates in all cases where disturbance had a significant effect in the ANOVA or disturbance plus one or more covariates had significant effects in the ANCOVA. By contrast, we interpreted results as 'indirect' effects of disturbance history in all cases where a significant disturbance effect in the ANOVA was replaced by one or more significant covariate effects in the ANCOVA, or where only one or more covariates (but not disturbance) had significant effects in the ANCOVA and these covariates were, in turn, significantly influenced by disturbance history in the ANOVA.

All analyses were calculated either in SPSS® version 12.0 (SPSS Inc., Chicago, USA) or in PAST (Hammer *et al.* 2001).

Results

Faunal composition

In the Eyach, the mayfly nymph *Baetis* spp. was the most abundant colonizer of the experimental tiles. This taxon contributed 40% to total invertebrate density (all samples combined), followed by chironomids (32%), the black fly *Simulium* spp. (5%), the caddisfly family Hydropsychidae (4%), and the stonefly *Leuctra* spp. (2%). Together, these five taxa comprised 83% of all invertebrates in the samples.

Colonisation of tiles versus stones

Experimental tiles were colonized by similar taxa as were natural surface stones. Invertebrate community structure (including rare taxa) on stable experimental tiles was similar to community structure on natural stones on all sampling dates (ANOSIM; $P > 0.10$ for each date).

Periods of increased stream flow

The high flow on day 22 coincided with reduced invertebrate density and richness at the time. Total invertebrate density ($P = 0.004$), taxon richness ($P < 0.001$) and densities of two of the common taxa (*Baetis* spp., $P = 0.005$; *Simulium* spp., $P = 0.02$) were all lower on day 22 than on day 8, the last previous sampling date (one-way ANOVAs; data from all disturbance treatments combined). Nevertheless, none of our experimental tiles was moved, and we also noticed no obvious movement of natural bed substrata in our experimental reach (M. Effenberger, personal observation). Further, epilithic algal biomass on tiles increased, rather than decreased, between day 8 and day 22 ($P < 0.001$; see Fig. 2). The small flow peak on day 50 coincided with a reduced density of *Baetis* spp. ($P < 0.001$) compared to that on day 36. By contrast, community evenness ($P = 0.002$) and the density of *Simulium* spp. ($P = 0.037$) increased from day 36 to day 50.

Effects of disturbance treatments on habitat parameters

Experimental scour and fill affected all five habitat parameters measured (Table 1; Fig. 2). Scouring mainly exposed finer substrata and caused local depressions in the stream bed characterized by slower near-bed current velocity. Velocity was at least twice as high in stable and fill as in scour patches on all six sampling dates. Water depth was generally highest in scour patches, followed by stable and fill patches. Substratum grain size underneath the sampled tiles was more than twice as large in stable and fill as in scour patches on most dates. On days 22 and 29, substratum grain size was largest in fill, intermediate in stable and smallest in scour patches. Epilithic algal biomass was higher in stable than in scour or fill patches on day 1, higher in stable and scour than in fill patches on day 8, and higher in scour than in fill patches on day 22. POM standing stock was higher in scour than in stable or fill patches on most dates, but significantly so only on days 1 and 8.

Effects on invertebrate community parameters

Directly after disturbance, invertebrate community structure (including rare taxa) differed between all three disturbance history categories (ANOSIM; $P < 0.004$ for each pairwise comparison; Fig. 3). One week later, communities in scour patches were still distinct from those in stable ($P < 0.001$) and fill patches ($P = 0.004$). The difference between scour and fill patches persisted throughout of the study (all P-values < 0.03), except for the final sampling date ($P = 0.08$). In addition to days 1 and 8, communities in scour and stable patches differed on day 36 ($P = 0.03$).

Total invertebrate density, taxon richness and evenness were affected by local disturbance history and/or related to habitat parameters on all sampling dates (Table 2). Total invertebrate density (Fig. 4) was higher in stable than in scour patches on days 1 and 50 and higher in stable than in fill patches on day 8. On days 22, 29 and 36, total density was higher in fill than in scour patches. Total density was positively correlated with POM and current velocity on three and five dates, respectively (Table 2). Taxon richness (Fig. 4) was higher in stable than in fill and/or scour patches on days 1 and 8. Richness was negatively correlated with substratum grain size on four dates and positively correlated with POM on five dates (Table 2). Community evenness (Fig. 4) was higher in scour than in stable and/or fill patches on days 1, 8, 36 and 50. Evenness was negatively correlated with current velocity on five dates (Table 2).

Effects on common invertebrate taxa

MANOVA revealed significant effects of disturbance history on the densities of the five common invertebrate taxa *Baetis* spp., *Simulium* spp., Hydropsychidae, Chironomidae and *Leuctra* spp. on all sampling dates (Table 3). Subsequent ANOVAs and ANCOVAs performed on the individual densities of these taxa revealed that almost all of them (except for the chironomids) were affected by disturbance history on three or more dates (including the final date), and that all of them were related to one or more habitat parameters on almost all dates (Fig. 4; Table 4). Two major distribution patterns could be distinguished for these common taxa:

(i) Three taxa (*Baetis* spp., *Simulium* spp. and Hydropsychidae) showed positive associations with near-bed current velocity on most dates. All three taxa were more common in fill than in scour patches from 3-4 weeks (or sooner) after disturbance until the end of the experiment, indicating long-term effects of local disturbance history on their distribution. These long-term effects can be explained at least partly by an 'indirect' mechanism: baetids, simuliids and hydropsychids all seemed to prefer microhabitats with relatively high current velocities and therefore aggregated in fill patches, which had consistently higher current velocities than scour patches (Fig. 2). During the second half of the experiment (from day 29 onwards), a significant disturbance history effect on one of these three taxa in the ANOVA was replaced by a positive correlation with current velocity in the ANCOVA in four cases (*Baetis* on day 29, *Simulium* on day 50, Hydropsychidae on days 29 and 36; Table 4). In addition, *Simulium* showed a positive relationship with current velocity on day 29. However, there were also two cases in which the positive correlation with current velocity did not result in the loss of a disturbance history effect in the ANCOVA (*Baetis* and *Simulium* on day 36).

(ii) Two taxa (chironomids and *Leuctra* spp.) were correlated positively with POM on most dates (Table 4). While chironomids showed only evidence for an initial, 'direct' (negative) effect of disturbance history (density was highest in stable patches on day 1) and no longer-term effects of disturbance, *Leuctra* was more common in scour than in fill patches on most sampling dates (Fig. 4). Again, the latter pattern can be at least partly explained as an 'indirect' effect of disturbance history: *Leuctra* seemed to prefer microhabitats with abundant POM and was therefore attracted to scour patches, which had higher quantities of POM than fill patches on all but the final date (Fig. 2). In two cases, a significant disturbance history effect on *Leuctra* in the ANOVA was replaced by a positive correlation with POM in the ANCOVA (on days 8 and 36; Table 4), and another positive relationship to POM was found on day 22 (when *Leuctra* density was also highest in fill patches but not quite significantly so; see Fig. 4). Nevertheless, there were also two cases for *Leuctra* where the disturbance history effect remained significant in spite of a positive correlation with POM in the ANCOVA (on days 29 and 50).

Discussion

Previous studies have shown that local disturbance history can be an important driver of the patchy microdistribution of stream organisms (Matthaei & Townsend 2000, Matthaei *et al.* 2003, Effenberger *et al.* 2006), but little is known about the specific mechanisms through which disturbance history affects benthic communities. Moreover, the link between disturbance history and habitat parameters that influence the microdistribution of stream biota is not very clear. To our knowledge, our experiment is the first manipulative study that specifically addressed 'indirect' effects of local disturbance history on benthic organisms (longer-term effects that occur as consequences of disturbance-mediated changes in physical habitat parameters and food resources).

As in previous research (Matthaei & Townsend 2000, Effenberger *et al.* 2006, Olsen *et al.* 2007), local disturbance history played an important role in structuring the invertebrate community in the Eyach and many of the previously described patterns were supported. However, in the earlier studies effects of disturbance history were never as common and rarely as persistent with time (up to seven weeks after disturbance) as in the present experiment. These differences may be partly due to the larger sample size and correspondingly greater statistical power of the present study. Invertebrate distributions were also often related to near-bed velocity, substratum grain size, epilithic algal biomass and POM, illustrating the well-known importance of these habitat parameters (e.g. Richards & Minshall 1988, Parker 1989, Peckarsky *et al.* 1990, Holomuzki & Messier 1993, Downes *et al.* 2000). Disturbance history influenced these habitat parameters frequently, which resulted in several 'indirect' effects of disturbance history on invertebrate distributions.

Directly after the experimental disturbance, we expected higher invertebrate densities in stable patches than in both disturbed patch types, because invertebrates had only one day to recolonize disturbed tiles. These expectations were largely fulfilled. Total invertebrate density, taxon richness and the densities of *Baetis* spp. and Chironomidae were higher in stable than in scour and fill patches on day 1. There was only one exception from this pattern. *Simulium* spp. showed higher densities in fill than in scour and/or stable patches from 1 day after disturbance until the end of the 7-week experiment, even though overall density of this taxon decreased steadily in all patch types with time (see below). The filter-feeding *Simulium* spp. is known to be an early colonizer of disturbed patches, favouring hard substrata in relatively fast-flowing areas (see e.g. Hemphill & Cooper 1983, Matthaei *et al.* 1996). Our findings agree with these earlier studies and suggest that while disturbance treatments directly removed biofilms and competitors from both scour and fill patches, only fill patches provided sufficiently high flow velocities to attract larger numbers of simuliids.

Evenness of the invertebrate community was, in contrast to taxon richness, higher in scour patches than in stable or fill patches for much of the experiment (see Fig. 4). This difference was caused by a numerical dominance of only one or two taxa in the fill and stable patches (*Simulium* spp. on day 1, *Baetis* spp. throughout the entire experiment, and Hydropsychidae from day 36 onwards) versus a more uniform distribution of taxa in the scour patches. This pattern might have changed after the end of our 7-week experiment, if the slow but steady increase of *Leuctra* spp. in the scour patches (see below) was to continue.

As expected from a previous study of natural floods (Effenberger *et al.* 2006), most of the differences between patch types changed little from one to eight days after the experimental disturbance. Disturbance effects on total invertebrate densities and *Baetis* spp. were slightly weaker on day 8 than on day 1 but still present. The stonefly *Leuctra* spp., which was also rare one day after the disturbance, showed a clear preference for scour patches from the second sampling date onwards until the end of the experiment.

Based on our earlier research on disturbance history (Matthaei & Townsend 2000, Effenberger *et al.* 2006), we had also expected at least some of the invertebrates to develop a preference for scour or fill patches with increasing time since disturbance. These expectations were supported for four of the five most common taxa. *Simulium, Baetis* spp. and Hydropsychidae were most common in fill patches from days 1, 22, and 29 onwards, respectively, whereas *Leuctra* spp. was most abundant in scour patches from day 29 on. While the former taxa were often correlated positively with near-bed current velocity, *Leuctra* was correlated positively with standing stocks of POM. These findings are in agreement with previous research showing that simuliids, baetids, and hydropsychids prefer fast-flowing habitats (Hemphill & Cooper 1983, Osborne & Herricks 1987, Mérigoux & Dolédec

2004) and *Leuctra* habitats that are rich in POM (Hildrew *et al.* 1980, Winterbottom *et al.* 1997, Robinson *et al.* 1998). Both of these habitat parameters were, in turn, affected by the disturbance treatments, suggesting that the longer-term distributional patterns of these four taxa among the different patch types were to some extent 'indirect' consequences of local disturbance history.

There is some circumstantial evidence that the mayfly *Baetis* spp. may have actively searched for fill patches from day 22 onwards. The early preference for stable patches (on days 1 and 8) may have been caused by higher algal biomass (and thus better food availability) in stable patches on these dates (see Fig.2). From day 22 onwards, the difference in food resources between stable and fill patches had disappeared due to faster algal growth in fill patches (see Table 1). The highly mobile *Baetis* (see Mackay 1992) is known to favour relatively fast-flowing habitats (e.g. preferred current velocity range 2-67 cm s^{-1} in Poff *et al.* 2003, and 5-45 cm s^{-1} in Wellnitz & Poff 2006) and to actively seek out high-quality food patches (Kohler 1984, 1985). Therefore, patches providing both fast current velocities and good food supply may be particularly attractive to *Baetis*, and such conditions were found in fill patches from day 22 onwards.

The shift from the highest total invertebrate densities in stable to highest densities in fill patches reflects at least partly the dominance of *Baetis* spp. and Hydropsychidae in the later part of the experiment. Interestingly, the density of the latter increased steadily with time in fill patches and replaced the faster-colonising *Simulium*, as had been found in earlier studies (Fisher *et al.* 1982, Hemphill & Cooper 1983). This pattern may reflect interference competition for space between these two taxa (see Hemphill & Cooper 1983, Hemphill 1991).

An important question is whether the effects of our experimental disturbance treatments on habitat parameters and invertebrate fauna are representative of natural floods. Let us first consider the habitat parameters. Near-bed current velocity was slowest and substratum size smallest in scour patches on all six sampling dates. Epilithic algal biomass was higher in stable patches directly after disturbance and in scour patches on day 22. Furthermore, POM standing stock was highest in scour patches during the first eight days after disturbance, probably because the relatively slow current velocities favoured deposition of POM. From the third sampling date on this trend was still visible but the difference was no longer significant, suggesting that the increased flow on day 22 washed out some POM from scour patches.

How do these experimental patterns compare to effects on these habitat parameters produced by natural floods? While there are numerous studies that investigated invertebrate re-colonisation after natural floods or experimental disturbances (see e.g. review papers by Wallace 1990, Mackay 1992, Lake 2000, Lepori & Hjerdt 2006), we are aware of only two that have documented effects of floods on invertebrate microhabitat parameters. Effenberger *et al.* (2006) investigated four floods in the Schmiedlaine, a stream of similar size as the Eyach (width 5-10 m), and Matthaei *et al.* (2003) studied two floods in the much larger River Isar (width 86-118 m). Effenberger *et al.* (2006) found disturbance effects on local habitat parameters that were largely similar (albeit not as strong and frequent) as the ones produced by our disturbance treatments; i.e. water depth was higher in scour than in fill patches and substratum size was larger in stable than in scour patches. Also similar to our experiment, water depth was higher in scour than in fill patches in the River Isar (Matthaei *et al.* 2003). In contrast to the present study, near-bed current velocity in the Isar was slower in fill than in stable and scour patches. This may be a consequence of the much larger size of the Isar, where individual scour, fill and stable patches covered larger areas and scour and fill were of larger magnitude (Matthaei *et al*. 2004). Further, the bed surface in the Isar was smoother than in the Eyach due to the smaller average substratum particle size in the Isar. Current velocity in large, homogeneous, free-flowing areas is usually positively related to water depth (Allan 1995), which may explain why current speed was slowest in fill patches in the Isar. Thus, the limited available evidence suggests that our results concerning the influence of disturbance history on habitat parameters may match the patterns found in smaller streams after patchy flood disturbances, whereas floods may have partly different effects on habitat parameters in larger rivers.

Concerning the effects on community parameters and common invertebrate taxa together, we found indications of 'direct' disturbance history effects in 22 out of 48 possible cases and of 'indirect' disturbance history effects in 17 out of 48 possible cases. Due to the strong influence of our experimental disturbance treatments on microhabitat parameters (and, consequently, the large number of 'indirect' disturbance history effects on invertebrates), the absolute frequency of disturbance history effects on the benthic invertebrate fauna in our experiment may have been somewhat higher than during natural floods. Nevertheless, we believe that the fundamental mechanisms demonstrated in our experiment should be similar to those operating during and after natural floods because the majority of disturbance effects on habitat parameters in the similar-sized Schmiedlaine (Effenberger *et al.* 2006) were comparable to the ones produced by our disturbance treatments (see previous paragraph).

Overall, the results from our manipulative experiment complement the findings of earlier, non-manipulative research. Our findings suggest that immediate, 'direct' (negative) effects of local disturbance on benthic invertebrates are often in the longer term replaced by 'indirect' effects mediated via disturbance-induced changes in habitat parameters such as current velocity, substratum size and resource availability. In such a scenario, high mortality and emigration in scour and fill patches would be the driving force for the microdistribution of invertebrates shortly after a flood. In the longer term, many mobile taxa may increasingly move from stable to scour and fill patches, where they may find microhabitat conditions that correspond better to their individual preferences.

It should be noted, however, that several effects of disturbance history remained significant in ANCOVAs towards the end of the experiment, suggesting that disturbance-driven habitat parameters cannot explain all longer-term effects of disturbance history on the invertebrate community. Disturbance and abiotic habitat conditions are also by no means the only factors influencing biological communities in running waters. Biotic interactions such as competition, grazing or predation can also be important in determining the structure and function of stream and river communities (e.g. McAuliffe 1984, Feminella & Resh 1991, Kohler & Wiley 1997, Englund & Evander 1999, Diehl *et al.* 2000). Future research should therefore investigate the interplay of these biotic processes with local disturbance history.

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Table 1. Summary (*P*-values) of disturbance history effects on habitat parameters as determined by two-way ANOVA. Only significant ($P < 0.05$) effects are listed, followed by the rankings of disturbance history types (scour, fill and stable) as determined by *post-hoc* tests (where only two patch types are ranked the third was not significantly different from either). Degrees of freedom in the ANOVA model were 2 (for the factor disturbance history) + 3 (block factor) + 42 (error; n = 48).

Date & dependent variable	**Factor** ***P***	**Ranking (*post-hoc*)**
Water depth		
Day 1	< 0.001	Scour > stable > fill
Day 8	< 0.001	Scour > stable > fill
Day 22	< 0.001	Scour > stable > fill
Day 29	< 0.001	Scour > stable > fill
Day 36	< 0.001	Scour > stable > fill
Day 50	< 0.001	Scour > (stable = fill)
Near-bed velocity		
Day 1	< 0.001	(Stable = fill) > scour
Day 8	< 0.001	(Stable = fill) > scour
Day 22	< 0.001	(Stable = fill) > scour
Day 29	< 0.001	(Stable = fill) > scour
Day 36	0.002	(Stable = fill) > scour
Day 50	0.005	(Stable = fill) > scour
Substratum size		
Day 1	< 0.001	(Stable = fill) > scour
Day 8	< 0.001	(Stable = fill) > scour
Day 22	< 0.001	Fill > stable > scour
Day 29	< 0.001	Fill > stable > scour
Day 36	< 0.001	(Stable = fill) > scour
Day 50	0.003	(Stable = fill) > scour
Epilithic algal biomass		
Day 1	< 0.001	Stable > (scour = fill)
Day 8	0.001	(Stable = scour) > fill
Day 22	0.007	Scour > fill
POM		
Day 1	< 0.001	Scour > (stable = fill)
Day 8	< 0.001	Scour > (stable = fill)

Table 2. Summary (P-values) of disturbance treatment effects on invertebrate community parameters as determined by two-way ANOVAs and ANCOVAs. Only significant ($P < 0.05$) effects are listed, followed by the rankings of disturbance history types (scour, fill and stable) as determined by *post-hoc* tests (where only two patch types are ranked the third was not significantly different from either). For each dependent variable, the results of ANOVAs resulting in significant factor effects are listed first, followed by the results of the corresponding ANCOVAs. If the same factor effect was found in the ANCOVAs as in the ANOVAs, only the ANCOVA results are shown. Only covariates with significant effects on the dependent variables are included (+ positive correlation; - negative correlation). Degrees of freedom were 2 (for the factor disturbance history) + 3 (block factor) + 42 (error) in the ANOVAs, and 2 (disturbance) + 3 (block) + 1 (for the covariate) + 41 (error) in the ANCOVAs (n = 48).

Date & dependent variable	**Covariate in ANCOVA**	**Covariate *P***	**Factor *P***	**Ranking (*post-hoc*)**
Total invertebrates				
Day 1	-	-	0.01	(Stable = fill) > scour
	Near-bed velocity (+)	0.002	-	-
Day 8	Near-bed velocity (+)	< 0.001	0.04	Stable > fill
Day 22	Epilithic algal biomass (+)	0.02	0.01	Fill > scour
	POM (+)	< 0.001	0.01	Fill > scour
Day 29	Near-bed velocity (+)	< 0.001	-	-
	POM (+)	0.02	0.02	Fill > scour
Day 36	-	-	0.04	Fill > scour
	Near-bed velocity (+)	< 0.001	-	-
	Epilithic algal biomass (+)	0.005		
Day 50	Near-bed velocity (+)	0.04	-	-
	Substratum size (+)	0.01	0.03	Stable > scour
	POM (+)	< 0.001	-	-
Taxon richness				
Day 1	-	-	< 0.001	Stable > (scour = fill)
Day 8	Epilithic algal biomass (+)	< 0.001	< 0.001	(Stable = scour) > fill
	Substratum size (-)	0.01	-	-
	POM (+)	0.02	-	-
Day 22	Substratum size (-)	0.04	-	-
	POM (+)	< 0.001	-	-
Day 29	POM (+)	< 0.001	-	-

Table 2 (continued)

Date & dependent variable	**Covariate in ANCOVA**	**Covariate** ***P***	**Factor** ***P***	**Ranking (*post-hoc*)**
Taxon richness *(cont.)*				
Day 36	Substratum size (-)	0.02	-	-
	POM (+)	< 0.001	-	-
Day 50	Near-bed velocity (+)	0.04	-	-
	Substratum size (-)	0.004	-	-
	Epilithic algal biomass (+)	< 0.001	-	-
	POM (+)	< 0.001	-	-
Community evenness				
Day 1	Near-bed velocity (-)	0.007	0.04	Scour > stable
Day 8	Near-bed velocity (-)	0.002	0.001	(Scour = fill) > stable
Day 29	Near-bed velocity (-)	< 0.001	-	-
Day 36	-	-	0.02	Scour > fill
	Near-bed velocity (-)	< 0.001	-	-
Day 50	Near-bed velocity (+)	0.001	0.04	Scour > (stable = fill)
	Substratum size (+)	0.001	0.04	Scour > (stable = fill)
	Epilithic algal biomass (-)	0.004	-	-

Table 3. Summary (*P*-values) of disturbance treatment effects on the invertebrate community (including rare taxa) as determined by one-way MANOVAs. *P*-values are based on statistics of Pillai´s trace tests. For more details see text.

Date	**Factor** ***P***
Day 1	< 0.001
Day 8	< 0.001
Day 22	0.002
Day 29	0.03
Day 36	0.006
Day 50	0.014

Table 4. Summary (*P*-values) of disturbance treatment effects on the five most common invertebrate taxa in the Eyach as determined by two-way ANOVAs and ANCOVAs. For more details see Table 2.

Date & dependent variable	**Covariate in ANCOVA**	**Covariate *P***	**Factor *P***	**Ranking (*post-hoc*)**
***Baetis* spp.**				
Day 1	Near-bed velocity (+)	0.002	< 0.001	Stable > (scour = fill)
Day 8	Near-bed velocity (+)	< 0.001	< 0.001	Stable > (scour = fill)
Day 22	POM (+)	0.02	< 0.001	Fill > scour
Day 29	-	-	0.004	Fill > scour
	Near-bed velocity (+)	< 0.001	-	-
Day 36	Near-bed velocity (+)	< 0.001	0.007	Fill > scour
	Epilithic algal biomass (+)	< 0.001	< 0.001	Fill > (stable = scour)
Day 50	POM (+)	< 0.001	0.007	(Stable = fill) > scour
***Simulium* spp.**				
Day 1	-	-	0.01	Fill > (stable = scour)
	Near-bed velocity (+)	< 0.001	-	-
Day 8	-	-	0.02	Fill > scour
	Near-bed velocity (+)	< 0.001	-	-
	Substratum size (+)	0.01	-	-
Day 22	Substratum size (+)	0.007	0.002	(Stable = fill) > scour
Day 29	Near-bed velocity (+)	< 0.001	-	-
Day 36	Near-bed velocity (+)	0.005	0.007	Fill > stable
Day 50	-	-	0.03	Fill > scour
	Near-bed velocity (+)	0.002	-	-
	Substratum size (+)	0.003	-	-
Hydropsychidae				
Day 1	Substratum size (+)	0.02	-	-
Day 8	Near-bed velocity (+)	0.002	-	-
Day 22	POM (+)	0.002	-	-
Day 29	POM (+)	0.009	0.04	Fill > scour
	Near-bed velocity (+)	< 0.001	-	-
Day 36	Epilithic algal biomass (-)	< 0.001	0.02	Fill > scour
	Near-bed velocity (+)	0.02	-	-
Day 50	POM (+)	0.001	0.03	Fill > scour
Chironomidae				
Day 1	-	-	< 0.001	Stable > (scour = fill)
	POM (+)	0.01	0.03	Stable > scour
Day 22	POM (+)	< 0.001	-	-
Day 29	POM (+)	0.006	-	-
Day 36	Near-bed velocity (+)	0.004	-	-
	POM (+)	0.04	-	-
Day 50	POM (+)	< 0.001	-	-

Table 4 (continued)

Date & dependent variable	**Covariate in ANCOVA**	**Covariate** ***P***	**Factor** ***P***	**Ranking (*post-hoc*)**
***Leuctra* spp.**				
Day 8	-	-	0.01	Scour > fill
	POM (+)	0.007	-	-
Day 22	Epilithic algal biomass (+)	0.04	-	-
	POM (+)	0.01	-	-
Day 29	POM (+)	< 0.001	0.04	Scour > fill
Day 36	-	-	0.02	Scour > fill
	Substratum size (-)	0.003	-	-
	POM (+)	0.002	-	-
Day 50	Substratum size (-)	0.02	-	-
	POM (+)	0.02	0.05	Scour > fill

Figure legends

Fig. 1. Schematic layout of one experimental block in the Eyach. Within each block, the four replicates of the three disturbance treatments were placed at random. One treatment unit showing six tiles is enlarged. Numbers on tiles indicate the sampling dates (1 = day 1; 2 = day 8; 3 = day 22; 4 = day 29; 5 = day 36; 6 = day 50) and the arrow indicates the flow direction.

Fig. 2. Water depth, near-bed velocity, substratum grain size, epilithic algal biomass and particulate organic matter in the Eyach. Error bars indicate standard errors. Asterisks indicate significant differences among disturbance treatments in the ANOVAs (*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). See Table 1 for exact *P*-values.

Fig. 3. Non-metric multidimensional scaling ordination plots of invertebrate community composition on experimental tiles on the six sampling dates.

Fig. 4. Total invertebrate density, taxon richness, community evenness and densities of the seven most common invertebrate taxa in the Eyach. Asterisks indicate significant differences among disturbance treatments in the ANOVAs and ANCOVAs (*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). See Tables 2 and 4 for detailed results of statistical analyses.

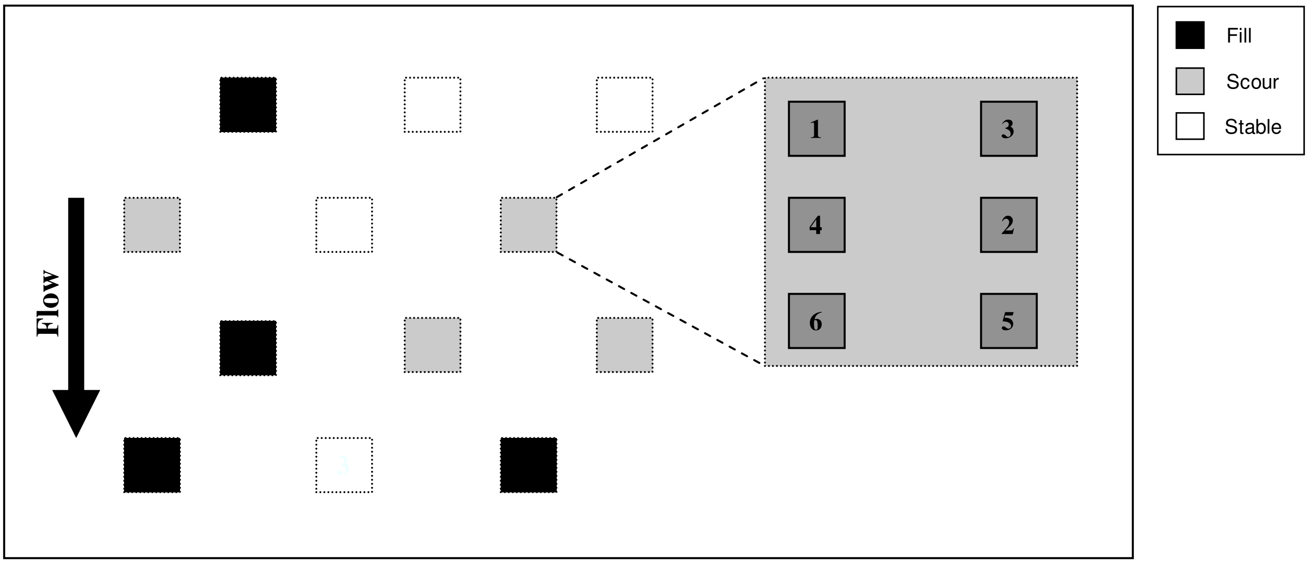


Fig. 1

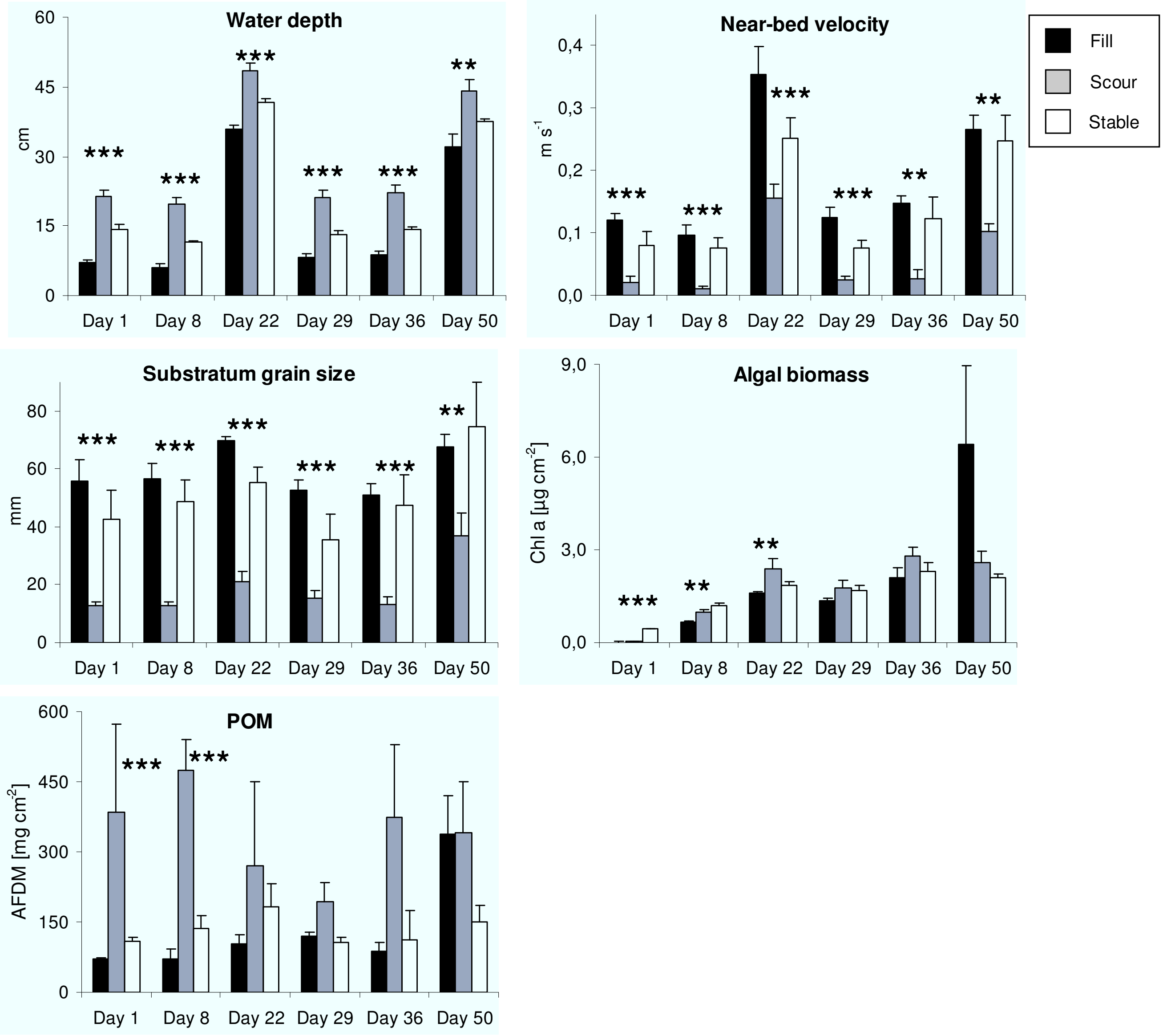

Water depth
cm
60
45
30
15
0
***
***
***
***
***
**
Day 1
Day 8
Day 22
Day 29
Day 36
Day 50
Near-bed velocity
$m\ s^{-1}$
0,4
0,3
0,2
0,1
0,0
***
***
***
***
**
**
Fill
Scour
Stable
Substratum grain size
mm
80
60
40
20
0
***
***
***
***
***
**
Algal biomass
Chl a [$\mu g\ cm^{-2}$]
9,0
6,0
3,0
0,0
***
**
**
POM
AFDM [$mg\ cm^{-2}$]
600
450
300
150
0
***
***

Fig. 2

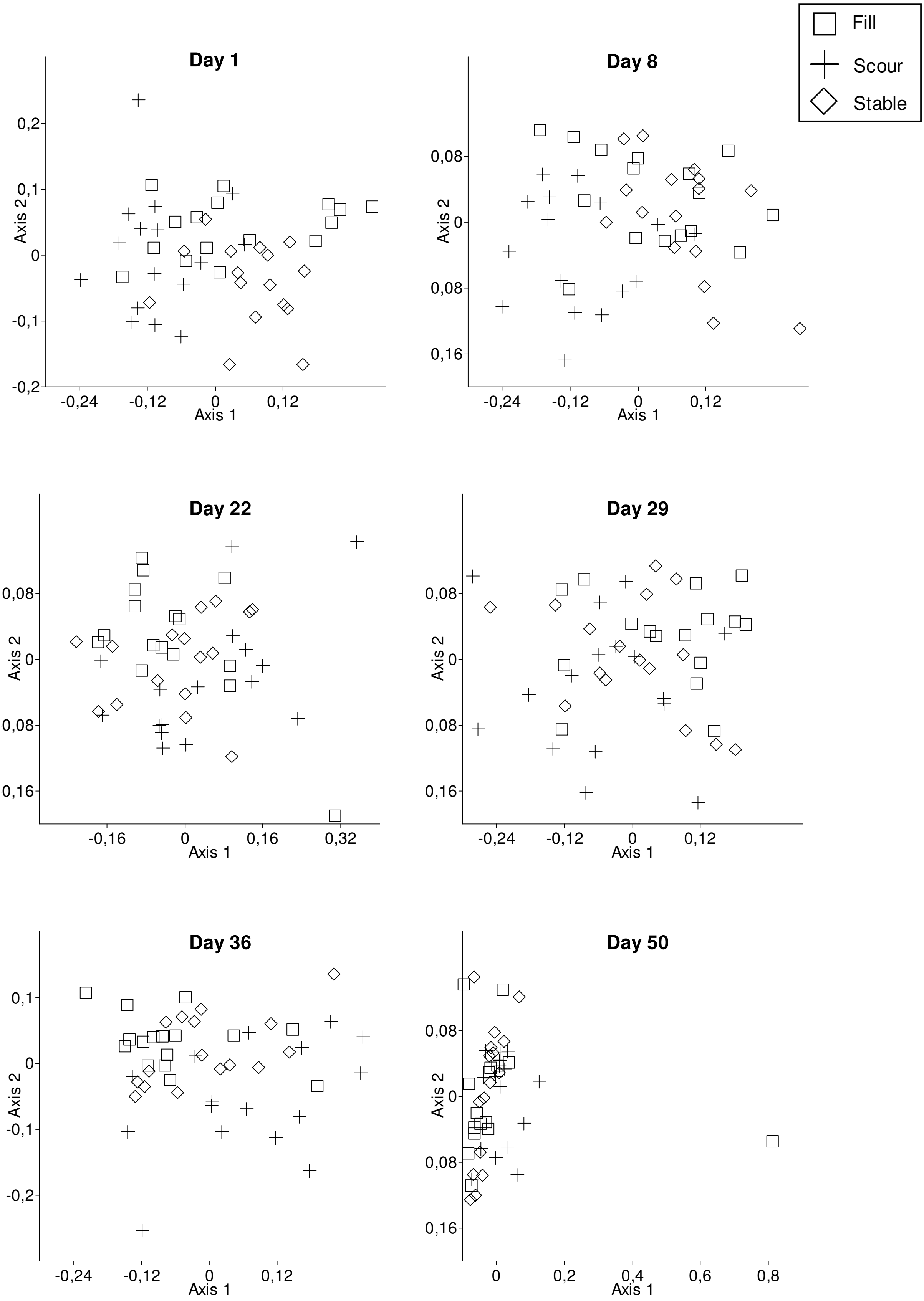

Fill
Scour
Stable
Day 1
Day 8
Day 22
Day 29
Day 36
Day 50
Axis 2
Axis 1
0,2
0,1
0
-0,1
-0,2
-0,24
-0,12
0,12
0,08
0,16
-0,16
0,32
0,2
0,4
0,6
0,8

Fig. 3

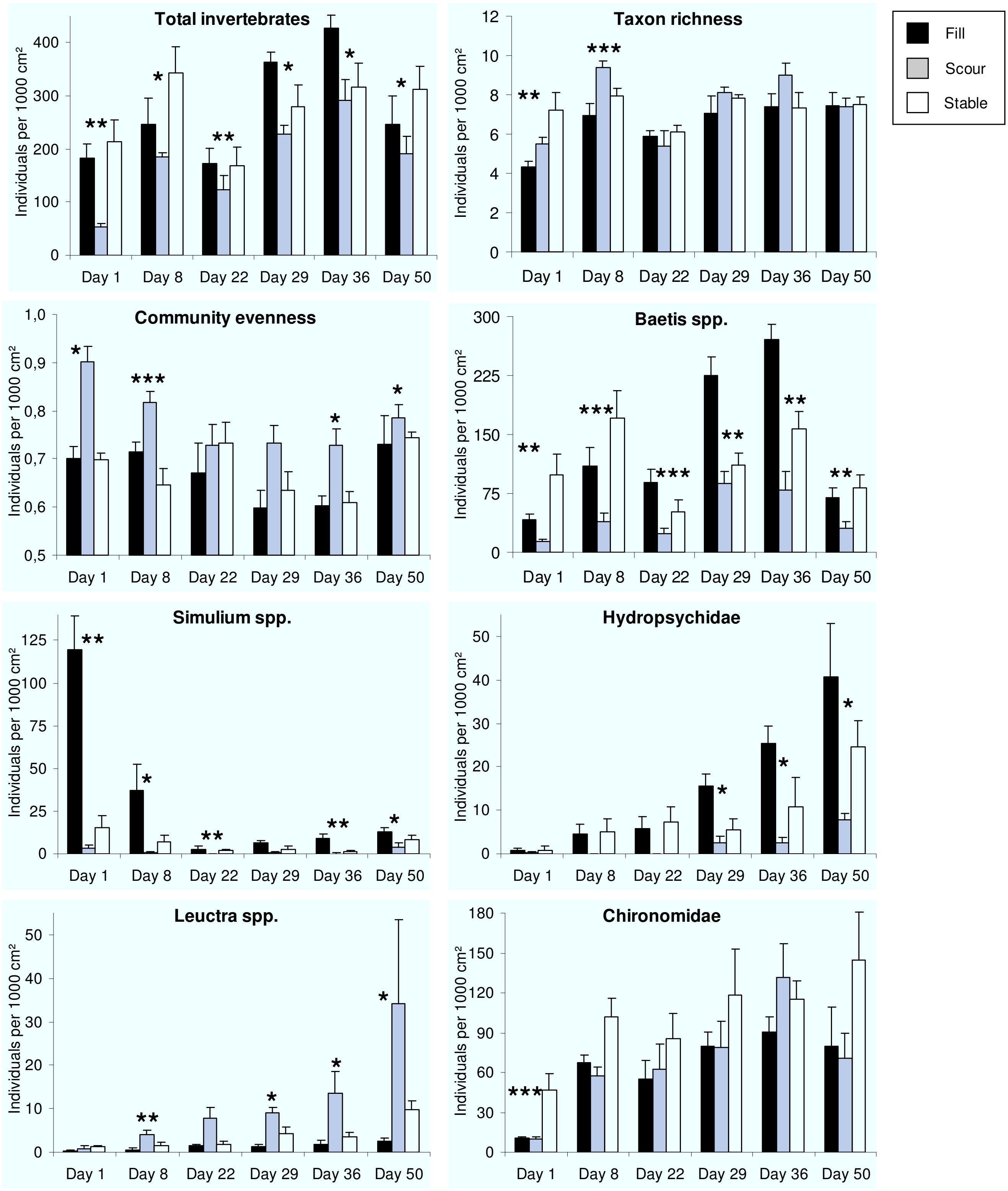
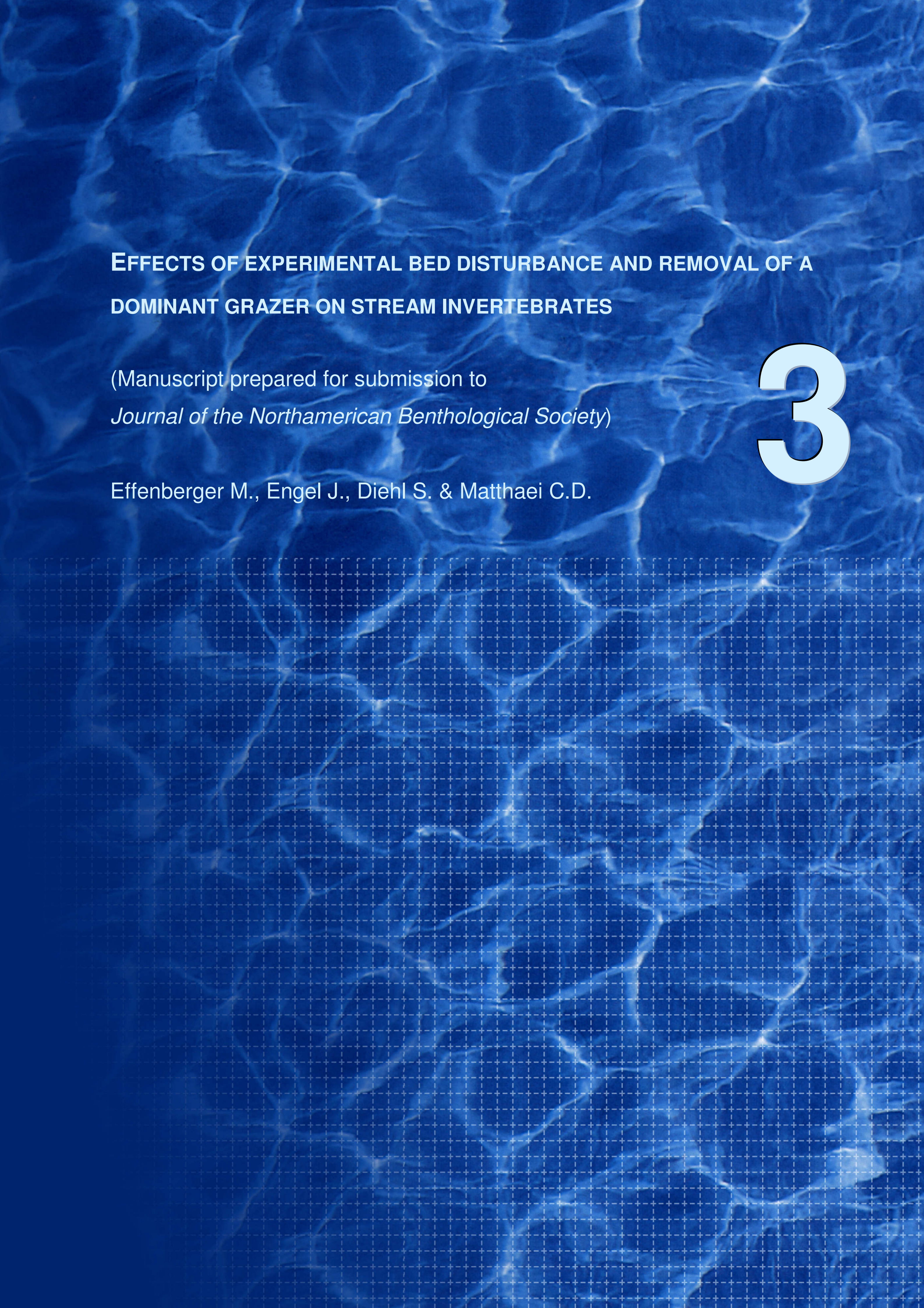

Total invertebrates
Taxon richness
Community evenness
Baetis spp.
Simulium spp.
Hydropsychidae
Leuctra spp.
Chironomidae
Individuals per 1000 cm²
Day 1
Day 8
Day 22
Day 29
Day 36
Day 50
Fill
Scour
Stable

Fig. 4



EFFECTS OF EXPERIMENTAL BED DISTURBANCE AND REMOVAL OF A DOMINANT GRAZER ON STREAM INVERTEBRATES

3

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Effenberger M., Engel J., Diehl S. & Matthaei C.D.

Effects of experimental bed disturbance and removal of a dominant grazer on stream invertebrates

Michael Effenberger[1], Johanna Engel[1], Sebastian Diehl[1]
& Christoph D. Matthaei[2]

[1]Department Biology II, Aquatic Ecology, University of Munich (LMU),
Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

[2]Department of Zoology, University of Otago, P.O. Box 56,
Dunedin, New Zealand

Corresponding author
E-mail: effenberger@zi.biologie.uni-muenchen.de
Fax: 0049-89-2180-74211

Abstract

It is widely believed that the importance of competitive interactions decreases with increasing frequency of abiotic disturbances. An alternative view suggests the opposite, because a population weakened by disturbances may be sensitive to even low densities of a competitor. We experimentally investigated the effects of a patchy flood disturbance and the removal of a potentially dominant competitor on the invertebrate community in a flood-prone stream. Bed movement during a moderate flood was simulated by scouring or filling stream bed patches (area 0.49 m^2) at the start of the experiment while leaving other patches undisturbed (stable). We then manipulated the density of the numerically dominant mayfly *Baetis* spp. on ceramic tiles (= sampling units) inside the experimental patches over a period of 50 days. Two removal treatments (*Baetis* removed every 3-4 days vs. controls) were crossed with the disturbance treatments (scour, fill, stable). Shortly after the disturbance, taxon richness and the densities of *Baetis* spp., chironomids, and total invertebrates were highest in stable patches. Several weeks later, *Baetis* spp. and simuliids were most abundant in fill and *Leuctra* spp. in scour patches. Community evenness was highest in scour patches on several sampling dates. In contrast to the frequent and lasting effects of disturbance treatments, effects of experimental *Baetis* removal occurred no more often than expected by chance alone. Our results thus confirm the importance of patchy disturbances for the microdistribution of stream invertebrates, whereas patchy removal of the numerically dominant taxon hardly influenced the invertebrate assemblages at the patch scale.

Keywords: local disturbance history, competition, invertebrate removal, experimental disturbance, stream invertebrates

Introduction

Disturbances are known to influence organism abundances and community structure in almost every ecosystem (Watt 1947, Connell 1978, Huston 1979). Most of the time, disturbances have a negative immediate impact on organisms, either directly by removing animals or indirectly by destroying or altering their habitats (Begon *et al.* 1996). On the other hand, disturbances create open space or release resources which can be used by re-colonizing individuals. Disturbances are therefore an important driver of spatial and temporal heterogeneity in ecosystems (White & Jentsch 2001).

Few ecosystems experience either the frequency or intensity of disturbances observed in running waters. Hence, disturbance is regarded as one of the dominant organizing factors in streams (Fisher *et al.* 1982, Power & Stewart 1987, Resh *et al.* 1988, Lake 2000). During floods, high shear forces suspend sediments, move bottom materials and kill or displace stream biota (Lake 2000). Consequently, significant decreases in the densities of benthic organisms, for instance macroinvertebrates, have been recorded after bed-moving floods (e.g. Grimm & Fisher 1989, Robinson *et al.* 2003, 2004, Effenberger *et al.* 2006). However, recent research has shown that floods can affect benthic organisms not just by killing or displacing them, but also in more subtle ways.

Floods can induce a patchy mosaic of bed disturbance, with some patches experiencing sediment scour and some deposition (fill) while others remain unchanged (Matthaei *et al.* 1999). Matthaei & Townsend (2000) termed the resulting small-scale patterns of scour, fill or no bed movement “local disturbance history” and demonstrated that this disturbance history influenced the small-scale distribution of benthic invertebrates in a frequently disturbed New Zealand stream for at least two months after a flood. A number of additional, descriptive studies have confirmed that local disturbance history can have long-lasting effects on the small-scale distributions of benthic invertebrates (Effenberger *et al.* 2006) and algae (Matthaei *et al.* 2003) in running waters. A recent field experiment focusing on stream invertebrates suggests that disturbance-induced changes in habitat parameters (e.g. current velocity, substratum size, food resources) are a likely mechanism contributing to such long-term effects of disturbance history (Effenberger *et al.* 2008).

As a second driver of spatial and temporal heterogeneity, biotic interactions such as competition (e.g. Hart 1987, Kohler 1992), grazing (Sarnelle *et al.* 1993, Roll *et al.* 2005) and predation (e.g. Wooster 1994, Diehl *et al.* 2000) are known to influence the distribution of stream biota (Cooper *et al.* 1998). However, although most streams are subject to considerable discharge variations (Poff & Ward 1989, Poff 1996), almost all field experiments investigating the interplay of disturbance and biotic interactions in running waters (except for Pringle & Hamazaki 1997, see Discussion) have been performed either in systems with relatively stable flow (e.g. lake outlet streams or small streams in low-gradient catchments with moderate rainfall; McAuliffe 1984, Kohler 1992, Kohler & Wiley 1997) or in periodically disturbed systems during periods of stable flow (Hemphill & Cooper 1983, Hemphill 1991). While biotic interactions are likely to be important in stable streams, Poff & Ward (1989) and Townsend (1989) proposed that the importance of such interactions should decrease with increasing frequency of disturbance. This conforms with general beliefs that the strength of biotic interactions decreases with decreasing population densities, and that there are trade-offs between traits conveying competitive ability vs. resistance against disturbance (Huston 1979, Menge & Sutherland 1987). On the other hand, Chesson and Huntly (1997) argued that biotic interactions can also play an important role in frequently disturbed ecosystems, because a relatively minor stress caused by competition or predation could be enough to push over the edge a population already weakened by abiotic disturbance. Also, intense disturbances may alter the nature of biotic interactions rather than override them, e.g. by setting initial conditions leading to alternative community trajectories (Power *et al.* 2008, Robinson *et al.* 2008). Clearly, there is a need to integrate hydrologic disturbance and biotic interactions in a common conceptual framework if we want to understand the effects of different disturbance regimes on stream communities (Power *et al.* 1995).

Theoretical and empirical studies suggest that the trajectory of community recovery after a flood disturbance depends on the severity of the disturbance, the productivity of the system, and the intensity of biotic interactions during the recovery phase (Nisbet *et al.* 1997, Power 1992, Marks *et al.* 2000, Roll *et al.* 2005). This view is supported by work in other systems exposed to periodic disturbances, such as rocky intertidal communities (Lubchenco 1983, Menge & Sutherland 1987, Worm *et* *al.* 2002) and temporarily drying pond systems (Wellborn *et al.* 1996, Kneitel & Chase 2004).

The aim of our study was to investigate the interplay between patchy bed disturbance and local biotic interactions in determining the microdistribution of benthic stream invertebrates in a frequently disturbed environment. To achieve this aim, we manipulated local disturbance history (to simulate bed movement during a flood) and the density of *Baetis* spp., the numerically dominant invertebrate taxon (to manipulate the intensity of competition between invertebrates) in a flood-prone German stream. Two invertebrate removal treatments (repeated removals of *Baetis* and no removal) were crossed with three disturbance treatments (scour, fill and stable) in a full-factorial design.

Based on evidence from previous studies of natural disturbances (e.g. Death & Winterbourn 1995, Death 1996, Matthaei *et al.* 2000), we expected experimental disturbance to cause both short-term (≤ 1 week) decreases and more complex longer-term (> 4 weeks) effects on invertebrate density and taxon richness (Matthaei *et al.* 2000, Effenberger *et al.* 2006). In stable bed patches, we expected removal of *Baetis* to cause increases in overall invertebrate taxon richness and the densities of non-manipulated taxa because of reduced competition for resources (Kohler 1992, Kohler & Wiley 1997). The scenarios suggested by Poff & Ward (1989), Townsend (1989) and Chesson & Huntly (1997) yield additional, and contrasting expectations concerning the overall importance of competition (in our case removal of *Baetis*) relative to disturbance and the interaction of disturbance and *Baetis* removal. Following Poff & Ward (1989) and Townsend (1989), competition should be relatively unimportant for invertebrate distributions due to the frequently disturbed nature of our study stream, and effects of *Baetis* removal should also be weaker in disturbed than in stable bed patches. Following Chesson & Huntly (1997), competition should be similarly important in our study stream as in more stable streams, and also in disturbed patches compared to stable patches within our stream.

Methods

Study site

Our study was carried out in the Eyach, a flood-prone, third-order stream in southern Germany. (For a detailed description of the stream and our study site see Effenberger *et al.* 2008.) The Eyach (47°46´N, 11°05´E) has a steep catchment (area ca. 27 km², altitude 570-930 m a.s.l.) that lies in a zone of fairly high rainfall at the northern edge of the Alps (mean annual rainfall in the catchment is 1210 mm; German Weather Service, station Hohenpeissenberg). Consequently, the Eyach has a harsh discharge regime with frequent floods that are often quite severe. The sediment supply into the Eyach is high because of the presence of several steep, unstable scree areas in the catchment. This high sediment input results in an unstable stream bed that is easily moved by floods.

Experimental disturbance and removal of invertebrates

Our study was conducted from June to August 2005. On 7 June, we exposed a total of 288 unglazed white tiles (9.8 × 9.8 × 0.8 cm; surface area 223 cm²) across a study reach of 200 m length and left them undisturbed for 12 days to allow natural colonization by stream organisms. These tiles were used as sampling units for macroinvertebrates and epilithic algae. Tiles were equipped with two silicon "feet" (1 × 1 × 0.5 cm) near their downstream edges to facilitate invertebrate colonization of tile undersides and to increase the hydraulic pressure holding the tiles on the substratum. Tiles were exposed in four blocks along the reach (Fig.1), each covering an area of 5 × 5 m. Blocks were spaced at intervals of 5 to 50 m. Within each block, tiles were organized in 12 experimental patches containing six tiles each. Each patch (area 0.7 × 0.7 m, inter-patch distance ≥ 1.5 m) was an independent experimental unit that was subjected to one of three randomly assigned disturbance treatments (scour, fill and stable) at the start of the experiment and to one of two repeated invertebrate removal treatments (see below). Subsequently, one tile from each patch was collected on each of six successive post-disturbance sampling dates.

For the disturbance treatments, the substratum in bed patches of 0.7 × 0.7 m was either scoured or filled to a depth of about 15-20 cm (scour and fill patches), or left unchanged (stable patches). The substratum for the fill patches was collected from dry gravel bars in the floodplain three days before the start of the experiment and stored in buckets on the stream bank to ensure that it contained no living stream invertebrates or algae (see Effenberger *et al.* 2008). Additionally, tiles in scour and fill patches were scrubbed with a soft brush (see McCabe & Gotelli 2000) to remove all invertebrates and a large proportion of epilithic algae. This experimental disturbance can simulate important aspects of a natural flood, such as local rearrangement of substrata and removal of invertebrates and algae from disturbed patches (see Matthaei *et al.* 1997).

In the removal treatment, we manipulated the density of the grazing mayfly *Baetis* spp., which dominated the invertebrate community numerically in a pilot study conducted two weeks before the experiment (M. Effenberger, unpublished data). We assumed that *Baetis* had the potential to locally compete for resources and possibly also space with the remaining invertebrates in our stream, because this taxon has negatively affected both resources and competitors in previous experiments (Kohler 1992, Diehl *et al.* 2000, Roll *et al.* 2005). *Baetis* also readily colonized experimental tiles and was easy to manipulate. Two treatments (removal of *Baetis* and unmanipulated controls) were applied to the experimental tiles at 3 to 4-day intervals, the shortest interval between invertebrate removals that we could maintain throughout the 50-day experiment. All individuals of *Baetis* were manually removed from the upper surface of each tile using forceps while the tile was left in its original position under water (as in McAuliffe 1984). The remaining invertebrates and algae on the tiles were disturbed as little as possible. All removed invertebrates were caught in a hand net (20 × 15 cm; mesh size 200µm) held immediately downstream of each tile and preserved with 70% ethanol in the field. Removed invertebrates were subsequently identified (most taxa to genus, dipterans to family) and counted under a stereomicroscope (WILD, Heerbrugg, Germany) at 6.5 – 40× magnification.

Our experiment started on 19 June with the creation of the bed disturbance mosaic and ended on 8 August (= day 50) with the last sampling occasion. *Baetis* removals began on 21 June, one day after the first sampling date, and continued twice per week until the end of the experiment. On days 22 and 50, moderate flow peaks (< twice the annual mean flow, M. Effenberger, personal observation) occurred in the Eyach. Both flow peaks did not move any of the experimental tiles.

Biological sampling

One randomly selected tile from each of the 48 patches was sampled 1, 8, 22, 29, 36 and 50 days after the experimental disturbance and 3 days after the previous invertebrate removal. All invertebrates were dislodged gently from the entire surface of each tile, caught in a hand net and preserved with 70% ethanol in the field. In the laboratory, invertebrate samples were processed as described above. To test whether colonization of our experimental tiles was similar to colonization of natural substrata we randomly selected one, roughly tile-sized, surface stone per block on each sampling date and sampled it in the same way as the tiles. Stone surface areas were determined by wrapping stones in aluminium foil of known mass per unit area and weighing the foil (Townsend *et al.* 1997). Invertebrate numbers on both stones and tiles were expressed per area of substrate surface (individuals per m^2), which includes the undersides of tiles.

Because *Baetis* is a grazer, we also assessed potential effects of *Baetis* removal on resource densities by measuring epilithic algal biomass on tiles and natural stones. Algal biomass was sampled by scraping the top surface of each tile with a tooth brush with shortened bristles. Algal samples were preserved immediately with formaldehyde solution (final concentration 4%) in the field, stored on ice in the dark and measured as chlorophyll *a* per cm^2 of tile surface area (using acetone for extraction; APHA 1998).

Effectiveness of invertebrate removal treatments

To test the effectiveness and selectivity of our invertebrate removal treatment, we calculated a “specific removal ratio”. For each tile, we counted the individuals of *Baetis* removed on each removal occasion, averaged these counts across the number of removals between two sampling dates and divided it by the benthic abundance of *Baetis* on the latter of these two dates. (Two removals were performed before sampling days 8, 29 and 36, and four removals before days 22 and 50.) We calculated a similar ratio for non-target taxa, which we lumped into a single group named “bycatch”. We considered the removal treatment as successful (= effective and selective), if the specific removal ratio of *Baetis* was > 1 in the treatment where we wished to remove it. Note that we could only remove invertebrates from the upper tile surfaces (area 96 cm^2), whereas benthic abundance measurements included invertebrates from all tile surfaces (223 cm^2). A removal ratio > 1 therefore implies a highly effective removal of invertebrates.

The specific removal ratio was 1.54 ± 0.32 (mean ± 1 SE) for *Baetis* and only 0.18 ± 0.03 for bycatch. Removal of *Baetis* was thus effective and selective. It should be noted that, although *Baetis* removal was successful, considerable recolonization of tiles by *Baetis* occurred in the intervals between removals. The effect of our removal treatment was therefore to intermittently rather than permanently reduce *Baetis* densities on tile surfaces (see Discussion).

Data analysis

The different components of our data analysis approach have been described in detail and justified in Effenberger *et al.* (2008). Therefore, we present only the main points of this analysis here. Invertebrate community structure was compared between experimental treatments on each of the six sampling dates using analysis of similarities (ANOSIM; Clarke 1993) on a Bray-Curtis similarity matrix obtained from $\log_{10}(x+1)$ transformed invertebrate density data. Differences between disturbance history categories (scour, fill and stable) and *Baetis* treatments (removal and no removal) on each date were interpreted from pairwise tests in the ANOSIM. The same procedure was used for comparison of invertebrate community structure between tiles from stable experimental patches and natural surface stones. Algal biomass values on tiles from stable patches and natural stones on the six dates were compared with separate t-tests.

Further comparisons between disturbance history and *Baetis* removal categories were conducted using ANOVA and MANOVA. Disturbance history and *Baetis* removal were treated as fixed factors and block (1-4) as a random factor. Treatment effects on algal biomass, total invertebrate density, taxon richness and community evenness (Shannon's equitability; Krebs 1985) were investigated with separate ANOVAs for each sampling date. Treatment effects on the densities of the six most common invertebrate taxa were analyzed with MANOVA followed by separate ANOVAs for each of these taxa. After exploratory analysis, data were log (x) or log (x+1) transformed where necessary to improve normality and homoscedasticity. Results for the factor block are not presented because they were not relevant for our research objectives.

If a disturbance history or removal effect was significant, we conducted pairwise Tukey HSD tests, except in cases of persisting heteroscedasticity (results of Levene´s test still significant after transformation) when we performed Games-Howell tests, which do not assume equal variances between groups (Quinn and Keough 2002). All analyses were calculated in SPSS® version 12.0 (SPSS Inc., Chicago, USA) or PAST (Hammer *et al.* 2001).

Results

Temporal patterns on tiles and natural stones

Experimental tiles were colonized by similar invertebrate taxa as were natural surface stones. Invertebrate community structure on stable tiles without *Baetis* removal was similar to community structure on natural stones (ANOSIM; $P > 0.10$ on all sampling dates). Epilithic algal biomass on natural stones was similar on day 8 but higher than on unmanipulated tiles on days 22, 29, 36 and 50 ($P \leq 0.002$). As in the pilot study, *Baetis* spp. was the most abundant invertebrate colonizer of the tiles. This taxon contributed 40% to total invertebrate density (all 288 tile samples combined), followed by Chironomidae (29%), the black fly *Simulium* spp. (5%), the caddisfly family Hydropsychidae (4%), the mayfly *Ecdyonurus* spp. (3%), and the stonefly *Leuctra* spp. (2%). Together, these six taxa comprised 83% of all invertebrates in the samples.

In disturbed patches, algal biomass, and the density and taxon richness of invertebrates increased from day 1 to day 8. The elevated stream flow on day 22 coincided with reduced invertebrate density and richness at that time. Total invertebrate density ($P = 0.004$), taxon richness ($P < 0.001$) and densities of two of the common taxa (*Baetis* spp., $P = 0.005$; *Simulium* spp., $P = 0.02$) were all lower on day 22 than on day 8, the last previous sampling date (one-way ANOVAs; data from all disturbance treatments combined). Nevertheless, none of our experimental tiles was moved, and we noticed no obvious movement of natural bed substrata in the experimental reach (M. Effenberger, personal observation). Further, epilithic algal biomass on tiles increased, rather than decreased, between day 8 and day 22 ($P < 0.001$; see Fig. 2). The small flow peak on day 50 coincided with a reduced density of *Baetis* spp. ($P < 0.001$) compared to that on day 36. By contrast, community evenness ($P = 0.002$) and the density of *Simulium* spp. ($P = 0.04$) increased from day 36 to day 50.

Treatment effects on invertebrate community structure, density and algal biomass

Overall, invertebrate densities and community structure were frequently affected by local disturbance history. In contrast, we found only one main effect and one interactive effect of *Baetis* removal on invertebrate parameters. Directly after the disturbance (day 1), the invertebrate communities in all three disturbance history categories differed from each other (ANOSIM; $P < 0.004$ for each pairwise comparison). While fill and stable patches were relatively similar from day 8 onwards ($P > 0.09$), the difference between scour and fill patches persisted throughout the study (all P-values < 0.03), except for the final sampling date ($P = 0.08$). In addition to day 1, communities in scour and stable patches differed on days 8 and 36 ($P \leq 0.03$). Invertebrate community structure on tiles where *Baetis* had been removed was similar to community structure on control tiles on all sampling dates (ANOSIM; $P > 0.66$ on each date).

Total invertebrate density was higher in stable and fill than in scour patches on day 1, higher in stable than in scour patches on day 8 and higher in fill than in scour patches on day 36 (Fig. 2, Table 1). Taxon richness was higher in stable than in fill and scour patches on day 1 and higher in scour than in fill patches on day 8 (Fig. 3, Table 1). Community evenness was higher in scour than in stable and fill patches on days 1, 8 and 36 (Fig. 3, Table 1). *Baetis* removal had no effect on any of the three community parameters, and no interactions between removal and disturbance history occurred for these parameters. Epilithic algal biomass was higher in stable than in fill and scour patches on day 1 and higher in stable and scour than in fill patches on day 8. On day 22, overall algal biomass was higher on scour tiles from which *Baetis* had been removed than on all other treatment tiles (Fig. 2, disturbance x removal interaction, Table 1).

MANOVA revealed significant effects of disturbance history on the densities of the six most common invertebrate taxa on five out of six sampling dates (Table 2). By contrast, no significant main or interactive effects of *Baetis* removal occurred (Table 2). Density of the mayfly *Baetis* spp. was higher in stable and fill than in scour patches on days 1, 8 and 36. On days 22, 29 and 50, this taxon was more abundant in fill than in scour patches (Fig. 4, Table 3). The black fly *Simulium* spp. reached higher densities in fill than in scour (and once also than in stable) patches on days 1, 8, 36 and 50 (Fig. 4, Table 3). Chironomidae were more common in stable than in scour and fill patches on day 1 (Fig. 4, Table 3). Hydropsychidae were more abundant in stable or fill than in scour patches on days 22 and 36, respectively; on day 22, there were more hydropsychids on tiles without *Baetis* removal than on tiles from which *Baetis* had been removed (Fig. 5, Table 3). The density of *Ecdyonurus* spp. was higher in stable and scour than in fill patches on day 8 (Fig. 5, Table 3). On day 36, disturbance history and *Baetis* removal had an interactive effect on this taxon, with fewer *Ecdyonurus* on tiles with *Baetis* removal than on tiles without removal in fill and stable patches, while the opposite pattern occurred in scour patches (Fig. 5, Table 3). The density of the stonefly *Leuctra* spp. was higher on scour than in stable and fill patches on day 8 and higher in scour than in fill patches on days 29 and 36 (Fig. 5, Table 3).

Discussion

The role of competition in stable versus frequently disturbed streams

To our knowledge, this study is the first field experiment investigating how local disturbance history (as defined by the mosaic of stable, scour and fill patches resulting from a (simulated) flood disturbance) and density manipulations of a numerically dominant invertebrate taxon interacted in their effects on a stream invertebrate community. Based on the predictions of Poff & Ward (1989) and Townsend (1989), competition should be generally relatively unimportant for invertebrate distributions due to the frequently disturbed nature of our study stream, and effects of *Baetis* removal should be stronger in stable than in disturbed bed patches. Based on the alternative hypothesis by Chesson & Huntly (1997), removal of a potentially dominant competitor should affect the remaining invertebrate community regardless of the frequently disturbed nature of our study stream, and effects should be similarly strong in disturbed patches compared to stable patches within the stream.

Most of our results are in better agreement with the predictions of Poff & Ward (1989) and Townsend (1989) than with those of Chesson & Huntly (1997). While significant effects of local disturbance history on invertebrate distributions were common (26 out of 54 possible cases), we observed only a single case in which *Baetis* removal statistically significantly influenced the density of any other common invertebrate taxon or the taxonomic composition of the invertebrate community across all disturbance treatments. This is less often than expected by chance alone. Interactions between disturbance and *Baetis* removal treatments, which would be expected if Poff & Ward's (1989) and Townsend's (1989) predictions can be applied to patches of differing bed stability within the same stream, also occurred in just a single case out of 54. However, this lack of interactions may be simply a consequence of the overall lack of *Baetis* removal effects and should therefore not be interpreted as supporting the hypotheses of Chesson & Huntly (1997). Moreover, while in other experimental settings *Baetis* has been shown to negatively affect algal resources (Kohler 1992, Diehl *et al.* 2000, Roll *et al.* 2005), algal biomass increased in our *Baetis* removal treatments in only one disturbance patch type and on only one sampling date out of six. Clearly, grazing pressure on algae did not decrease consistently on tiles where *Baetis* was removed, again in agreement with the expectations of Poff & Ward (1989) and Townsend (1989).

The general lack of *Baetis* removal effects in stable patches contrasts with the results of the few studies available for direct comparison. Hemphill & Cooper (1983) and Hemphill (1991) found strong evidence that frequent experimental disturbance reduced competition for space between two filter-feeding stream insects (simuliids and hydropsychids) during periods of stable flow in a Californian stream. Likewise, McAuliffe (1984) showed that physical disturbance (the overturning of individual stones) prevented the monopolization of space by the sedentary caddis fly larva *Leucotrichia* in a stable lake outlet stream in Montana, in which this caddis fly can reach very high densities. It is worth noting that the spatial scales of invertebrate removal and disturbance units in these three studies were very similar to those manipulated in our experiment, and that the intervals between invertebrate removals were more than twice as long as in our experiment.

The three earlier experiments differ from the present study in that they were conducted during periods of hydrological stability when relatively sessile invertebrate taxa, which compete primarily for space, were able to reach high densities. In contrast, the highly mobile *Baetis* competes primarily for benthic food resources (see Kohler 1992, Kuhara *et al.* 1999), moves rapidly between favourable and unfavourable habitats (Kohler 1984) and recolonizes bare patches quickly after disturbance (Mackay 1992, Matthaei *et al.* 1996). Further, invertebrate densities in the Eyach may be generally kept so low by frequent floods that resources for grazers rarely become limiting and, consequently, additional density reductions of *Baetis* have only marginal effects on the community. Recall that two minor high-flow events occurred during the 50 days of our experiment, both of which coincided with reduced invertebrate densities. Throughout our experiment, invertebrate densities on natural surface stones were indeed rather low in comparison to more stable streams. For instance, Baetis densities were 3-12 times lower than in other streams during periods of stable flow conditions (Kohler and Wiley 1997, Matthaei *et al.* 1997, Diehl *et al.* 2000, Robinson & Uehlinger 2008; note that densities per stone surface area in Figs. 2-5 must be divided by a factor of 2-3 to yield densities per surface area of stream bed).

Clearly the streams investigated by Hemphill & Cooper (1983), Hemphill (1991) and McAuliffe (1984) are relatively near the stable end of the gradient of disturbance frequency and intensity occurring in natural streams, whereas the Eyach is probably closer to the “frequently disturbed” end of this gradient (see Poff & Ward 1989 and Poff 1996). Collectively, the results from all three streams therefore conform with the predictions of Poff & Ward (1989) and Townsend (1989), according to which the importance of biotic interactions in shaping aquatic communities should decrease with increasing frequency or intensity of disturbance. The generality of these patterns is, however, far from clear. For example, when Pringle & Hamazaki (1997) excluded grazing fishes from small bed patches of a flood-prone tropical stream over a period spanning several high flow events, they found strong fish effects on algal community structure and invertebrate density. One reason for the differences to our study may be that grazing by fish is directed towards sedentary organisms, which recolonize manipulated patches from the unmanipulated environment much more slowly than do mobile invertebrates. Furthermore, floods in this tropical lowland stream were not accompanied by bed movement. Bed movement, however, may be one of the most important criteria determining whether or not a flood represents a disturbance for the benthic community (Poff 1992).

Limitations of our experiment

The ability of our experiment to discriminate among the conceptual models of Poff & Ward (1989), Townsend (1989), and Chesson & Huntly (1997) was limited by the spatial and temporal scales of our experiment. We investigated effects of bed disturbances and invertebrate removals occurring in a small-scale mosaic of patches and the application of experimental treatments was limited to a single stream reach and a period of 50 days. By contrast, all three conceptual models compare different disturbance scenarios occurring at the spatial scale of entire systems and the temporal scale of several generation times. However, these spatial and temporal scales are much less amenable to manipulative experimentation. We also want to emphasize that the spatial scale of our disturbance manipulations is highly relevant to many natural situations, because bed-moving floods often result in patchy bed movements as simulated in our experiment (Matthaei *et al.* 1999, Effenberger *et al.* 2006).

While the spatial scale of our disturbance treatments is thus of clear relevance, it would have been desirable to manipulate *Baetis* densities at larger spatial scales. *Baetis* were able to recolonize the relatively small removal patches from the surrounding, unmanipulated stream bed. This recolonization reduced the strength of the *Baetis* removal treatment. The high removal ratio indicates, however, that *Baetis* removal was highly effective on the day of removal, resulting in intermittently reduced *Baetis* densities on the manipulated tiles. We can assess the rate at which *Baetis* recolonized removal tiles by comparing *Baetis* densities on disturbed versus stable tiles on day 1 of our experiment. Invertebrates had been removed from scour and fill tiles, but not from stable tiles, during the experimental disturbance performed on the previous day. Compared to stable tiles, *Baetis* densities on day 1 were still reduced by 86% on scour tiles and by 57% on fill tiles, suggesting that the effect of *Baetis* removal lasted for at least one day. Later in the experiment, when algal biomass had increased on tiles, recolonization rates of *Baetis* removal tiles may have been faster.

Effects of experimental disturbance

In contrast to *Baetis* removals, local disturbance history treatments had many effects on the microdistribution of invertebrates in the Eyach, several of which lasted for weeks. The mechanisms through which disturbance history affected the benthic community have been investigated in a companion paper (Effenberger *et al.* 2008) which included an analysis of the contributions of biotic and abiotic habitat parameters (e.g. current velocity, substratum size, food resources) to the observed distributional patterns. Thus, we discuss disturbance history effects only briefly here and refer to Effenberger *et al.* (2008) for a more comprehensive discussion.

Habitat parameters were frequently influenced by disturbance history in our experiment. For example, scouring generally exposed finer substrata and caused local depressions in the stream bed characterized by slower near-bed current velocity (Effenberger *et al.* 2008). Invertebrate distributions were, in turn, often related to these and other habitat parameters. Directly after the experimental disturbance, we expected higher invertebrate densities in stable patches than in both disturbed patch types, because invertebrates had only one day to recolonize disturbed patches. These predictions were largely fulfilled. As expected from a previous study of natural floods (Effenberger *et al.* 2006), most of the differences between patch types also changed little from one to eight days after the experimental disturbance. The only taxon showing higher densities in disturbed than in stable patches from early on was *Simulium* spp., which was most common in fill patches where current velocities were highest. Several other invertebrate taxa developed preferences for scour or fill patches later in the experiment, as has been observed in earlier, descriptive studies (Matthaei & Townsend 2000, Effenberger *et al.* 2006). For example, *Leuctra* spp. became most common in scour patches with slower current speeds, which accumulated higher levels of particulate organic matter. Conversely, *Baetis* spp. and Hydropsychidae became most abundant in fill patches, which had the highest current speeds. Overall, these results suggest that several 'direct' initial effects of local disturbance history on the invertebrates were subsequently replaced by 'indirect' effects of disturbance history acting via disturbance-induced changes in habitat parameters such as current velocity or food availability.

Outlook

In our experiment, conducted in a naturally flood-prone stream, small-scale removals of the numerically dominant invertebrate taxon showed hardly any effects on the remaining invertebrate community and on benthic algae. By contrast, initial small-scale bed disturbances affected the microdistribution of the most common invertebrate taxa in a lasting manner, i.e. throughout the entire 50-day experiment. These results add to the very limited data addressing the methodologically challenging question to which extent biotic interactions influence stream invertebrate communities under frequently disturbed conditions. Because all existing manipulative experiments investigating the interplay between bed disturbances and biotic interactions (including ours) were unreplicated at the stream level (owing to the prohibitive effort involved), more experiments with similar study designs are needed to examine the generality of our results. Together, these experiments should span a large range of natural disturbance regimes (from highly stable to very frequently disturbed). Future experimental research should also focus on removing invertebrates from larger areas and using even shorter intervals between removals of potentially dominant competitors when highly mobile species are targeted, and possibly also on disturbing larger stream bed patches and/or longer sections of stream bed.

Other biotic factors such as predation and productivity have been found to alter the effects of disturbance on community structure in streams (Wooton *et al.* 1996, Thomson *et al.* 2002, Cardinale *et al.* 2006) and several other ecosystems (e.g. Kneitel & Chase 2004, Svensson *et al.* 2007). So far, these factors have been largely examined in isolation or in two-factorial designs, although theoretical and empirical evidence suggests that these factors can interact strongly (Proulx & Mazumder 1998, Kondoh 2001, Worm *et al.* 2002, Sih *et al.* 2004). Exploring the interaction of disturbance with multiple biotic factors should therefore be a priority in future community ecology.

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Table 1. Summary (*P*-values) of treatment effects on the invertebrate communities as determined by separate ANOVAs on each sampling date. Only statistically significant results are presented ($P < 0.05$) plus rankings of main treatment effects as determined by *post-hoc* tests. The results for the block factor are not shown because they were not relevant for our hypotheses. Dist = Disturbance, B = *Baetis* removal.

Date & dependent variable	**Disturbance *P***	**Ranking (post-hoc)**	**Removal *P***	**Ranking (post-hoc)**	**Significant interactions *P***
Epilithic algal biomass					
Day 1	< 0.001	Stable > (scour = fill)	-	-	-
Day 8	< 0.001	(Stable = scour) > fill	-	-	-
Day 22	0.002	Scour > fill	0.006	Rem > No rem	0.004 (Dist x B)
Total invertebrates			-	-	-
Day 1	< 0.001	(Stable = fill) > scour	-	-	-
Day 8	0.02	Stable > scour	-	-	
Day 36	0.04	Fill > scour			
Taxon richness			-	-	-
Day 1	< 0.001	Stable > (scour = fill)	-	-	-
Day 8	0.001	Scour > fill	-	-	-
Community evenness					
Day 1	< 0.001	Scour > (stable=fill)	-	-	-
Day 8	< 0.001	Scour > (stable=fill)	-	-	-
Day 36	0.02	Scour > (stable = fill)			

Table 2. Summary (*P*-values) of treatment effects on the invertebrate communities as determined by three-way MANOVAs. The results for the block factor are not shown because they were not relevant for our hypotheses. Because all results for *Baetis* removal and factor interactions were non-significant ($P > 0.22$; $P > 0.07$), these results are not shown. *P*-values are based on statistics of Pillai´s trace tests.

Date	**Disturbance**
	P
Day 1	< 0.001
Day 8	< 0.001
Day 22	0.01
Day 29	0.16
Day 36	0.003
Day 50	0.02

Table 3. Summary (P-values) of treatment effects on the six invertebrate taxa as determined by separate ANOVAs on all sampling dates. Only statistically significant results are presented ($P < 0.05$) plus rankings of main treatment effects as determined by post-hoc tests. The results for the block factor are not shown because they were not relevant for our hypotheses. Dist = Disturbance, B = Baetis removal.

Date & dependent variable	Disturbance *P*	Ranking (post-hoc)	Removal *P*	Ranking (post-hoc)	Significant interactions *P*
***Baetis* spp.**					
Day 1	< 0.001	(Stable = fill) > scour	-	-	-
Day 8	< 0.001	(Stable = fill) > scour	-	-	-
Day 22	0.001	Fill > scour	-	-	-
Day 29	0.005	Fill > scour	-	-	-
Day 36	< 0.001	(Stable = fill) > scour	-	-	-
Day 50	0.03	Fill > scour	-	-	
***Simulium* spp.**					
Day 1	0.02	Fill > scour	-	-	-
Day 8	0.01	Fill > scour	-	-	-
Day 22	0.04	Fill > scour	-	-	-
Day 36	< 0.001	Fill > (stable = scour)	-	-	-
Day 50	0.04	Fill > scour	-	-	-
Chironomidae					
Day 1	< 0.001	Stable > (scour = fill)	-	-	-

Table 3 continued

Date & dependent variable	Disturbance *P*	Ranking (post-hoc)	Removal *P*	Ranking (post-hoc)	Significant interactions *P*
***Ecdyonurus* spp.**					
Day 8	0.007	(Stable = scour) > fill	-	-	-
Day 36	-	-	-	-	0.02 (Dist x B)
Hydropsychidae					
Day 22	0.02	Stable > scour	0.05	No rem > rem	-
Day 36	0.004	Fill > scour	-	-	-
***Leuctra* spp.**			-	-	
Day 8	0.01	Scour > (stable = fill)	-	-	-
Day 29	0.03	Scour > fill	-	-	-
Day 36	0.02	Scour > fill	-	-	-

Figure legends

Fig. 1. Schematic layout of one experimental block in the Eyach. Within each block, the combinations of the two experimental factors were placed at random. One treatment unit showing 6 tiles is enlarged. Numbers on tiles indicate sampling dates (1 = Day 1; 2 = Day 8; 3 = Day 22; 4 = Day 29; 5 = Day 36; 6 = Day 50) and the arrow indicates the direction of flow. B = *Baetis* removal, No = No removal.

Fig. 2. Total invertebrate density and density of epilithic chlorophyll *a* in *Baetis* removal and disturbance treatments in the Eyach. Error bars indicate standard errors. Significant differences among treatments in the ANOVAs are shown by asterisks (*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Dist = disturbance; Rem = *Baetis* removal; Int = interaction between removal and disturbance). See Table 1 for exact *P*-values.

Fig. 3. Taxon richness and community evenness in *Baetis* removal and disturbance treatments in the Eyach. See Table 3 for exact *P*-values. Symbols are as in Fig. 2.

Fig. 4. Densities of *Baetis* spp., *Simulium* spp. and Chironomidae in *Baetis* removal and disturbance treatments in the Eyach. See Table 3 for exact *P*-values. Symbols are as in Fig. 2.

Fig. 5. Densities of *Ecdyonurus* spp., Hydropsychidae and *Leuctra* spp. in *Baetis* removal and disturbance treatments in the Eyach. See Table 3 for exact *P*-values. Symbols are as in Fig. 2.

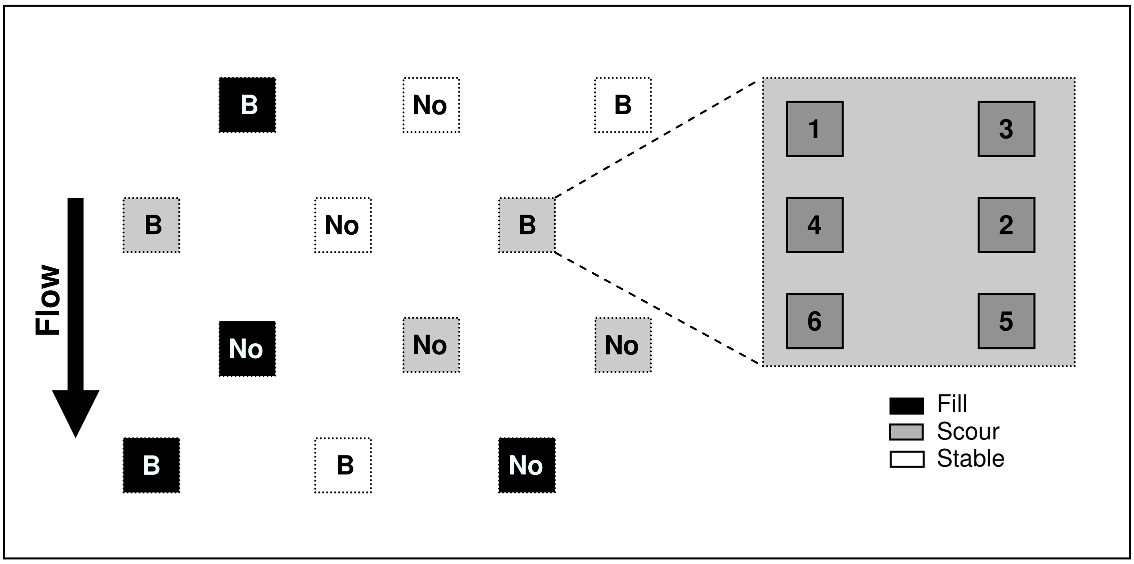


Fig. 1

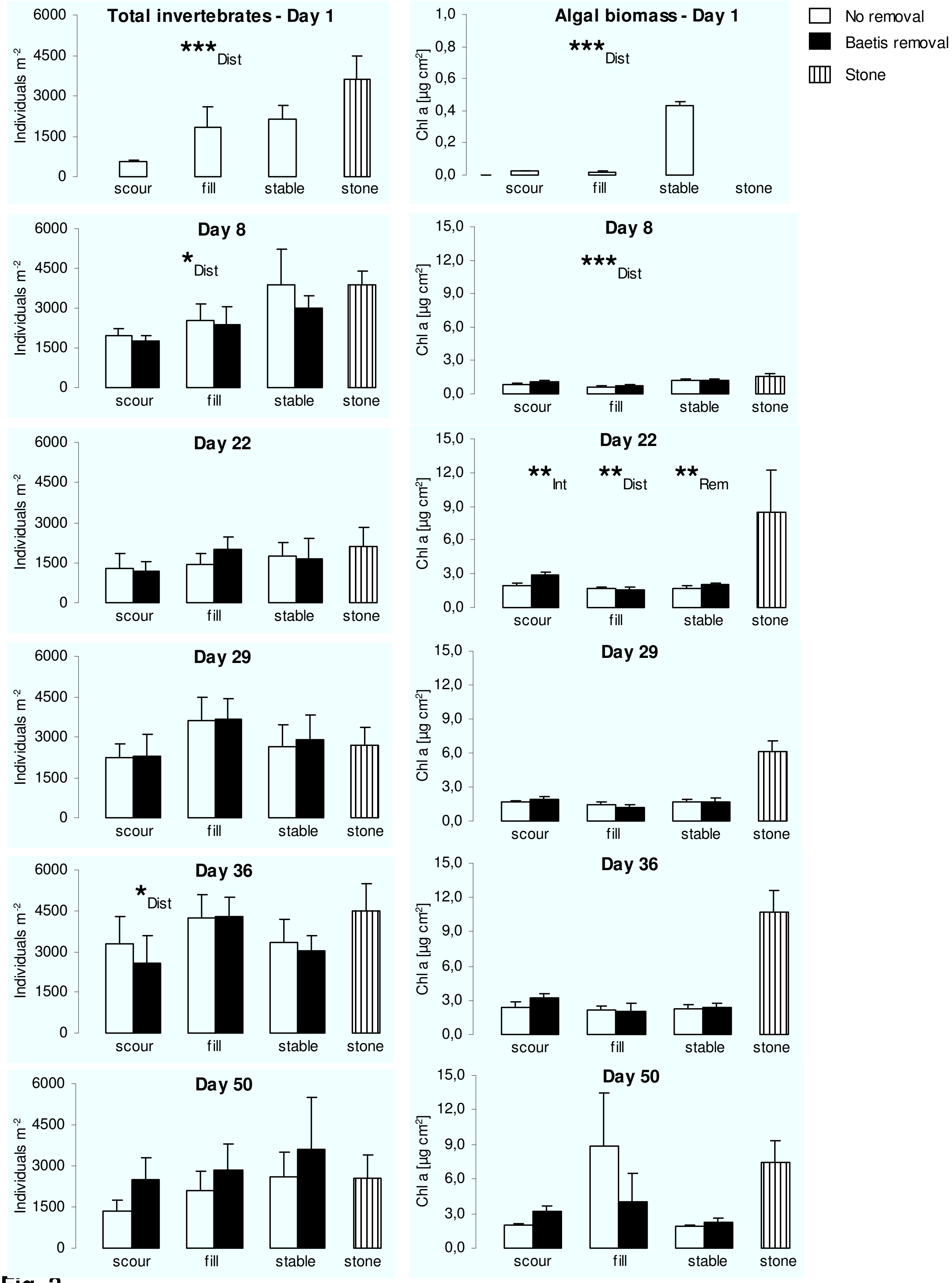

Total invertebrates - Day 1
Algal biomass - Day 1
No removal
Baetis removal
Stone
Individuals m^{-2}
Chl a [µg cm^{-2}]
***Dist
*Dist
**Int
**Dist
**Rem
Day 8
Day 22
Day 29
Day 36
Day 50
scour
fill
stable
stone
0
1500
3000
4500
6000
0,0
0,2
0,4
0,6
0,8
1,0
3,0
6,0
9,0
12,0
15,0

Fig. 2

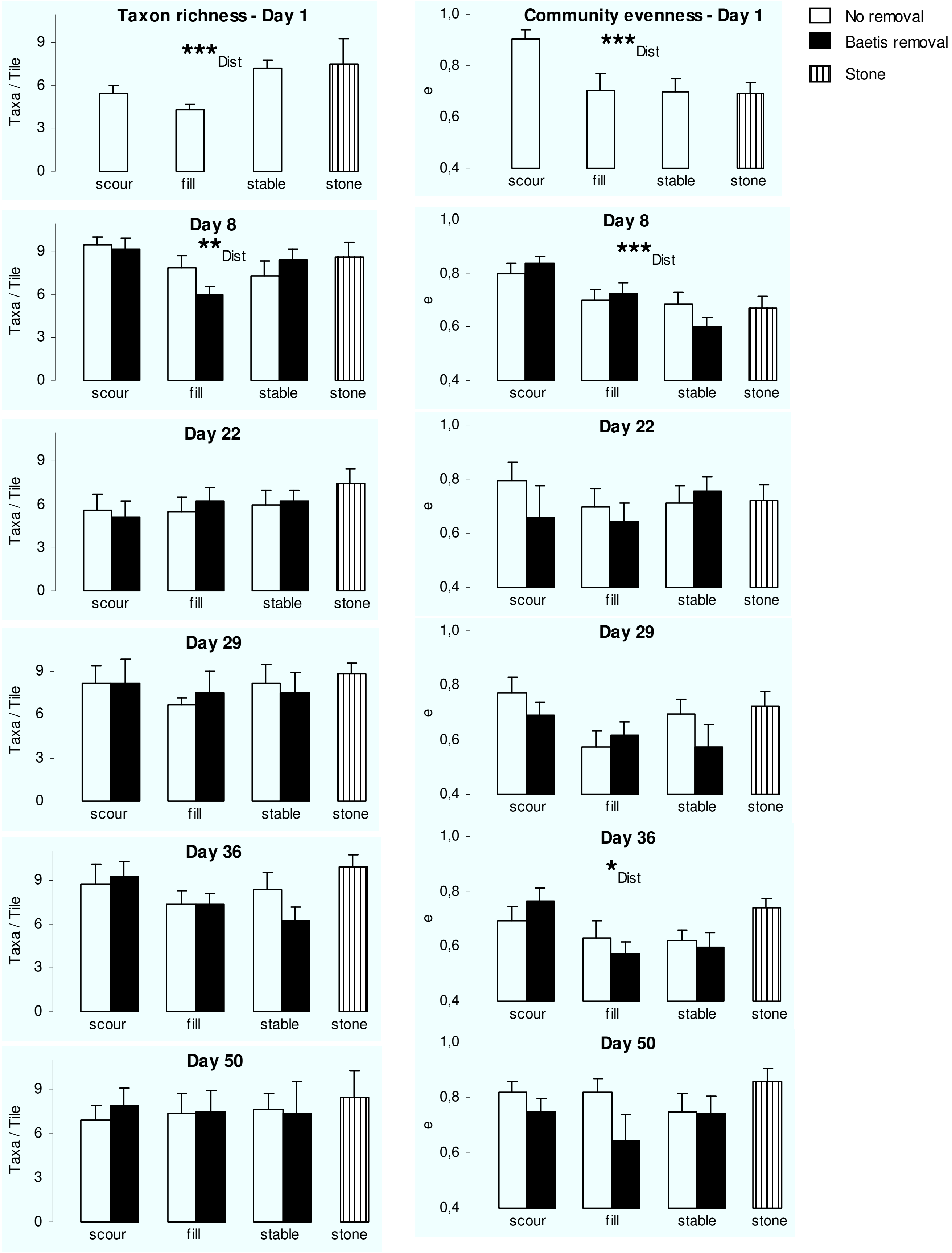

Taxon richness - Day 1
***Dist
Taxa / Tile
0
3
6
9
scour
fill
stable
stone
Community evenness - Day 1
***Dist
e
0,4
0,6
0,8
1,0
No removal
Baetis removal
Stone
Day 8
**Dist
***Dist
Day 22
Day 29
Day 36
*Dist
Day 50

Fig. 3

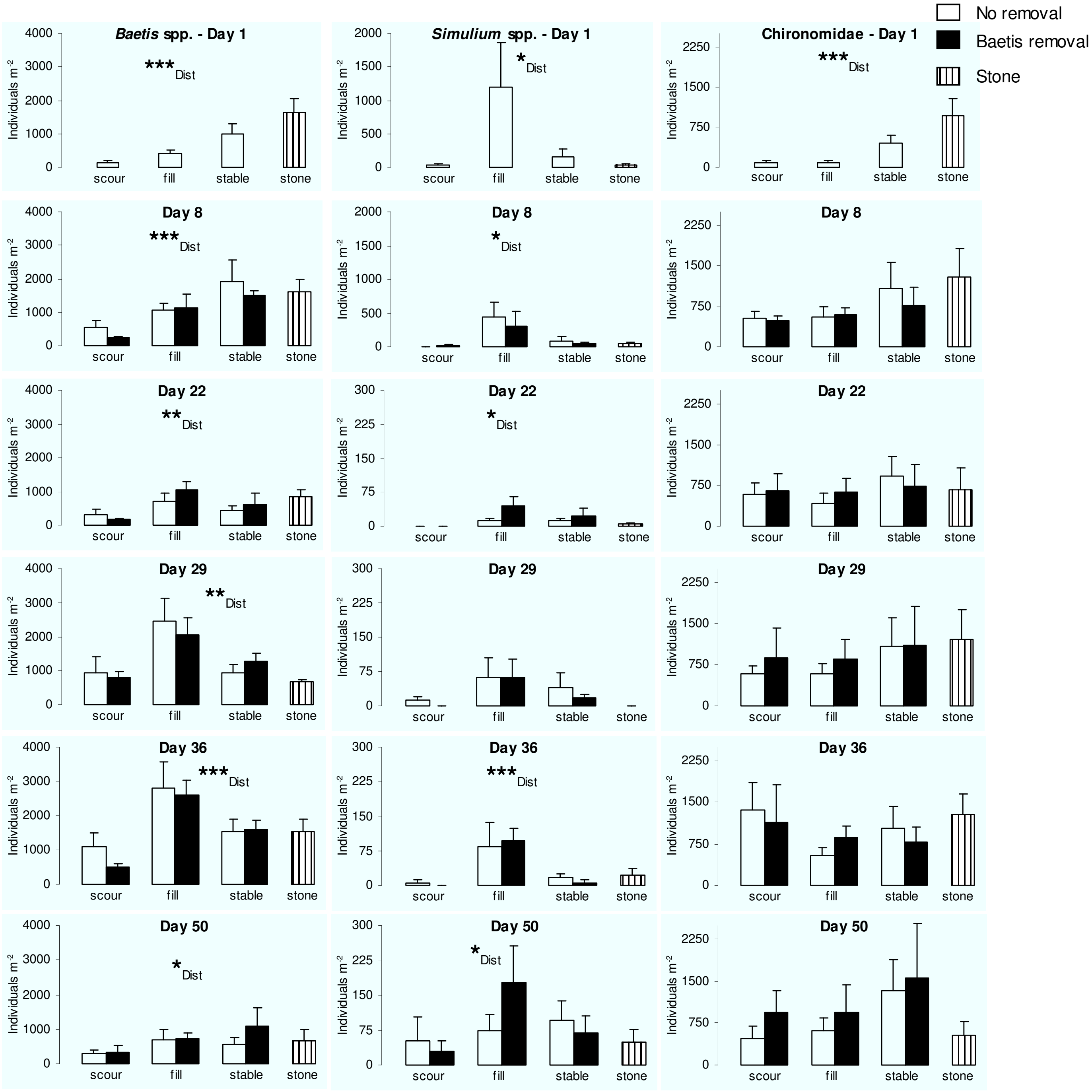

No removal
Baetis removal
Stone
Baetis spp. - Day 1
Simulium spp. - Day 1
Chironomidae - Day 1
Day 8
Day 22
Day 29
Day 36
Day 50
***Dist
**Dist
*Dist
Individuals m-2
0
1000
2000
3000
4000
500
1500
75
150
225
300
750
2250
scour
fill
stable
stone

Fig. 4

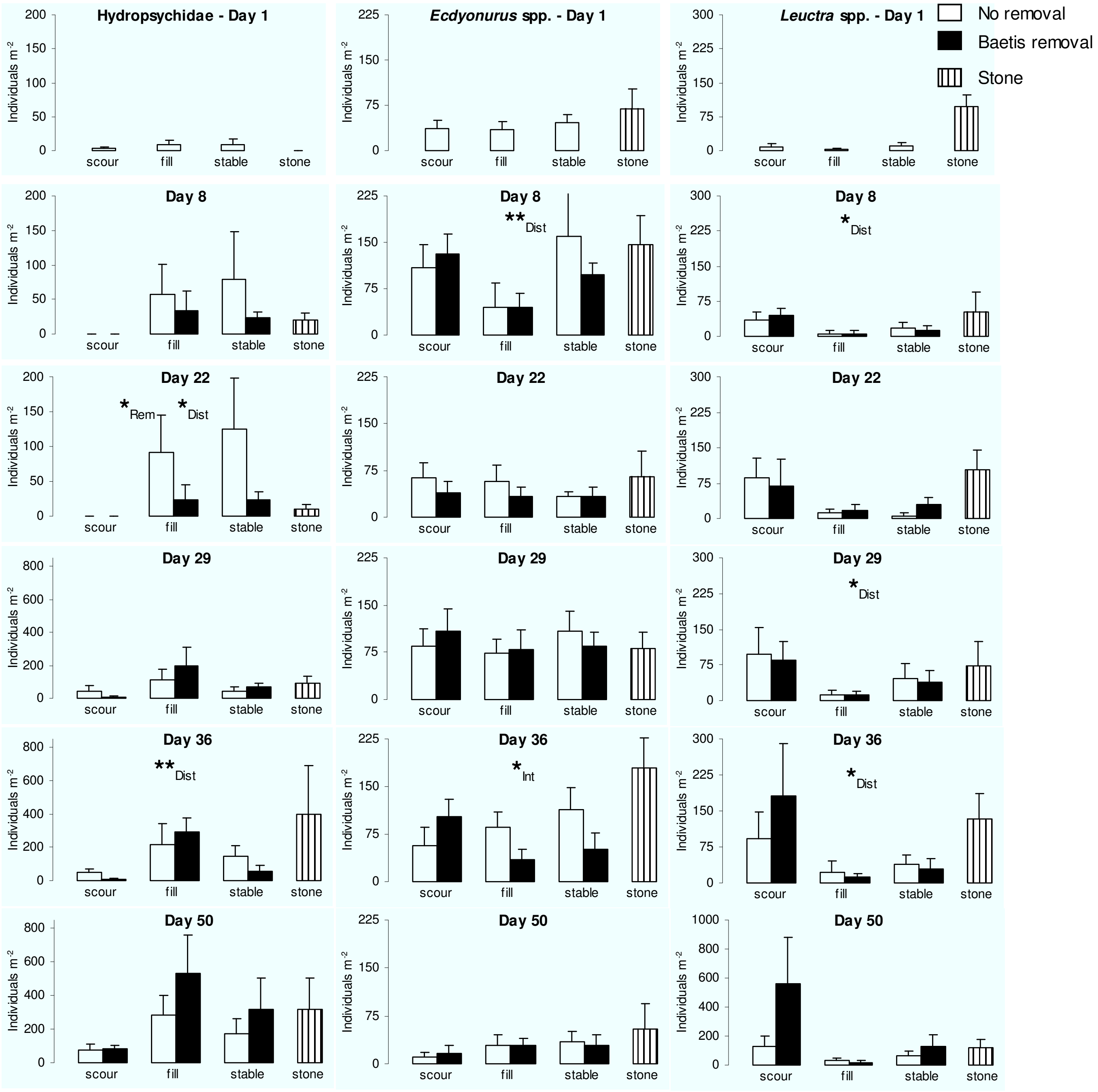
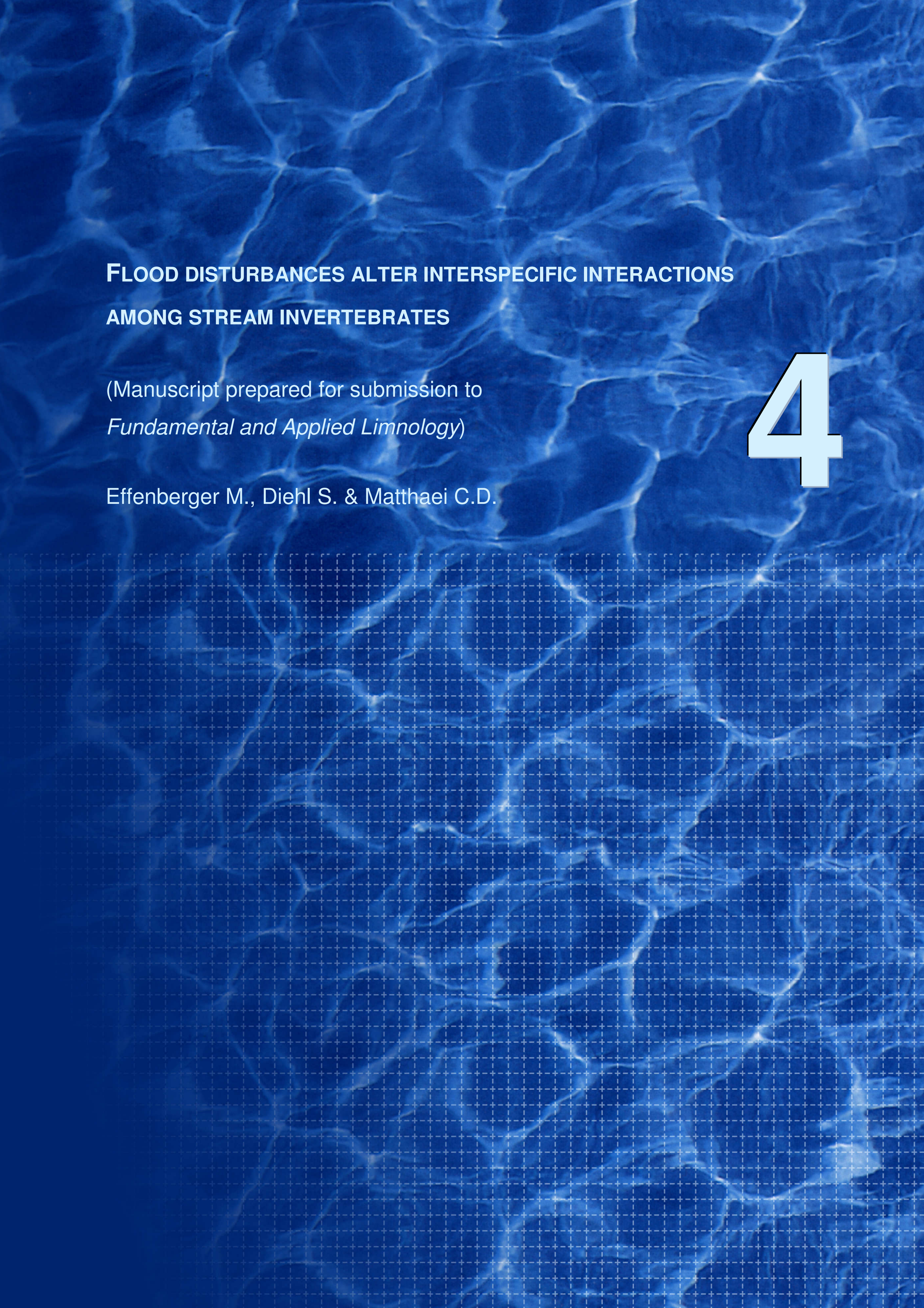

Hydropsychidae - Day 1
Ecdyonurus spp. - Day 1
Leuctra spp. - Day 1
No removal
Baetis removal
Stone
Day 8
**Dist
*Dist
Day 22
*Rem
*Dist
Day 29
*Dist
Day 36
**Dist
*Int
*Dist
Day 50
Individuals m-2
0
50
75
100
150
200
225
300
400
600
800
1000
scour
fill
stable
stone

Fig. 5



FLOOD DISTURBANCES ALTER INTERSPECIFIC INTERACTIONS AMONG STREAM INVERTEBRATES

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Effenberger M., Diehl S. & Matthaei C.D.

Flood disturbances alter interspecific interactions among stream invertebrates

Michael Effenberger[1], Sebastian Diehl[1] & Christoph D. Matthaei[2]

[1]Department Biology II, Aquatic Ecology, University of Munich (LMU),
Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

[2]Department of Zoology, University of Otago,P.O. Box 56,
Dunedin, New Zealand

Corresponding author
E-mail: effenberger@zi.biologie.uni-muenchen.de
Fax: 0049-89-2180-74211

Abstract

We investigated the influence of abiotic disturbance on interactions among invertebrates in 2 streams (Würm and Eyach) using ceramic tiles. In each stream, half the tiles (and an area of 0.16 m^2 surrounding each tile) were disturbed every 2 weeks to simulate patchy disturbance by minor floods; the other half remained undisturbed. We simultaneously manipulated densities of common invertebrates on the tiles (Würm: *Simulium* spp. and *Brachycentrus montanus*; Eyach: *Baetis* spp. and Heptageniidae). Three treatments (taxon 1 removed, taxon 2 removed, and controls) were applied and invertebrates removed *in situ* every 3 days. We repeatedly sampled 8 tiles from each treatment and determined invertebrate faunal composition. In the Würm, effects of disturbance and invertebrate removal were largely independent: disturbance reduced densities of common invertebrates (*Simulium*, *Brachycentrus*, *Baetis*, Hydropsychidae); removal of *Simulium* resulted in lower taxon richness and fewer *Lepidostoma hirtum* but more *Brachycentrus.* In contrast, disturbance and removal interacted frequently in the Eyach, where total density, taxon richness, and densities of *Baetis*, Heptageniidae and Chironomidae were higher in removal treatments, but only without disturbance. Our results show that the interplay between disturbance and biotic interactions can play an important role in shaping stream invertebrate communities.

Keywords: competition, biotic interactions, disturbance, patch dynamics, flood, invertebrate removal, streams,

Introduction

The patchy distribution of organisms in space and time is a striking feature of natural ecosystems and the identification of factors that drive these “patch dynamics” is a central concern of ecology (Pickett & White 1985). Research on patch dynamics has been conducted in various ecosystems and on a broad range of organisms. During the past 2 decades patch dynamics research has been extended to lotic ecosystems (e.g. Pringle *et al.* 1988, Townsend 1989, Downes 1990, Poff & Ward 1990).

It is well known that the microdistributions of invertebrates and algae on the stream bed are correlated with abiotic factors including water depth, substratum size, and current velocity (e.g. Barmuta 1989, Holomuzki & Messier 1993, Peckarsky *et al.* 1990). By contrast, the potential importance of flood disturbance in generating patchy distributions has received less attention. In many streams, physical disturbance of the stream bed occurs frequently during spates and floods (Poff & Ward 1989). Recent studies suggest that disturbance can contribute to patchiness in the distribution of lotic invertebrates and algae (Matthaei & Townsend 2000, Matthaei *et al.* 2000, 2003, Effenberger *et al.* 2006).

Biotic interactions such as competition (e.g. Hart 1987, Kohler 1992), grazing (Sarnelle *et al.* 1993) and predation (Wooster 1994, Englund & Evander 1999) can also be important determinants of the distribution of stream biota (Cooper *et al.* 1998). However, although most streams are subject to considerable discharge variation (Poff & Ward 1989, Poff 1996), almost all experimental studies of biotic interactions in running waters have been performed either in systems with permanently stable flow or in periodically disturbed systems during periods of stable flow (Hemphill & Cooper 1983, McAuliffe 1984, Kohler 1992, Kohler & Wiley 1997, Cardinale & Palmer 2002). While biotic interactions are likely to be important in stable streams, Poff & Ward (1989) and Townsend (1989) proposed that their importance should decrease with increasing frequency of disturbance. On the other hand, Chesson & Huntly (1997) argued that biotic interactions can also play an important role in frequently disturbed ecosystems, because a relatively minor stress caused by competition or predation could be enough to “push over the edge” a population already weakened by abiotic disturbance. Given that humans influence flow regimes of streams and rivers worldwide on an unprecedented scale through activities such as dam-building, river channelization and anthropogenic climate change (Poff 2002, Lytle & Poff 2004), we need to integrate disturbance and biotic interactions in a common conceptual framework if we want to understand the influences of altered flow regimes on stream communities (Power *et al.* 1995).

Theoretical and empirical studies suggest that the trajectory of community recovery after a flood disturbance depends on the severity of the disturbance, the productivity of the system, and the intensity of biotic interactions during the recovery phase (Nisbet *et al.* 1997, Power 1992, Marks *et al.* 2000, Roll *et al.* 2005). This view is supported by work in other systems exposed to periodic disturbances, such as rocky intertidal communities (Lubchenco 1983, Menge & Sutherland 1987, Worm *et al.* 2002) and temporarily drying pond systems (Wellborn *et al.* 1996, Kneitel & Chase 2004).

The purpose of our study was to investigate the interplay between frequent abiotic disturbance and biotic interactions in determining benthic community composition in an experimental situation. Specifically, we manipulated substrate stability and the densities of 2 common invertebrate taxa in 2 simultaneously conducted field experiments. In each experiment, 3 invertebrate removal treatments (taxon 1 removed, taxon 2 removed and unmanipulated controls) were crossed with 2 disturbance treatments (no disturbance and simulated substrate abrasion) in a full-factorial design. Based on evidence from previous studies (e.g. Death & Winterbourn 1995, Death 1996, Matthaei *et al.* 2000), we expected experimental disturbance to cause decreases in invertebrate density, taxon richness and algal biomass. In the undisturbed treatments, we expected invertebrate removals to cause increases in overall invertebrate taxon richness and the densities of unmanipulated taxa, because of reduced competition for resources (Kohler 1992, Kohler & Wiley 1997) or space (Hemphill & Cooper 1983, McAuliffe 1984). The scenarios suggested by Townsend (1989) and Chesson & Huntly (1997) yield additional, and contrasting, expectations concerning the interaction of disturbance and invertebrate removal. Following Townsend (1989), effects of invertebrate removal should be stronger under undisturbed than under frequently disturbed conditions; following Chesson & Huntly (1997), effects of invertebrate removal should be similar (or even stronger) under frequently disturbed conditions.

Methods

Based on the findings of previous disturbance research in streams (see citations in Introduction), we believe that the effects of an experimental manipulation of disturbance and species densities are likely to depend on the natural disturbance regime and resulting adaptations of the local community. We therefore performed our experiment simultaneously in two streams that differed in their natural disturbance regime (temporally stable vs. variable discharge) and benthic community structure. However, given the complex design and the high level of treatment replication within each stream (see below), it was logistically impossible to replicate the experiment at the level of stream type (discharge regime). So, albeit our results may hint at some general differences among these stream types (see Discussion), our study does not allow a rigorous comparison of streams with different natural disturbance regimes. Nevertheless, we find it useful to present both experiments in a single paper because they enhance the data base in an area of disturbance research in which manipulative field experiments are quite rare.

Study sites

Both study streams are located in southern Germany. The Eyach (47°46´N, 11°05´E) has a steep catchment (area ca. 27 km^2, altitude 570-930 m a.s.l.) that lies in a zone of fairly high rainfall at the northern edge of the Alps (mean annual rainfall in the catchment is about 1210 mm; German Weather Service [DWD], station Hohenpeissenberg). Consequently, the Eyach has a harsh discharge regime with frequent floods that are often quite severe. Mean flow is about 0.5 m^3/s, baseflow about 0.05 m^3/s, and water temperature is low (< 17°C in summer; M. Effenberger, unpublished data). The sediment supply into the Eyach is high because of the presence of several steep, unstable scree areas in the catchment. This high sediment input results in an unstable stream bed that is easily moved by floods. The stream bed consists mainly of large pebbles and small cobbles (particle width 32-128 mm) interspersed with small- and medium-sized boulders (256-1024 mm). About 70 % of the catchment is covered by forest, and the remaining area is pasture lightly grazed by cattle.

The Würm (48°02´N, 11°21´E) is the outlet of Lake Starnberg. The catchment of the Würm at the lake outlet is about 314 km² (altitude 570-700 m a.s.l.). The relatively small ratio of catchment area to lake area (57 km²) results in a marked buffering of flow extremes in the Würm. Further, annual rainfall in the area (about 804 mm; DWD, station Munich) is lower than in the catchment of the Eyach, and the relief is less steep. As a result, the Würm has a far more stable flow regime than the Eyach, with hardly any bed-moving floods. Such a stable flow regime is a feature of most lake outlet streams (see e.g. Poff & Ward 1989, Poff 1996, Hieber *et al.* 2005). Mean annual flow at the study reach is 4.7 m³/s and baseflow about 0.97 m³/s (Bavarian Water Management Authority [WWA] Munich, unpublished data). Water temperature in the Würm in summer is >17°C (M. Effenberger, unpublished data). The stream bed consists mainly of gravels or small pebbles (2-32 mm). Vegetation in the Würm catchment is a mixture of forest and agricultural land. The study site was located about 5 km downstream of the lake outlet.

Apart from their different flow regimes, the 2 streams share several similar characteristics: width at baseflow is about 5-10 m, flow regime and channel morphology are more or less natural, and water depth at the study sites is about 15-25 cm. Both streams run through largely v-shaped valleys with steep slopes of 50 m height on at least 1 bank. In each stream, we selected a single study reach of about 50 m length. While the Würm is somewhat more nutrient-rich than the Eyach (average total phosphorus concentration 43 vs. 11µg/l), its streambed is less exposed to direct sunlight (canopy cover at the study sites was 70-90% in the Würm and 30-50% in the Eyach). In spite of these differences, epilithic algal biomass at our study sites was similar in both streams (see Results).

Experimental disturbance and removal of invertebrates

Our study was conducted from June to August 2004. On 15 June, we exposed 144 unglazed, white tiles (9.8 × 9.8 × 0.8 cm; surface area 223.4 cm²) in 8 blocks of 18 tiles in each of the 2 streams (Fig. 1). Blocks of tiles were spaced in intervals of 6-7 m to cover a wide range of habitats within each study reach. Within blocks, tiles were placed 1 meter apart from each other. Tiles were equipped with two silicon “feet” (1 × 1 × 0.5 cm) near their downstream edges to facilitate invertebrate colonization of tile undersides and to increase the hydraulic pressure holding the tiles on the substratum.

After being left undisturbed for two weeks to allow natural colonization, tiles were randomly assigned to disturbed or non-disturbed treatments, cross-classified with the 3 invertebrate removal treatments (Fig. 1). The disturbance treatment was intended to mimic repeated, patchy bed movement as would be caused by a series of minor spates (Matthaei *et al.* 1999). In another pre-alpine river similar to our study streams, the Swiss River Necker, such disturbances occur on average at least every 22 days (Matthaei *et al.* 1996). Our disturbance consisted of scrubbing tiles with a soft brush (see McCabe and Gotelli 2000) every two weeks to remove all invertebrates and a large proportion of the algae. Additionally, the substrate in a 40 × 40 cm area around the tile was disturbed to a depth of 10-15 cm for 1.5 minutes using a screwdriver (see Matthaei *et al.* 1997).

In the invertebrate removal treatment (see Hemphill & Cooper 1983), we manipulated the densities of two numerically dominant invertebrate taxa in each stream, the mayflies *Baetis* spp. and Heptageniidae (mainly *Ecdyonurus* spp. plus a few individuals of *Rhithrogena* spp.) in the Eyach, and the black fly *Simulium* spp. and the caddisfly *Brachycentrus montanus* (Klapalek) in the Würm. Because it was impossible to distinguish between early instars of Heptageniidae in the field, we treated them as a single taxon. We assumed that the selected taxa in each stream had the potential to locally compete with each other and with the remaining invertebrate community. The two mayfly taxa are the most abundant grazers in the Eyach and can therefore be expected to compete mainly for periphyton, whereas the more sessile *Brachycentrus* and *Simulium* in the Würm are possibly limited by space rather than by jointly used food resources. Besides their abundance (all four had been among the most common taxa in their respective stream in 2003, the year before our experiment; M. Effenberger, unpublished data), these taxa were chosen for removal because they readily colonized experimental tiles and were easy to manipulate.

Three treatments (removal of taxon 1, removal of taxon 2 and unmanipulated controls) were applied to the experimental tiles at 3-day intervals (the shortest interval between invertebrate removals that we could maintain throughout the experiment). This interval was considerably shorter than in earlier field experiments where invertebrates had been selectively removed (Hemphill & Cooper 1983: two weeks, McAuliffe 1984: one week). All individuals of the targeted taxon were manually removed *in situ* using forceps (as in McAuliffe 1984). Each manipulated tile was lifted slightly out of the water, and all target organisms were removed as quickly as possible (the average time needed for this manipulation was about 20 sec). By contrast, control tiles were left in the stream and not manipulated at all. Removed invertebrates were caught in a hand net (20 × 15 cm; mesh size 200µm) held immediately downstream of each tile and were preserved with 70% ethanol in the field. The remaining invertebrates and algae were disturbed as little as possible, and the tile was gently placed back in its original position on the stream bed. Removed invertebrates were subsequently identified (most taxa to genus, dipterans to family), counted, and measured to the nearest millimeter (head-to-body-length) under a stereomicroscope (WILD, Heerbrugg, Germany) at 6.5 – 40x magnification.

Our experiment started on 29 June with the first disturbance, followed by a second disturbance on 15 July and a third on 30 July. It ended with the third sampling date on 13 August. Invertebrate removals started on 2 July and continued every three days until the end of the experiment. Each period between experimental disturbances thus included four invertebrate removals. In the Eyach, a bed-moving flood caused some changes to this schedule (see below).

Biological sampling

Six tiles (1 per treatment) were randomly selected from each block (in total 48 tiles per stream and sampling date) and sampled on 14, 29 July and 13 August (2, 4 and 6 weeks after the first experimental disturbance).

Shortly after the first sampling date (on 20 July), a local thunderstorm caused a major flood (> 5 times mean discharge) in the Eyach, thus demonstrating the harsh disturbance regime of this river. This flood washed downstream or buried all 96 remaining experimental tiles. Because of the discharge-buffering effect of Lake Starnberg, similar thunderstorms did not produce any flooding in the Würm. To continue our experiment, we exposed a second set of 48 clean tiles in the disturbed reach of the Eyach on 29 July. After one week of colonization (on 4 August), we experimentally disturbed this second set of tiles and resumed invertebrate removal as described above three days later. These tiles were sampled on 13 August.

During biological sampling, all invertebrates were dislodged gently from the entire surface area of each tile, caught in a hand net, and preserved with 70% ethanol in the field. In the laboratory, invertebrate samples were processed as described above. Epilithic algal biomass was sampled by scraping the entire top side area of each tile with a tooth brush with shortened bristles. Algal samples were preserved immediately with formaldehyde solution (final concentration 4%) in the field, stored on ice in the dark and measured as chlorophyll *a* (APHA 1998) per cm^2 of tile surface area.

To test whether colonization of our experimental tiles was similar to colonization of natural substrata in our study streams, we randomly selected 1 surface stone per block on each sampling date and sampled it in the same way as the experimental tiles. Stone surface areas were determined by wrapping stones completely with a mono-layer of aluminium foil of known mass per unit area and weighing the foil (Townsend *et al.* 1997). For graphical illustration of the results, invertebrate numbers on both stones and tiles were converted to densities per 1000 cm^2.

Data analysis

For each of the two experiments, we evaluated effects of disturbance and removal treatments using 2-way analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA). Disturbance (disturbed or undisturbed) and removal (removal of taxon 1, removal of taxon 2, or unmanipulated controls) served as fixed factors and block (1-8) as a random factor. Treatment effects on epilithic algal biomass, total invertebrate density, and invertebrate taxon richness were investigated with separate ANOVAs. Treatment effects on the densities of the six most common invertebrate taxa in each stream were analyzed with a MANOVA followed by separate ANOVAs for each of these taxa.

After exploratory analysis, all data were log (x) or log (x+1) transformed where necessary to improve normality and homoscedasticity. Because the flood in the Eyach resulted in a different set of tiles being sampled on each collection date (see above), we analyzed these two dates separately. The data from the Würm were analyzed in the same way to facilitate comparisons between streams. If a main effect was statistically significant, we conducted pairwise post-hoc comparisons with Tukey´s HSD tests, except in cases of persisting heteroscedasticity (results of Levene´s test still significant after transformation), where we performed Games-Howell tests (Quinn & Keough 2002), which do not assume equal variances between groups. In all cases with significant interactions between disturbance and invertebrate removal, we calculated additional one-way (M)ANOVAs within disturbance categories to determine the shape of these interactions.

To test the effectiveness and selectivity of our invertebrate removal treatments, we calculated a “specific removal ratio”. For each tile, we counted the numbers of different invertebrates removed on each removal occasion. For the target taxa of our removals, we then averaged these numbers across the last four removals preceding a sampling and divided it by the abundance of the taxon on that sampling date. We calculated a similar ratio for non-target taxa, which we lumped into a single group named “bycatch”. To assess the selectivity of the removal treatments, we compared target taxon-specific removal ratios between the two invertebrate removal treatments in each stream using t-tests. We considered a removal treatment as successful (= effective and selective), if the specific removal ratio of target taxon 1 was > 0.5 in the treatments where we wished to remove 1 and if the (accidental) removal ratio of 1 was significantly lower in the treatments where we wished to remove taxon 2. Note that this removal ratio of > 0.5 is quite conservative, because it means that at least twice the number of individuals found on a given tile had been removed from this tile since the last previous sampling occasion (0.5 x 4 removals).

Invertebrate community structure between non-manipulated experimental tiles and natural surface stones in each stream was compared using analysis of similarities (ANOSIM; Clarke 1993) on a Bray-Curtis similarity matrix obtained from $\log_{10}(x+1)$ transformed invertebrate density data. Differences between tiles and stones on each sampling occasion were interpreted from pairwise tests in the ANOSIM. We also used t-tests to compare total densities, taxon richness, and the densities of the most common invertebrate taxa on non-manipulated experimental tiles with the communities on natural surface stones in each stream.

All analyses were calculated in SPSS® version 12.0 (SPSS Inc., Chicago, USA) or PAST (Hammer, Harper & Ryan, 2001). We set the significance level at $p = 0.05$, but report all cases where $0.05 < p < 0.1$. To help avoid type II errors, we also give exact p-values and statistical power for all cases (Toft & Shea 1983).

Results

Success of invertebrate removal

Eyach. Specific removal ratios were greater than 0.5 for *Baetis*, but lower than 0.2 for Heptageniidae in both treatments (Table 1). Moreover, removal ratios of the 2 target taxa and of the bycatch did not differ significantly between the *Baetis* and Heptageniidae treatments (Table 1). Because the removals lacked selectivity for the target taxa, we combined the two removal treatments in all following analyses into a single 'global' removal treatment.

Würm. Specific removal ratios of *Brachycentrus* and *Simulium* were greater than 0.5 in the treatments where these taxa were selectively removed, but significantly lower in the treatments where they were only accidentally removed (Table 2). The removal ratio for bycatch was less than 0.5 in both treatments, but somewhat higher in the *Simulium* than in the *Brachycentrus* removal treatment. Overall, the two removal treatments were thus largely successful and sufficiently specific to be treated separately in all following analyses.

Faunal composition

As in our surveys in 2003 (M. Effenberger, unpublished data), the four manipulated target taxa were among the numerically dominant invertebrates in both streams during our experiment. In the Eyach, *Baetis* was the most abundant colonizer of the experimental tiles. *Baetis* contributed 43% to total invertebrate density (all samples combined), followed by Chironomidae (17%), the mayfly *Ephemerella ignita* (Poda; 7%), the stonefly *Nemoura* spp. (6%), Heptageniidae (4%) and larvae of the beetle *Esolus* spp. (4%). Together, these six taxa accounted for 81% of all invertebrates. Tiles in the Würm were dominated by *Simulium*, which contributed 51% to total invertebrate counts, followed by *Baetis* (14%) and *Brachycentrus* (6%). Further abundant taxa were the caddis flies *Lepidostoma hirtum* (Fabricius; 5%) and Hydropsychidae (4%) plus the mayfly *Ecdyonurus* spp. (3%). Together, these six taxa accounted for 83% of all invertebrates.

Colonization of tiles versus stones

In the Eyach, invertebrate community structure on stable experimental tiles was different to community structure on natural surface stones on one sampling date (ANOSIM; 14 July, $p = 0.04$; 8 August, $p = 0.14$), whereas in the Würm it was different on all sampling dates (ANOSIM; 14 July, $p = 0.03$; 29 July, $p = 0.006$; 8 August, $p = 0.005$). However, invertebrate taxon richness and densities of the most common invertebrate taxa were generally similar on artificial and natural substrata, with the following exceptions: In the Eyach, total invertebrate density and densities of *Baetis* and Chironomidae were lower on non-manipulated tiles (no disturbance + no removal) than on natural stones on 14 July ($p = 0.03$; see Figs 2 and 3). In the Würm, taxon richness was higher on non-manipulated tiles than on stones on 29 July and 13 August ($p \leq 0.005$), and *Baetis* was more common on stones than on tiles on 14 July ($p = 0.03$; see Figs 4 and 5).

Specific effects of experimental disturbance and invertebrate removal

Eyach. In the Eyach, we found few main effects of our experimental treatments, but interactions between disturbance and removal treatments were common (Figs 2 and 3; Table 3). Overall, we found six different patterns of treatment effects (indicated by superscripts **1** - **6** in Table 3). First, MANOVA indicated higher invertebrate densities of the six most common taxa on disturbed than on undisturbed tiles on 14 July; moreover, Heptageniidae and *Esolus* larvae on 14 July and *Nemoura* on 13 August were more common on disturbed than on undisturbed tiles (superscript **1** in Table 3; Fig. 3). Epilithic algal biomass (Fig. 2) was higher on undisturbed tiles than on disturbed tiles on 13 August (**2** in Table 3). On 13 August, Chironomidae densities were higher on non-manipulated tiles than on tiles where *Baetis* and Heptageniidae had been removed (**3** in Table 3). On 14 July, disturbance and removal interacted with each other in several cases. Algal biomass was higher on tiles without removal than on tiles where *Baetis* and Heptageniidae had been removed, but only on undisturbed tiles (**4** in Table 3). Furthermore, total density of invertebrates, the combined densities of the 6 most common invertebrate taxa (MANOVA), and the densities of *Baetis* and Chironomidae (Figs 2 and 3) were higher in the removal treatment than on tiles with no removal, but only in the absence of experimental disturbance, and Heptageniidae and invertebrate taxon richness (Fig. 2) showed the same pattern on 13 August (**5** in

Table 3). On 13 August, *Nemoura* densities (Fig. 3) were higher on tiles where no invertebrates had been removed than on tiles with removal, but only in the presence of disturbance (**6** in Table 3). Density of *Ephemerella* (Fig. 3) was not influenced at all by the experimental treatments.

Würm. In contrast to the Eyach, interactions among the removal and disturbance treatments were rare in the Würm (see treatment effect patterns labeled **10** and **11** in Table 4), whereas main treatment effects were fairly common (patterns **2**, **7** and **8** in Table 4). Experimental disturbance reduced epilithic algal biomass and the combined densities of the six most common invertebrate taxa (MANOVA) on all sampling dates; total invertebrate density, and the densities of *Brachycentrus*, *Simulium*, *Baetis* and Hydropsychidae were reduced on at least one sampling date (**2** in Table 4; Figs 4 and 5). The removal of *Simulium* reduced taxon richness and the abundance of *Lepidostoma* on one sampling date each (**7** in Table 4; Figs 4 and 5), whereas the removal of *Brachycentrus* reduced *Brachycentrus* density on all three sampling dates (**8** in Table 4). Algal biomass was higher on tiles with *Simulium* removal on 29 July (**9** in Table 4). In four cases, disturbance and invertebrate removal interacted in idiosyncratic ways to affect invertebrate densities (Table 4). On 14 July, *Simulium* and *Ecdyonurus* (Fig. 5) were more common on tiles with *Simulium* removal than on tiles without removal, but only in the presence of experimental disturbance (**10** in Table 4). On 29 July, taxon richness and the density of *Brachycentrus* (Fig. 5) were higher on tiles with *Simulium* removal than on tiles with *Brachycentrus* removal, but only in the absence of disturbance (**11** in Table 4).

Discussion

Impact of experimental disturbance

Based on evidence from previous studies (e.g. Death & Winterbourn 1995, Death 1996, Matthaei *et al.* 2000), we expected our experimental disturbance to cause a decrease in invertebrate density and taxon richness. This expectation was frequently borne out in the Würm, for both relatively sessile (e.g. *Brachycentrus*) and highly mobile taxa (e.g. *Baetis*), even though the latter are considered to be fast colonizers (Mackay 1992). In contrast, disturbance did not have any negative effects on invertebrate densities in the Eyach, and there were even a few positive effects (Table 4). There are at least two (non-exclusive) explanations for this difference between streams. First, it seems plausible that the invertebrate community of a frequently disturbed stream is better adapted to fast recolonization of disturbed patches than the community of a stream with stable discharge. Second, negative effects of disturbance became more prevalent in the stable Würm over the course of the experiment, suggesting that effects of repeated local disturbances in a matrix of undisturbed stream bed may accumulate over time (Hemphill & Cooper 1983). In contrast, the Eyach experienced a large-scale disturbance (a natural flood) after our first sampling date, forcing us to restart the experiment. Consequently, cumulative effects of our experimental disturbance could not be expressed in the Eyach. Algal biomass was also reduced significantly by the experimental disturbance on at least one sampling date in each stream, but once again the impact was stronger in the Würm. Because of its dense canopy cover, the experimental reach in the Würm receives low levels of incident radiation. Therefore after a disturbance, algal biomass may take longer to recover to pre-disturbance levels than in the considerably sunnier Eyach.

Interactions between disturbance and invertebrate removal

Our study is one of the first field experiments that investigated how frequent abiotic disturbances and density manipulations of selected taxa interact in their effects on benthic communities in streams. To our knowledge, highly mobile taxa such as *Baetis* and Heptageniidae have never been used as target species in such an experiment. Disregarding the marginally significant cases ($0.05 < p < 0.1$) and the negative effect of *Brachycentrus* removal on its own density in the Würm, we did not observe a single case in which invertebrate removals influenced invertebrate densities across *both* disturbance treatments. In contrast, disturbance and invertebrate removal interacted significantly with each other in several cases, indicating that the influence of biotic interactions was often dependent on physical disturbance. Based on the predictions of Poff & Ward (1989) and Townsend (1989), disturbance and invertebrate removal should interact with each other, with weaker effects of invertebrate removal under frequently disturbed conditions (in our terms, treatment patterns **3** and **4** in Table 3). Based on the alternative hypothesis by Chesson & Huntly (1997), one would expect either no or a different interaction, because invertebrate removal should affect the remaining species regardless of the presence or absence of disturbance, or maybe even more so under frequently disturbed conditions.

Our findings from the Eyach support mainly the first hypothesis, whereas our results from the Würm support neither hypothesis. In the Eyach, total invertebrate density, taxon richness, and the densities of Chironomidae, *Baetis* and Heptageniidae all showed a significant interaction between disturbance and invertebrate removal on one of two sampling dates each (pattern **5** in Table 3). All five variables showed higher values on tiles where Heptageniidae and *Baetis* had been removed than on tiles without removal (indicating that the removed taxa may have competed with the remaining invertebrate fauna on the experimental tiles), but only in the absence of disturbance. For total density, taxon richness and Chironomidae, these results are in agreement with Poff & Ward's (1989) and Townsend's (1989) hypothesis that the effects of competition (in our case on the small-scale distribution of stream invertebrates) should be weaker under frequently disturbed conditions. In two of the few studies available for comparison, Hemphill & Cooper (1983) and Hemphill (1991) also found that frequent experimental disturbance reduced competition between two filter-feeding stream insects, *Simulium* and the net-spinning caddisfly *Hydropsyche*, during periods of stable flow in a stream that experiences winter flooding. Likewise, McAuliffe (1984) showed that physical disturbances can prevent the monopolization of space by the sedentary caddisfly *Leucotrichia*. For *Baetis* and Heptageniidae, the higher densities on tiles where these taxa had been removed illustrates the high mobility and fast recolonising ability of these mayflies (see also Mackay 1992). This result also implies that, for unknown reasons, the two taxa preferentially recolonized tiles from which their conspecifics had been recently removed.

In the Würm, we found one case (*Ecdyonurus* on 14 July) where a removal treatment had a positive effect on another taxon only in the presence of disturbance. At first glance, this might be interpreted as support for the hypothesis of Chesson & Huntly (1997), but the argument is contradicted by the fact that the removed taxon (*Simulium*) (marginally significantly) showed the same pattern and was actually more abundant in disturbed patches from which it was removed. Furthermore, although the absence of further significant interaction terms in the Würm is in conflict with the interaction pattern predicted by Townsend (1989), it also does not support the hypothesis of Chesson & Huntly (1997). The latter would require that species removals did affect at least some invertebrate taxa, which was not the case.

Differences between streams and concluding remarks

The interplay between disturbance and biotic interactions in their influence on the benthic fauna differed in several ways between our two study streams, the flood-prone Eyach and the stable lake outlet Würm (see above). At least some of these differences could be linked to the different disturbance regimes of the two streams. Although the lack of replication at the stream level does not allow us to investigate this hypothesis rigorously, a few striking patterns should be pointed out: In the stable Würm we found many (and exclusively) negative effects of disturbance on stream biota. Most of the affected taxa are relatively sedentary (algae, *Brachycentrus*, *Simulium*, Hydropsychidae) and only *Simulium* and *Baetis* are fast colonizers. In the flood-prone Eyach, we found negative effects of disturbance on sedentary algae, but positive effects on the most common invertebrate taxa (MANOVA), in particular the mobile taxa *Nemoura* and Heptageniidae. Moreover, positive effects of removal were frequent, but only in undisturbed patches.

The results of our two manipulative experiments add to the very limited data addressing the open question to which extent biotic interactions can influence stream invertebrate communities under frequently disturbed conditions. Because of their character as pioneer studies, our experiments inevitably had certain shortcomings. For instance, our experimental invertebrate removals were only partly successful, even though intervals between removals were considerably shorter than in similar field experiments (Hemphill & Cooper 1983, McAuliffe 1984) and, for three of the four target taxa, at least twice the number of individuals found on a given tile had been removed from this tile since the last previous sampling occasion. In most cases, our target taxa recolonized rapidly between consecutive removal dates and removal led only to temporary density reductions but not to persistent elimination in the corresponding treatments. Shortening the intervals between removals even further would have been logistically impossible in our study because we conducted the two experiments simultaneously. However, removing target invertebrates every two days or even daily might reveal more or stronger evidence of competitive interactions in future experiments. Further, we investigated effects of small-scale disturbances and removals in the present study, whereas the conceptual models of Poff & Ward (1989), Townsend (1989) and Chesson & Huntly (1997) strictly describe situations where disturbances occur at larger spatial scales (which are much harder to reproduce in manipulative experiments). In spite of these limitations, we believe that our experiment represents a step ahead in a difficult field of research. Besides using shorter intervals between removals, future research on abiotic disturbances and biotic interactions should include experiments during unusual flow conditions (e.g. long stable periods in frequently disturbed streams) and comparisons between replicated streams with different disturbance regimes.

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Table 1. Specific removal ratios (= average no of individuals removed per removal occasion divided by standing stock sampled) in the two invertebrate removal treatments in the Eyach. *P*-values indicate results of t-tests between removal treatments. See text for further details.

Taxon removed	**Treatment**	**Removal ratio**		
		Mean	**SE**	***p*/ power**
Baetis spp.	*Baetis* removal	0.57	0.18	
	Heptageniidae removal	1.03	0.39	0.122/ 0.330
Heptageniidae	*Baetis* removal	0.05	0.05	
	Heptageniidae removal	0.17	0.05	0.135/ 0.308
Bycatch	*Baetis* removal	0.31	0.17	
	Heptageniidae removal	0.92	0.58	0.326/ 0.148

Table 2. Specific removal ratios (= average no of individuals removed per removal occasion divided by standing stock sampled) in the two invertebrate removal treatments in the Würm. *p*-values indicate results of t-tests between removal treatments. See text for further details.

Taxon removed	**Treatment**	**Removal ratio**		
		Mean	**SE**	***p*/ power**
B. montanus	*B. montanus* removal	0.55	0.24	
	Simulium removal	0.08	0.04	**0.011/ 0.803**
Simulium spp.	*B. montanus* removal	0.15	0.09	
	Simulium removal	0.52	0.13	**0.016/ 0.738**
Bycatch	*B. montanus* removal	0.16	0.08	
	Simulium removal	0.46	0.09	**0.008/ 0.845**

Table 3. Effects of invertebrate removal and disturbance treatments in the Eyach. Shown are *p*-values of two-way-(M)ANOVAs and of abundance rankings ($p < 0.1$) based on *post-hoc*-tests (main treatments effects) and on one-way-(M)ANOVAs within disturbance categories (removal x disturbance interactions). Results for the factor 'block' are not shown because they are irrelevant to our hypotheses. D = disturbed, U = undisturbed, No = no removal, BH= *Baetis* and Heptageniidae removal. Qualitatively similar effect patterns share common numbers in the superscript.

Date & dependent variable	**Removal *p*/ power**	**Ranking (post-hoc)**	**Disturbance *p*/ power**	**Ranking (post-hoc)**	**Interaction (Removal x Disturbance) *p*/ power**	**Ranking (1-way-ANOVAs)**
14 July						
Epilithic algal biomass	n.s.	-	n.s.	-	**0.049/ 0.510**	U BH < U No ^{4} D BH = D No
Total invertebrates	n.s.	-	n.s.	-	**0.025/ 0.623**	U BH > U No ^{5} D BH = D No
MANOVA	n.s.	-	0.053/ 0.725	U < D ^{1}	**0.028/ 0.801**	U BH > U No ^{5} D BH = D No
Baetis spp.	n.s.	-	n.s.	-	0.083/ 0.412	U BH > U No ^{5} D BH = D No
Heptageniidae	n.s.	-	**0.020/ 0.659**	U < D ^{1}	n.s.	-
Chironomidae	n.s.	-	n.s.	-	**0.001/ 0.936**	U BH > U No ^{5} D BH = D No

Table 3 (continued)

Date & dependent variable	Removal *p*/ power	Ranking (post-hoc)	Disturbance *p*/ power	Ranking (post-hoc)	Interaction (Removal x Disturbance) *p*/ power	Ranking (1-way-ANOVAs)
14 July (cont.)						
Esolus spp. (larvae)	n.s.	-	**0.012**/ **0.734**	U < D [1]	n.s.	-
13 August						
Epilithic algal biomass	n.s.	-	**0.003**/ **0.879**	U > D [2]	n.s.	-
Taxon richness	n.s.		n.s.	-	0.055/ 0.490	U BH > U No [5] D BH = D No
Heptageniidae	n.s.	-	n.s.	-	**0.030**/ **0.594**	U BH > U No [5] D BH < D No
Chironomidae	0.080/ 0.419	no > BH [3]	n.s.	-	-	-
Nemoura spp.	n.s.		**0.048**/ **0.513**	U < D [1]	0.076/ 0.428	U BH = U No [6] D BH < D No

Table 4. Effects of invertebrate removal and disturbance treatments in the Würm. Shown are *p*-values of two-way-(M)ANOVAs and abundance rankings ($p < 0.1$) based on *post-hoc*-tests (main treatments effects) and on one-way-(M)ANOVAs within disturbance categories (removal x disturbance interactions). Results for the factor 'block' are not shown because they are irrelevant to our hypotheses. D = disturbed, U = undisturbed, No = no removal, B = *Brachycentrus* removal, S = *Simulium* removal. Qualitatively similar effect patterns share common numbers in the superscript.

Date & dependent variable	**Removal *p*/ power**	**Ranking (post-hoc)**	**Disturbance *p*/ power**	**Ranking (post-hoc)**	**Interaction (Removal x Disturbance) *p*/ power**	**Ranking (1-way-ANOVAs)**
14 July						
Epilithic algal biomass	n.s.	-	**0.047**/ **0.515**	U > D^{2}	n.s.	-
Taxon richness	0.083/ 0.496	(no = B) > S^{7}	n.s.	-	n.s.	-
MANOVA	n.s.	-	**0.028**/ **0.801**	U > D^{2}	n.s.	-
Simulium spp.	n.s.	-	n.s.	-	0.090/ 0.481	U S = U No^{10} D S > D No
B. montanus	0.082/ 0.497	S > B^{8}	**0.007**/ **0.803**	U > D^{2}	n.s.	-
Ecdyonurus spp.	n.s.	-	n.s.	-	**0.042**/ **0.611**	U B = U S = U No^{10} D S > (D B = D No)

Table 4 (continued)

Date & dependent variable	Removal *p*/ power	Ranking (post-hoc)	Disturbance *p*/ power	Ranking (post-hoc)	Interaction (Removal x Disturbance) *p*/ power	Ranking (1-way-ANOVAs)
29 July						
Epilithic algal biomass	0.056/ 0.566	S > no [9]	**< 0.001/ 0.983**	U > D [2]	n.s.	-
Taxon richness	n.s.	-	n.s.	-	0.073/ 0.519	U B < U S [11] D B = D S
MANOVA	n.s.	-	**0.003/ 0.952**	U > D [2]	n.s.	-
B. montanus	**0.024/ 0.697**	(no = S) > B [8]	**< 0.001/ 0.999**	U > D [2]	**0.031/ 0.657**	U B < U S [11] D B = D S
13 August						
Epilithic algal biomass	n.s.	-	**0.007/ 0.791**	U > D [2]	n.s.	-
Total invertebrates	n.s.	-	**0.040/ 0.545**	U > D [2]	n.s.	-
MANOVA	n.s.	-	**0.029/ 0.797**	U > D [2]	n.s.	-
Simulium spp.	n.s.	-	**0.003/ 0.881**	U > D [2]	n.s.	-
B. montanus	0.085/ 0.491	no > B [8]	**0.030/ 0.594**	U > D [2]	n.s.	-
Baetis spp.	n.s.	-	0.073/ 0.436	U > D [2]	n.s.	-
L. hirtum	0.088/ 0.486	no > S [7]	n.s.	-	n.s.	-
Hydropsychidae	n.s.	-	0.053/ 0.495	U > D [2]	n.s.	-

Figure legends

Fig. 1. Schematic layout of one experimental block representative for both study streams. Within each block, the three replicates of the six different treatments were placed at random. Numbers indicate sampling dates (1 = 14 July; 2 = 29 July; 3 = 13 August), and the arrow indicates the flow direction.

Fig. 2. Epilithic algal biomass, total invertebrate densities and taxon richness in invertebrate removal and disturbance treatments in the Eyach. Error bars indicate standard errors. Significant differences among treatments in the ANOVAs are shown by asterisks above the mean values ($^{(*)}p < 0.10$; $^{*}p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; Remo = invertebrate removal; Dist = disturbance; Int = interaction between removal and disturbance). See Table 3 for exact *p*-values.

Fig. 3. Densities of *Baetis* spp., Heptageniidae, Chironomidae, *Esolus* spp., *E. ignita* and *Nemoura* spp. in invertebrate removal and disturbance treatments in the Eyach. See Table 3 for exact *p*-values. Symbols are as in Fig. 2.

Fig. 4. Epilithic algal biomass, total invertebrate densities and taxon richness in invertebrate removal and disturbance treatments in the Würm. See Table 4 for exact *p*-values. Symbols are as in Fig. 2.

Fig. 5. Densities of *Simulium* spp., *B. montanus, Ecdyonurus* spp., *L. hirtum*, *Baetis* spp. and Hydropsychidae in invertebrate removal and disturbance treatments in the Würm. See Table 4 for exact *p*-values. Symbols are as in Fig. 2.

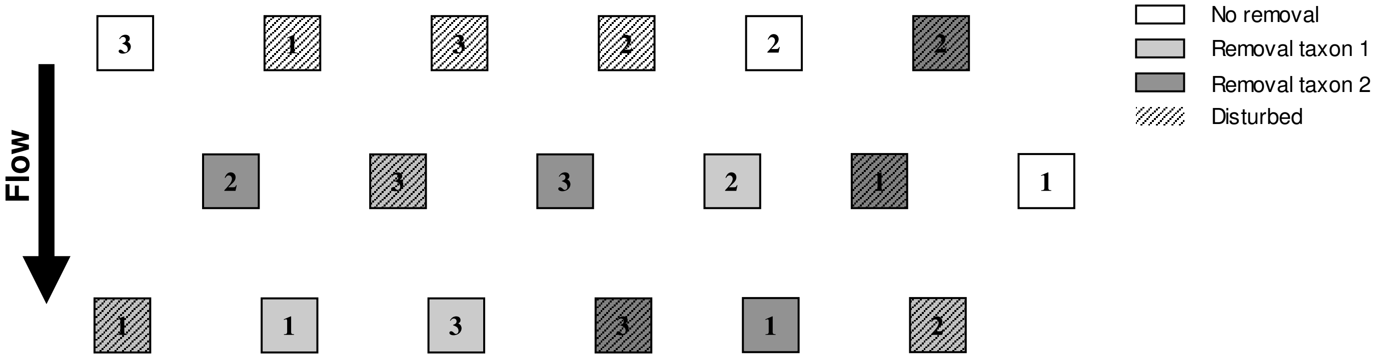
3
1
3
2
2
2
Flow
2
3
3
2
1
1
1
1
3
3
1
2
No removal
Removal taxon 1
Removal taxon 2
Disturbed

Fig. 1

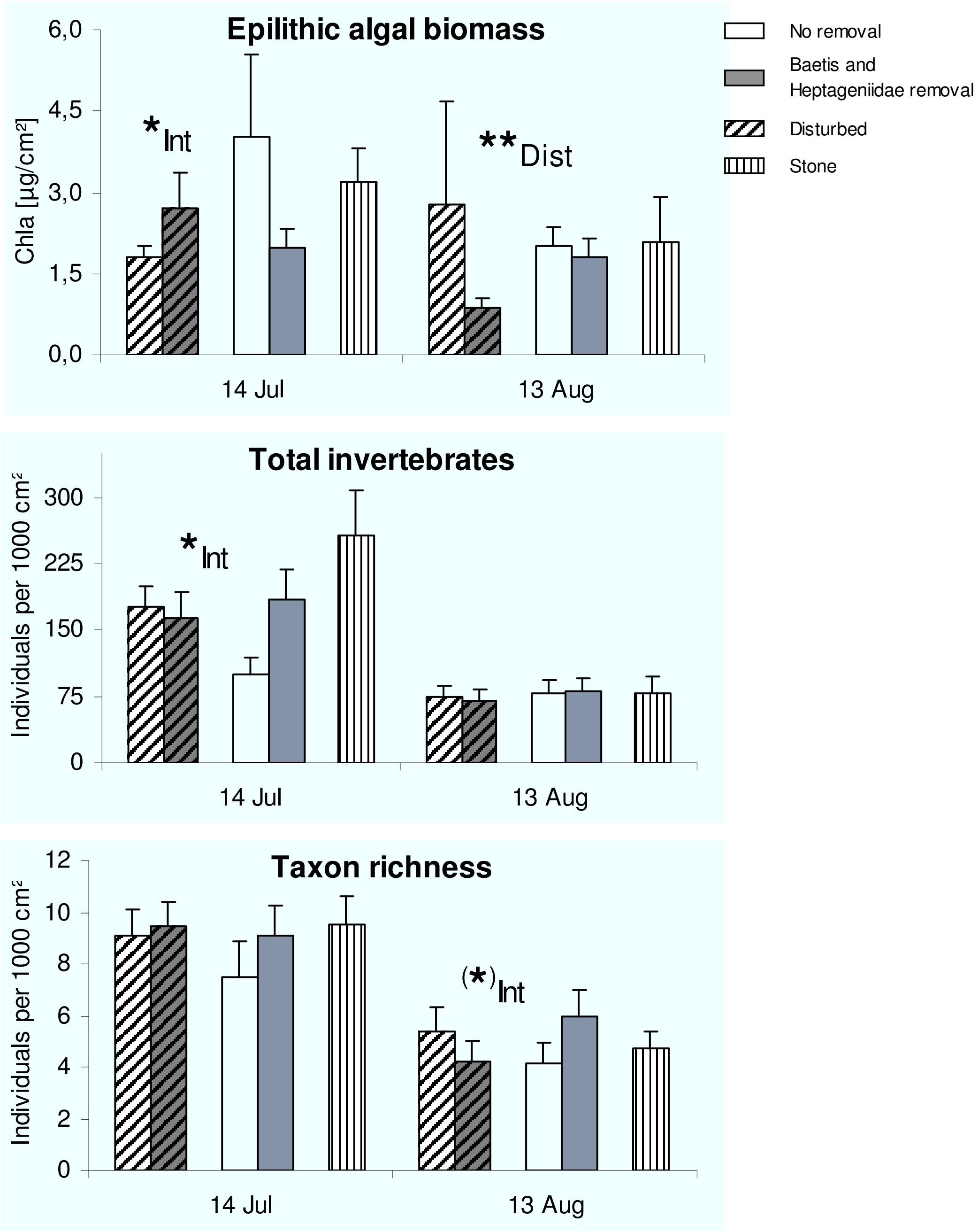
Epilithic algal biomass
Chla [µg/cm²]
6,0
4,5
3,0
1,5
0,0
*Int
**Dist
14 Jul
13 Aug
No removal
Baetis and Heptageniidae removal
Disturbed
Stone
Total invertebrates
Individuals per 1000 cm²
300
225
150
75
0
*Int
14 Jul
13 Aug
Taxon richness
Individuals per 1000 cm²
12
10
8
6
4
2
0
(*)Int
14 Jul
13 Aug

Fig. 2

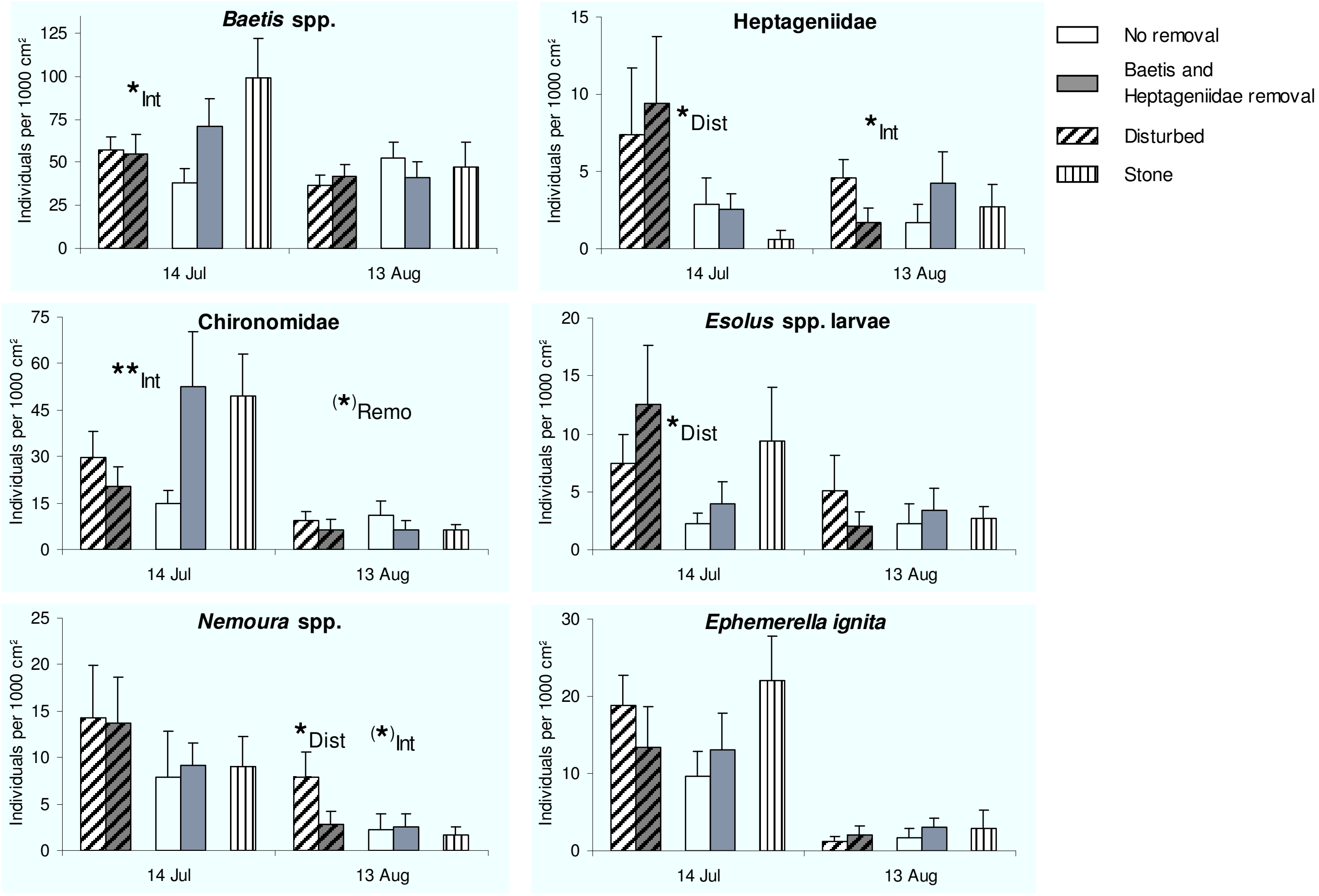
Baetis spp.
Individuals per 1000 cm²
0
25
50
75
100
125
*Int
14 Jul
13 Aug
Heptageniidae
0
5
10
15
*Dist
*Int
No removal
Baetis and Heptageniidae removal
Disturbed
Stone
Chironomidae
0
15
30
45
60
75
**Int
(*)Remo
Esolus spp. larvae
0
5
10
15
20
*Dist
Nemoura spp.
0
5
10
15
20
25
*Dist
(*)Int
Ephemerella ignita
0
10
20
30

Fig. 3

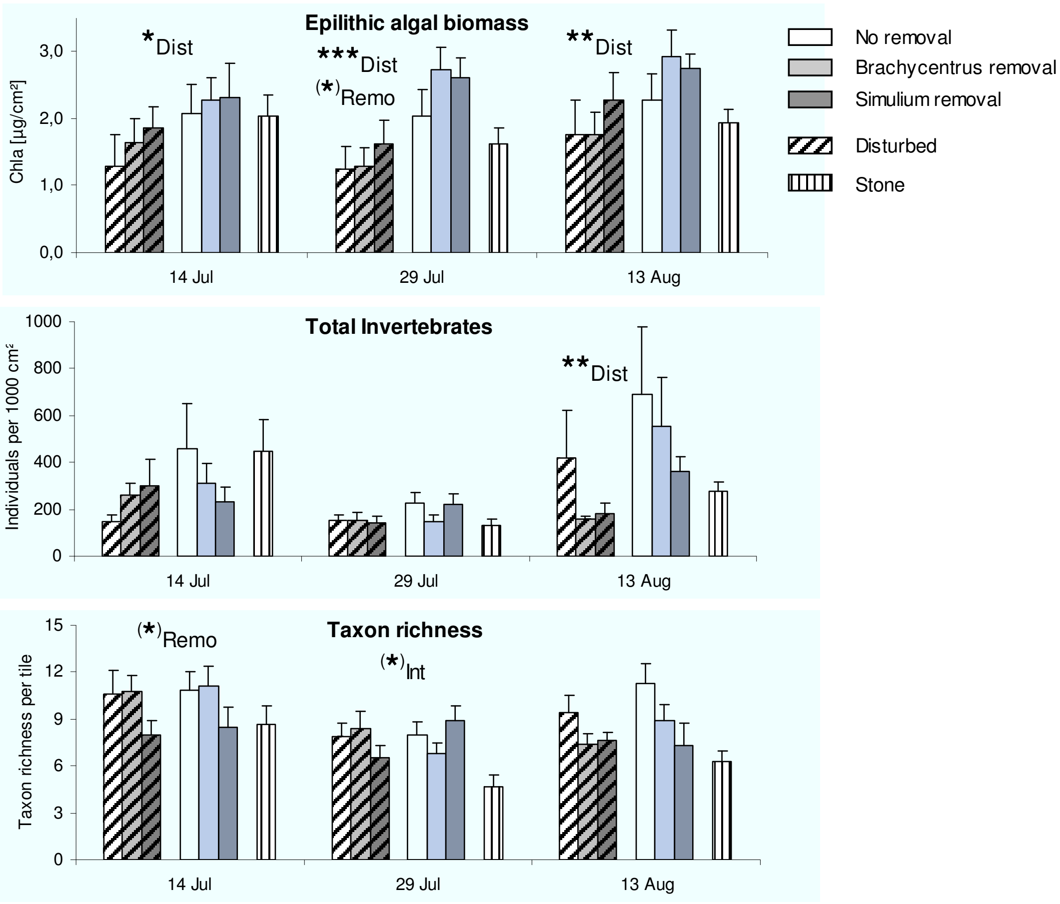
Epilithic algal biomass
Chla [µg/cm²]
0,0
1,0
2,0
3,0
*Dist
***Dist
(*)Remo
**Dist
14 Jul
29 Jul
13 Aug
No removal
Brachycentrus removal
Simulium removal
Disturbed
Stone
Total Invertebrates
Individuals per 1000 cm²
0
200
400
600
800
1000
**Dist
14 Jul
29 Jul
13 Aug
Taxon richness
Taxon richness per tile
0
3
6
9
12
15
(*)Remo
(*)Int
14 Jul
29 Jul
13 Aug

Fig. 4

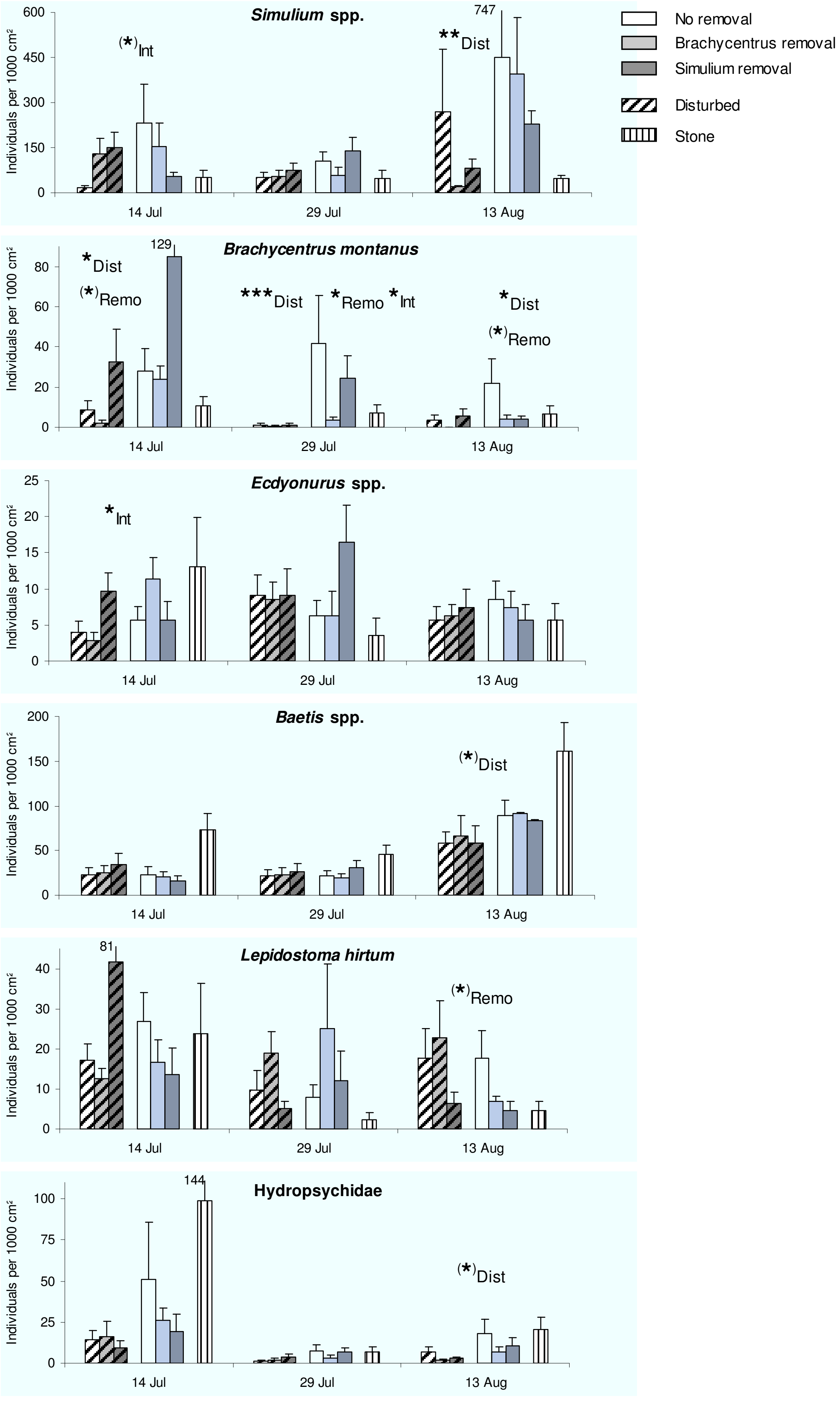
No removal
Brachycentrus removal
Simulium removal
Disturbed
Stone
Simulium spp.
Individuals per 1000 cm²
600
450
300
150
0
(*)Int
**Dist
747
14 Jul
29 Jul
13 Aug
Brachycentrus montanus
Individuals per 1000 cm²
80
60
40
20
0
129
*Dist
(*)Remo
***Dist
*Remo
*Int
*Dist
(*)Remo
14 Jul
29 Jul
13 Aug
Ecdyonurus spp.
Individuals per 1000 cm²
25
20
15
10
5
0
*Int
14 Jul
29 Jul
13 Aug
Baetis spp.
Individuals per 1000 cm²
200
150
100
50
0
(*)Dist
14 Jul
29 Jul
13 Aug
Lepidostoma hirtum
Individuals per 1000 cm²
40
30
20
10
0
81
(*)Remo
14 Jul
29 Jul
13 Aug
Hydropsychidae
Individuals per 1000 cm²
100
75
50
25
0
144
(*)Dist
14 Jul
29 Jul
13 Aug

Fig. 5

EXPERIMENTAL BED DISTURBANCE AND FISH EXCLUSION INFLUENCE THE DISTRIBUTION OF STREAM INVERTEBRATES AND ALGAE

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Effenberger M., Gerth M., Diehl S. & Matthaei C.D.

Experimental bed disturbance and fish exclusion influence the distribution of stream invertebrates and algae

Michael Effenberger[1], Maximilian Gerth[1], Sebastian Diehl[1],
& Christoph D. Matthaei[2]

[1]Department Biology II, Aquatic Ecology, University of Munich (LMU),
Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

[2]Department of Zoology, University of Otago, P.O. Box 56,
Dunedin, New Zealand

Corresponding author
E-mail: effenberger@zi.biologie.uni-muenchen.de
Fax: 0049-89-2180-74211

Abstract

We investigated the separate and interactive influences of disturbance by floods and predation by fish on a stream benthic community. We used electric fields to exclude fish predators from half of 48 stream bed patches (area 0.49 m^2) with contrasting disturbance treatments. Three types of bed disturbance were created by either scouring or filling patches to a depth of 15-20 cm or by leaving the patches undisturbed, thus mimicking the mosaic of scour and fill caused by a moderate natural flood. Benthic invertebrates and algae were sampled repeatedly until 57 days after the disturbance. Disturbance influenced all 10 investigated biological response variables, whereas predation affected five variables. Averaged across time, invertebrate taxon richness and total invertebrate abundance were highest in stable patches. Algal biomass and the densities of simuliids, *Sericostoma* spp., hydropsychid caddis flies, *Baetis* spp., and chironomids were higher in fill than in scour patches, whereas *Leuctra* spp. and *Agapetus* spp. were more abundant in scour and stable than in fill patches. Several invertebrates were more abundant in fish exclusion patches either throughout the experiment (*Baetis* spp., *Agapetus* spp.) or on single occasions (*Simulium* spp. and *Sericostoma* spp.). Reduced densities of invertebrate grazers in fish access patches coincided with a moderate increase in algal biomass, suggesting a weak trophic cascade. Overall, our results highlight the importance of patchy disturbances for the microdistribution of stream organisms and indicate a notable, but less prevalent, influence of fish exclusion at the patch scale. Disturbance and predation treatments interacted only once, suggesting that the observed predation effects were largely independent of local disturbance history.

Keywords: bed movement, fish, local disturbance history, predation, stream.

Introduction

In most ecosystems, both organisms and resources are distributed patchily in space and time across a heterogeneous environment. Identification of factors driving these “patch dynamics” is a central concern of ecology (Pickett & White 1985) and stream ecology in particular (Pringle *et al.* 1988, Townsend 1989). At the level of the community, disturbance and predation have received particular attention as drivers of community composition. The relative importance of these two factors in shaping communities and the interplay between them has been subject to long-standing debates (Menge & Sutherland 1976, Connell 1978, Huston 1979, Pickett & White 1985, Chesson & Huntly 1997, Chase *et al.* 2002). While there are conceptual similarities between abiotic disturbance and predation (e.g. both cause increased mortality), their community impacts may frequently diverge, because prey defenses that are effective against predators may not be effective against abiotic disturbances and vice versa. Also, disturbances occur by definition as pulsed, discrete events, whereas predation may act as a more continuous press on prey populations.

In streams, the spatial distribution of benthic invertebrates and algae is extremely patchy and known to be influenced by abiotic factors such as current velocity and bed substratum size (Barmuta 1989, Peckarsky *et al.* 1990, Holomuzki & Messier 1993). In the last decade, the role of flood disturbances in generating such patchy organismal distributions has received increasing attention (Palmer *et al.* 1992, Lancaster & Hildrew 1993, Robinson *et al.* 2003). Recent research has shown that high-flow events often create a mosaic of small (≤ 1 m^2) bed patches that have experienced sediment scour, deposition, or remained undisturbed (Matthaei *et al.* 1999, Matthaei *et al.* 2003). In addition to direct, short-term reductions in density or biomass, this 'local disturbance history' can have longer-lasting (> 4 weeks) effects on the microdistribution of algae and invertebrates (Matthaei & Townsend 2000, Matthaei *et al.* 2003, Effenberger *et al.* 2006). A recent field experiment suggests that changes in habitat parameters (e.g. current velocity, substratum size, food resources) induced by bed movement in combination with active microhabitat choice by benthic invertebrates are a likely mechanism contributing to such long-term effects of local disturbance history (Effenberger *et al.* 2008).

Numerous experiments have shown that predation can also be an important determinant of the density of stream populations (Cooper *et al.* 1990, Wootton & Power 1993, Englund & Olsson 1996, Diehl *et al.* 2000). Furthermore, there is evidence that predation can affect the degree of patchiness in the distribution of stream organisms. For example, Crowl *et al.* (1997) observed that the spatial variance of benthic invertebrates in New Zealand streams reflected the spatial distribution of the dominant predators. Whether prey populations respond measurably to patchy differences in predation risk depends largely on the relative importance of local, within-patch predation versus between-patch exchange rates. Thus, the distributional response of prey populations could be dominated by local predation rates (in the case of sedentary prey species), they could be amplified by strong local prey emigration responses, or they could be swamped by high overall prey immigration rates (Cooper *et al.* 1990, Wooster & Sih 1995, Englund 1997, Nisbet *et al.* 1997).

Although the majority of streams and rivers are subject to considerable discharge variation (Poff & Ward 1989, Poff 1996), most experiments investigating community impacts of predation in running waters have been performed under conditions of relatively stable flow. While predation has been shown to be important under such conditions, Poff & Ward (1989) and Townsend (1989) hypothesized that the importance of biotic interactions should decrease with increasing frequency of disturbance. On the other hand, Chesson & Huntly (1997) argued that biotic interactions may play an important role also in frequently disturbed ecosystems, because a relatively minor stress caused by competition or predation could be enough to push over the edge a population already weakened by abiotic disturbance. Hence, disturbance could either relieve organisms from stress caused by biotic interactions or make them even more vulnerable to this stress (Thomson *et al.* 2002).

With respect to predation, the hypothesis that disturbance weakens the influence of biotic interactions has been called the ‘harsh-benign hypothesis’, which posits that predation should be less important in frequently disturbed or physically harsh environments, because predators are believed to be more sensitive to disturbance and physical stress than many of their prey (Menge 1976, Menge & Olson 1990). Studies in streams have, with about equal frequency, supported or contradicted the harsh-benign hypothesis, thus questioning its general applicability (Peckarsky *et al.* 1990, Lancaster 1996, Thomson *et al.* 2002). These studies focused on hydraulic stress (enhanced current and drag) as the abiotic disturbance. To our knowledge, it has not been investigated how bed movement during high-flow events, arguably the most pervasive type of disturbance in running waters (Poff 1992), affects the impact of predators on prey communities. Bed-movement related effects may differ from those of increased hydraulic stress alone because bed movements occur as discrete, pulsed disturbances that create a spatial pattern of initial conditions of scour, fill and stable patches. In conjunction with spatial variation in predation or grazing, these heterogeneous initial conditions can lead to alternative community trajectories at scales from small patches to entire streams (Hart 1992, Roll *et al.* 2005, Power *et al.* 2008, Robinson & Uehlinger 2008).

We examined the separate and interactive effects of patchy bed disturbance and predation on benthic invertebrates and algae in a field experiment. We manipulated local disturbance history (to simulate the pulsed, patchy bed movement during a flood) and the access of fish to experimental bed patches (to manipulate the intensity of fish predation on invertebrates). Three disturbance treatments were crossed with two fish access treatments in a full-factorial design. Based on the results of previous, related studies, we expected patchy bed disturbances to have both short-term and long-term effects on the microdistribution of benthic organisms. We further expected fish predation to generally reduce invertebrate densities. We were particularly interested in testing whether disturbance and predation treatments would interact, as would be expected if biotic interactions were more important in stable patches compared to recently disturbed ones (as predicted by Poff & Ward 1989 and Townsend 1989).

Methods

Study site

The study was carried out in the Ach, a third-order, gravel-bed stream in southern Germany (47°43´N, 11°08´E). The Ach is the outlet of Lake Staffelsee that lies in a zone of fairly high rainfall at the northern edge of the Alps (mean annual rainfall in the catchment is about 1210 mm; German Weather Service [DWD], station Hohenpeissenberg). Mean annual discharge downstream of the study reach is 2.65 m^3s^{-1} and mean annual baseflow 0.74 m^3s^{-1} (Bavarian Water Management Authority [WWA] Munich). The Ach has a moderately harsh discharge regime with floods exceeding mean annual baseflow by a factor of 20 occuring on average once per year (extrapolation from flow data from 1951-2001, WWA Munich, unpublished data). About 50 % of the catchment (area 113 km^2, altitude 580-860 m a.s.l.) is covered by forest, and the remainder is pasture grazed by cattle. Our study reach has a fairly high sediment supply from unstable scree areas in the catchment, and this sediment supply results in a stream bed that is easily moved by floods. The stream bed consists mainly of small cobbles (particle width 64-128 mm) interspersed with some large cobbles (128-256 mm). Stream width at baseflow is about 5-10 m and water depth at the study reach ranged from 15-50 cm. The water is relatively nutrient-rich as indicated by average phosphate concentrations of 78 µg/l (n=3; data collected between May and August 2006). We did not quantify fish density in the study reach, but we observed many fishes every time we worked in the stream. Among the most frequently sighted species were barb (*Barbus barbus*), rainbow trout (*Oncorhynchus mykiss*) and chub (*Leuciscus cephalus*; M. Effenberger, field observations). Other common species in the Ach are spirlin (*Alburnoides bipunctatus*), eel (*Anguilla anguilla*), carp (*Cyprinus carpio*) and pike (*Esox lucius*; WWA Munich, unpublished data).

Experimental disturbance, removal of invertebrates and fish exclusion

Our study was conducted from June to August 2006. On 12 June, thirteen days before the start of the experiment, we exposed 288 unglazed white tiles (9.8 × 9.8 × 0.8 cm; surface area 223 cm^2) across a study reach of 100 m length. These tiles were subsequently used as sampling units for benthic invertebrates and algae. Tiles were tied in groups of six into 48 rectangular frames (50 × 50 cm) made out of PVC-pipe (inside diameter 1 cm). These PVC-frames were exposed in four blocks in riffles along the experimental reach (Fig.1). Blocks were spaced at intervals of 5 -15 m. Within each block, PVC frames were organized in two rows of six frames each. Each PVC frame was held in the center of a 0.7 × 0.7 m experimental plot by steel tent pegs. Each plot was an independent experimental unit (seperated by ≥ 1.5 m from neighbouring plots).

The experiment started on 25 June with the experimental disturbance and ended on 21 August (day 57). Fish were excluded from 27 June, one day after the first sampling date (see below), until the end of the experiment. On 25 June, each plot was subjected to one of three disturbance treatments cross-classified with two fish access treatments (see below). Within blocks, plots were randomly assigned to these six different treatment combinations, and one tile from each plot was collected on each of six successive post-disturbance sampling dates.

For the disturbance treatments, the bed substratum in the plots was either scoured or filled to a depth of about 15-20 cm (scour and fill plots), or left unchanged (stable plots). The magnitude of these manipulations was based on the bed movement patterns observed during natural floods in the Eyach, a similarly-sized river located about 6 km from the Ach (see Effenberger *et al.* 2008). The substratum for the fill patches was collected from dry gravel bars in the floodplain and contained no living stream invertebrates or algae (see Olsen, Matthaei & Townsend 2007, Effenberger *et al.* 2008). Scour patches were created by removing the surface sediment of the stream bed using a shovel. Additionally, tiles in scour and fill patches were scrubbed with a soft brush (see McCabe & Gotelli 2000) to remove all invertebrates and a large proportion of epilithic algae. These experimental disturbance treatments simulate important aspects of a moderate natural flood, such as patchy rearrangement of substrata and removal of invertebrates from disturbed patches (see Matthaei, Uehlinger & Frutiger 1997).

Electrified ‘fences’ (Pringle & Hamazaki 1997) were used to keep fish out of 'fish exclusion' plots. They consisted of 50 × 50 cm PVC frames lined with three parallel electrodes made of 12-gauge copper wire stripped of its insulation cover, one anode along the middle, and two cathodes along the sides (Peter B. Herrmann, unpublished data). Battery-powered electric fence chargers (Gallagher B160, Gallagher, Hamilton, New Zealand) were installed on the stream bank. Each fence charger was connected to the exclusion fences via two 12-gauge insulated copper wires (positive and ground terminals). Electric fence chargers produce continuous pulses (DC), 54-55 times per minute, with a pulse duration of 2 nanoseconds. Each fence charger supplied three electrified fences. The configuration of the wire lines within electrified fences produces strong pulses in the area inside the fence and extending 4-10 cm outside its perimeter. These electric pulses repel fish very effectively but do not affect invertebrate colonization of the areas inside the fence (Pringle & Hamazaki 1997, Peter B. Herrmann, unpublished data). In comparison to the cage exclosures traditionally used by stream ecologists, electric exclusion fences have several important advantages: (1) low resistance to stream current, which greatly reduces washout risk during high flow events; (2) avoidance of cage artefacts such as reduced current velocity and increased sedimentation; and (3) reduced maintenance work while in the stream (see Schofield *et al.* 2004). 'Control' fences were identical to 'fish exclusion' fences but were not connected to fence chargers.

Biological sampling

One randomly selected tile from each of the 48 patches was sampled 1, 8, 15, 29, 43 and 57 days after the experimental disturbance. All invertebrates were dislodged gently from the entire surface of each tile, caught in a hand net and preserved with 70% ethanol in the field. In the laboratory, invertebrate samples were identified (most taxa to genus, dipterans to family) and counted under a stereomicroscope at 6.5 – 40× magnification. Invertebrate numbers were expressed per area of tile surface, which included the undersides of tiles. Epilithic algal biomass was sampled by scraping the entire top side area of each tile with a tooth brush with shortened bristles. Samples were preserved immediately with formaldehyde solution (final concentration 4%) in the field, stored on ice in the dark and measured as chlorophyll a (using acetone for extraction; APHA 1998) per area of upper tile surface.

Data analysis

Invertebrate community structure (including rare taxa) was compared between disturbance and fish exclusion treatments on each of the six sampling dates using analysis of similarity (ANOSIM; Clarke 1993) on a Bray-Curtis similarity matrix obtained from $\log_{10}(x+1)$ transformed invertebrate density data. Differences between the three disturbance history types and the two fish exclusion treatments on each date were interpreted from pairwise tests in the ANOSIM.

Treatment effects on algal biomass, invertebrate taxon richness, total invertebrate density, and the densities of the seven most common invertebrate taxa were analyzed further with two-way, repeated-measures ANOVA, with ‘disturbance’ and ‘fish exclusion’ as between-subject factors and sampling date as the within-subjects factor. After exploratory analysis, all data were log (x) or log (x+1) transformed where necessary to improve normality and homoscedasticity. In cases where the assumption of data sphericity was violated, the results of the within-subjects analyses were corrected with the Greenhouse–Geisser method (Quinn & Keough 2002). If the factor disturbance had a significant effect, we conducted pairwise comparisons with Tukey’s HSD post hoc tests, except in cases of persisting heteroscedasticity where we used Games–Howell tests which do not assume equal variances between groups (Quinn & Keough 2002). Results for the factor time were statistically significant for all investigated response variables ($P \leq 0.001$). These results are not presented in further detail because they were not relevant for our research objectives. For brevity and because we were not interested in temporal dynamics per se, we present all data as grand means averaged across all sampling dates. Where treatment effects changed over time (statistically significant time x treatment interactions), we also present treatment means on individual sampling dates. All analyses were calculated in SPSS® version 12.0 (SPSS Inc., Chicago, USA) or PAST (Hammer, Harper & Ryan 2001).

Results

Faunal composition on tiles

Averaged across the entire 57-day experiment, larvae of the black fly *Simulium* spp. were the most abundant colonizers of the experimental tiles. This taxon contributed 16% of total invertebrate density (all 288 samples combined), followed by the two caddis fly taxa *Sericostoma* spp. (15%) and Hydropsychidae (13%), the stonefly *Leuctra* spp. (13%), the mayfly *Baetis* spp. (8%), midges (Chironomidae; 8%) and the caddis fly *Agapetus* spp. (6%). Together, these seven taxa made up 79% of all invertebrates on the tiles and were therefore abundant enough to be analyzed for treatment effects.

Treatment effects on invertebrate community parameters and algal biomass

On the first three post-disturbance sampling dates, the invertebrate communities in the three disturbance history categories all differed from each other (ANOSIM; $P < 0.03$ for each pairwise comparison). On the remaining three dates, the communities in scour patches were still distinct from those in fill patches ($P < 0.006$ for each date). Moreover, community composition in stable patches differed from fill patches on day 43 ($P = 0.009$) and from scour patches on day 57 ($P = 0.02$). By contrast, invertebrate community structure was similar in patches with and without fish access on all six sampling dates (ANOSIM; $P > 0.21$ for each date).

Overall, epilithic algal biomass (Fig. 2) was highest in stable, intermediate in fill and lowest in scour patches (Table 1, between-subjects effects). The differences between the three disturbance treatments changed, however, over time (Fig. 3; all pairwise specific contrasts for the time × disturbance interaction on successive sampling dates were significant; Table 1, within-subjects effects). Overall, algal biomass was reduced in fish exclusion patches, the difference to patches with fish access being marginally statistically significant ($P = 0.07$, power = 0.43; Table 1). This pattern did not change between sampling dates (no significant contrasts for the time × fish interaction).

Overall, total invertebrate density and invertebrate taxon richness (Fig. 2) were both higher in stable than in fill and scour patches. Significant time × disturbance contrasts indicated that the differences between disturbance treatments changed from day 1 to day 8, day 15 to day 29 and day 36 to day 57 for both parameters (Table 1). While total densities in stable and scour patches first increased and then decreased in parallel, densities in fill patches oscillated between the densities in the other two patch types (Fig. 3). Taxon richness remained highest in stable patches on the first five sampling dates. Richness in both disturbed patch categories recovered almost to stable levels between day 1 to day 8, then decreased again (at least in fill patches) from day 15 to day 28, and eventually reached the levels in stable patches between day 36 and day 57 (Fig. 3). The overall effects of disturbance and fish exclusion on taxon richness interacted, with the number of taxa in fill patches being higher in fish access than in fish exclusion treatments and the pattern being reversed in scour and stable patches (Fig. 2; Table 1).

Effects of disturbance history and fish exclusion on single invertebrate taxa

Overall, *Simulium* spp. (Fig. 2) reached higher densities in fill than in scour patches. This difference developed on day 8, persisted on day 15, and disappeared from day 29 onwards, when *Simulium* densities were very low in all three patch categories (Fig. 3; significant time × disturbance contrasts between day 1 and day 8 and between day 15 and day 29; Table 2). Three significant contrasts for the time × fish interaction indicated that *Simulium* was more abundant in patches where fish were excluded on days 15 and 43, but not overall (Fig. 4, Table 2).

Sericostoma spp. (Fig. 2) was more common in stable and fill than in scour patches overall. *Sericostoma* responded weakly to fish exclusion, with higher densities in the fishless treatment on day 1, but not on any other date (Fig. 4; significant contrast for the time × fish interaction between day 1 and day 8; Table 2).

Overall, densities of Hydropsychidae (Fig. 2) were higher in stable and fill patches than in scour patches. This difference became apparent from day 8 onwards, a change from the initial pattern on day 1 when Hydropsychidae were more common in stable patches than in both disturbed patch categories (Fig. 3; significant contrast between day 1 and day 8 for the time × disturbance interaction; Table 2).

Leuctra spp. (Fig. 2) was more abundant in stable and scour patches than in fill patches overall (Table 2). Significant time × disturbance contrasts indicated changing disturbance history patterns from day 1 to day 8 (faster recovery towards stable levels in scour than in fill patches) and from day 36 to day 57 (a shift from lowest *Leuctra* densities in fill patches to similar densities in all three patch categories; Fig. 3, Table 2).

Overall, densities of *Baetis* spp. (Fig. 2) were highest in stable, intermediate in fill and lowest in scour patches (Table 2). In addition, the differences between the disturbance treatments changed from day 1 to day 8 (when densities in the two disturbed patch categories started to recover relative to stable levels) and from day 8 to day 15 (when densities in fill patches recovered faster towards stable levels than densities in scour patches; Fig. 3, Table 2). Overall, there were also more *Baetis* larvae in patches from which fish had been excluded, the difference to patches with fish access being marginally statistically significant ($P = 0.055$, power = 0.49; Table 2).

The densities of Chironomidae (Fig. 2) were higher in stable and fill than in scour patches overall. On day 1, however, midges were still rarer in both disturbed patch types than in stable patches (Fig. 3; significant contrast for the time × fish interaction between day 1 and day 8; Table 2).

Finally, overall densities of *Agapetus* spp. (Fig. 2) were higher in stable and scour than in fill patches. This difference between disturbance categories disappeared between day 43 and day 57 (Fig. 3; significant contrast for the time × disturbance interaction between these two dates, Table 2). Overall, this caddisfly also reached higher densities in fish exclusion patches; this pattern was not yet present on day 1 when *Agapetus* was similarly rare in both fish treatments (Fig. 4; significant contrast for the time × fish interaction between day 1 and day 8; Table 2).

Discussion

We have investigated effects of bed disturbance and fish exclusion occurring in a small-scale mosaic of patches. While major differences in fish predation pressure within a stream primarily occur on a somewhat larger spatial scale (e.g. between riffles and pools), it seems very likely that there is also spatially predictable, small-scale patchiness in fish predation pressure because many fish species have (size-dependent) preferences for specific microhabitat conditions (Crowl *et al.* 1997, Skyfield & Grossman 2008). With respect to disturbance, the spatial scale of our manipulations is also relevant to many natural situations, because bed-moving floods often result in patchy bed movements as simulated in our experiment (Matthaei *et al.* 1999, Effenberger *et al.* 2006). Our treatments were, however, unavoidably embedded in a matrix of an unmanipulated stream bed. Fast exchange rates between patches and the matrix could thus have swamped responses of mobile organisms to patch-scale conditions (Cooper *et al.* 1990, Englund 1997). Still, the seven most abundant invertebrate taxa (most of which are highly mobile) did respond to our patch scale manipulations. We begin with a discussion of the direct and indirect, patch-scale effects of disturbance and fish predation before addressing their interactions and relative importance.

Direct and indirect effects of disturbance history and fish predation

In accordance with previous disturbance history research (Effenberger *et al.* 2006, 2008), our experimental disturbance had strong and lasting effects on the benthic community. Averaged across the entire 57-day experiment, epilithic algal biomass, total invertebrate density, taxon richness and the densities of all seven common invertebrate taxa were reduced significantly in at least one of the two disturbed treatments (scour or fill patches) relative to stable patches (see between-subjects effects in Tables 1 and 2). Moreover, nine significant interactions between time and disturbance plus many significant pair-wise contrasts for this interaction term in the repeated-measures ANOVA (see within-subjects effects in Tables 1 and 2) indicate that these patterns often changed over time since the experimental disturbance.

In the longer term, several of the common invertebrate taxa were more abundant in fill than in scour patches or vice versa (see Fig. 3). Most of these patterns are consistent with previous studies of natural and experimental flood disturbances and can be explained by preferences of these invertebrates for patches with particular habitat conditions (Effenberger *et al.* 2006, 2008). For example, in an earlier study we found higher densities of baetids, hydropsychids, and simuliids in fill than in scour patches up to 50 days after an experimental bed disturbance, which could be explained with a consistently higher near-bed current velocity in fill patches (Effenberger *et al.* 2008). Conversely, the stonefly *Leuctra* spp. was more abundant in scour patches where their food, particulate organic matter, accumulated because of reduced current velocity (Effenberger *et al.* 2008). These findings correspond well with earlier descriptions of habitat preferences of these taxa (Hildrew *et al.*1980, Hemphill & Cooper 1983, Osborne & Herricks 1987, Winterbottom *et al.* 1997, Robinson *et al.* 1998, Mérigoux & Dolédec 2004). We found exactly the same patterns in this study: First, current velocity was higher in fill patches (mean ± 1 SE across all sampling dates: 0.25 ± 0.02 m/s) than in scour patches (0.12 ± 0.01), the difference being statistically significant ($P < 0.002$) on all but the final date. Second, baetids, hydropsychids, and simuliids were more abundant in fill than in scour patches, whereas leuctrids showed the opposite pattern. The results of our two studies are thus highly consistent, supporting our earlier proposition that longer-term effects of local disturbance history occur as consequences of disturbance-mediated changes in physical habitat parameters and food resources (Effenberger *et al.* 2008).

Based on previous studies (Cooper *et al.* 1990, Wooster 1994, Englund & Olsson 1996), we had expected invertebrate densities to be higher in patches from which fish were excluded because prey mortality and/or prey emigration should have been higher in patches to which fish had access. Moreover, fish should have had an indirect positive impact on algal growth by reducing invertebrate grazing pressure on algae (see e.g. Power 1990, McIntosh & Townsend 1996, Diehl *et al.* 2000).

Both expectations were at least partly fulfilled. First, the densities of two invertebrate taxa (*Agapetus*, *Baetis*) were reduced in patches with fish access throughout the entire 57-day experiment. Two further taxa (*Simulium*, *Sericostoma*) showed reduced densities in fish patches on at least one sampling date. Second, algal biomass tended to be higher in patches to which fish had free access. Reduction of the numerically dominant grazers *Baetis* and *Agapetus* may have facilitated algal growth in fish access patches, suggesting a trophic cascade from fish to algae (see

Power 1990, 1992, Flecker & Townsend 1994, McIntosh & Townsend 1996, Dahl *et al.* 1998, Diehl *et al.* 2000).

In contrast to fish effects, indirect effects of disturbance history could have propagated either up or down the food chain or both. Algal biomass in running water ecosystems is often positively related to current speed (Biggs *et al.* 1998, Blanchet *et al.* 2008). Current speed was 50% slower in scour compared to stable and fill patches, which could explain why algal biomass was lowest in scour patches. The time-averaged densities of *Baetis*, in turn, showed a pattern remarkably similar to that of algal biomass (stable > fill > scour). This congruence would be compatible with a current velocity-mediated bottom-up effect of the disturbance treatments on this grazer. However, the other major grazer *Agapetus* showed a partly opposite distribution, with the highest *Agapetus* densities coinciding with the lowest algal biomass in the scour patches. Consequently, an alternative explanation for the lower algal biomass in scour patches could be that a behavioral preference of *Agapetus* for scour patches led to enhanced grazing losses. The latter scenario would require *Agapetus* to be a more effective grazer than *Baetis*, with the former locally reducing algae and thus contributing to the patchy mosaic of algal densities, and the latter merely tracking between-patch differences in algal density. This hypothesis is consistent with differences in feeding mode and in mobility between the two taxa. The heavy-cased *Agapetus* is a thorough scraper largely limited to crawling and *Baetis* is a much less thorough grazer but a highly mobile drifter and swimmer (Kohler 1984, 1992, Becker 2001). Empirical and theoretical studies have demonstrated that thorough but slow-moving grazers can indeed produce patchiness in their resource even in the absence of environmental patchiness, whereas less thorough but more mobile grazer tend to be better at tracking resource patchiness (Nisbet *et al.* 1997, Wilson *et al.* 1999, Richards *et al.* 2000, Chase *et al.* 2001).

Relative importance of disturbance history and fish predation

In our experiment, local disturbance history affected all nine invertebrate community parameters plus algal biomass, whereas local fish exclusion only influenced five of these variables and some of them only on a single sampling date. This result suggests that local disturbance history was relatively more ‘important’ as a driver of the microdistribution of stream organisms than fish predation. Our results indicate that changes in habitat parameters (e.g. current velocity) induced by bed movement can be local cues for the active habitat choice of benthic invertebrates (Effenberger *et al.* 2008, the present study). On the other hand, invertebrates may be less able to distinguish reliably between patches with reduced or sustained fish predation risk at a very small spatial scale (0.5 m^2) when the surrounding water contains chemical cues of fish. Interestingly, the two taxa that most consistently responded to the fish treatment (*Baetis* and *Agapetus)* occupy different ends of the invertebrate mobility spectrum, suggesting that different mechanisms may be responsible for their density reductions in fish patches. *Agapetus* is a very slow-moving, non-drifting epibenthic grazer. Its density reduction in fish patches was therefore most likely a direct consequence of fish predation. In contrast, high drift immigration rates of highly mobile invertebrates such as baetids tend to swamp the effects of local consumption by predators at very small spatial scales (Cooper *et al.* 1990, Englund 1997). Therefore, the density reductions of baetids in fish patches were most likely a consequence of increased drift emigration from predator patches, as has been demonstrated in previous experiments (Kratz 1996, Forrester *et al.* 1999, Diehl *et al.* 2000).

Studies in streams focusing on hydraulic stress (enhanced current and drag without bed movement) as the abiotic disturbance have given mixed support for the harsh-benign hypothesis. For example, in a careful descriptive study Lancaster (1996) found that the impact of invertebrate predators on their prey decreased during periods of increased flow variability and enhanced current speed for one predator taxon (an alderfly) but not for another (a caddisfly). Further, while Peckarsky *et al.* (1990) found that the effects of invertebrate predators on their prey increased with a reduction in current speed, Thomson *et al.* (2002) observed the opposite phenomenon. Both studies were experimental and used taxonomically similar predators (stoneflies) and prey (grazing mayflies), suggesting that the harsh-benign hypothesis has limited generality with respect to hydraulic stress as the relevant type of disturbance.

Our experiment may be the first in which the influence of a pulsed bed disturbance on predation has been studied experimentally in a full-factorial design. We found that effects of fish predation on invertebrate and algal densities were generally present or absent regardless of the disturbance history of the investigated patches of stream bed. Invertebrate taxon richness was the only response parameter for which disturbance history and fish treatments interacted. In stable patches, taxon richness was higher in the absence than in the presence of fish, while the opposite pattern was observed in fill patches. Nevertheless, in this case bed disturbance did not influence predation effects in a consistent way because richness in the other disturbance treatment (scour patches) showed the same pattern as in stable patches. Overall, our results thus do not support the hypothesis that predation effects are dampened in the wake of a bed disturbance, at least at the relatively small spatial scale of our manipulations.

Conclusions and outlook

In our experiment, both bed disturbance and fish predation affected the benthic invertebrate and algal communities at the patch scale, even though predation effects occurred less often than disturbance effects. Overall, these results add to the very limited data addressing the question to which extent biotic interactions influence stream invertebrate communities under frequently disturbed conditions. However, there is still a need to expand the two-factorial designs used in all previous related experiments, and exploring the interaction of disturbance with multiple biotic factors (e.g. predation plus competition) should be a priority in future community ecology. It is also known from other ecosystems that the productivity of a system can change the relationship between predation or disturbance and diversity (Rosenzweig & Abramsky 1993, Kondoh 2001, Worm *et al.* 2002, Currie *et al.* 2004). Hence, productivity should also be included in future investigations of the interplay between abiotic disturbances and biotic interactions. Moreover, we investigated effects of bed disturbances and fish exclusion occurring in a small-scale mosaic of patches. By contrast, the conceptual models by Poff & Ward (1989), Townsend (1989) and Chesson & Huntly (1997) all compare different disturbance scenarios occurring at the spatial scale of entire systems. Even though these spatial scales are much less amenable to manipulative experimentation, a true challenge for future experimental research would to combine patchy bed disturbances with fish exclusions from replicated stream reaches (see e.g. Nakano *et al.*1999)

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Table 1. Summary of treatment effects and time by treatment interactions on epilithic algal biomass, total invertebrate densities and taxon richness as determined by repeated-measures-ANOVAs and subsequent post-hoc tests and specific contrasts. Only treatment effects and interactions with *P*-values ≤ 0.10 are shown. Results for the factor 'time' are not presented because they were not relevant for our hypotheses. *P*-values for the time × disturbance interactions represent the overall results (including all sampling dates). Specific contrasts for the time × disturbance-interactions indicate differences between paired sampling dates (1 = day 1; 2 = day 8; 3 = day 15; 4 = day 29; 5 = day 43; 6 = day 57). Dist = Disturbance, Fish = Fish exclusion.

Dependent variable	***P*-value**	**Ranking (*post-hoc* test or specific contrasts)**
Epilithic algal biomass		
Between subjects		
Dist	< 0.001	Stable > fill > scour
Fish	0.074	Fish > no fish
Within subjects		
Time x Dist	< 0.001	1 vs. 2; 2 vs. 3; 3 vs. 4; 4 vs. 5; 5 vs. 6
Total invertebrates		
Between subjects		
Dist	< 0.001	Stable > (fill = scour)
Within subjects		
Time x Dist	< 0.001	1 vs. 2; 3 vs. 4; 5 vs. 6
Taxon richness		
Between subjects		
Dist	< 0.001	Stable > (fill = scour)
Dist x Fish	0.01	Fill: Fish > no fish; Stable, scour: no fish > fish
Within subjects		
Time x Dist	< 0.001	1 vs. 2; 3 vs. 4; 5 vs. 6

Table 2. Summary of treatment effects and time by treatment interactions on the densities of the seven most common invertebrate taxa as determined by repeated-measures-ANOVAs. For treatment (= between-subjects) effects. and time by treatment interactions (= within-subjects effects) only *P*-values ≤ 0.10 are shown. For time by treatment interactions all listed specific contrasts between subsequent sampling dates were statistically significant at $P < 0.05$. For more details see Table 1.

Dependent variable	***P*-value**	**Ranking (*post-hoc* test or specific contrasts)**
***Simulium* spp.**		
Between subjects		
Dist	0.02	Fill > scour
Within subjects		
Time x Dist	< 0.001	1 vs. 2; 3 vs. 4
Time x Fish	0.10	3 vs. 4; 4 vs. 5; 5 vs. 6
***Sericostoma* spp.**		
Between subjects		
Dist	0.02	(Stable = fill) > scour
Within subjects		
Time x Fish	0.22	1 vs. 2
Hydropsychidae		
Between subjects		
Dist	0.001	(Stable = fill) > scour
Within subjects		
Time x Dist	0.15	1 vs. 2
***Leuctra* spp.**		
Between subjects		
Dist	< 0.001	(Stable = scour) > fill
Within subjects		
Time x Dist	0.001	1 vs. 2; 5 vs. 6

Table 2 continued

Dependent variable	***P*-value**	**Ranking (*post-hoc* test or specific contrasts)**
***Baetis* spp.**		
Between subjects		
Dist	< 0.001	Stable > fill > scour
Fish	0.055	No fish > fish
Within subjects		
Time x Dist	< 0.001	1 vs. 2; 2 vs. 3
Chironomidae		
Between subjects		
Dist	< 0.001	(Stable = fill) > scour
Within subjects		
Time x Dist	0.009	1 vs. 2
***Agapetus* spp.**		
Between subjects		
Dist	< 0.001	(Stable = scour) > fill
Fish	0.02	No fish > fish
Within subjects		
Time x Dist	< 0.001	5 vs. 6
Time x Fish	0.28	1 vs. 2

Figure legends

Fig. 1. Schematic layout of one experimental block. Within each block, two replicates of each treatment combination (three disturbance history treatments x two fish treatments) were placed at random. Numbers on tiles indicate the sampling dates (1 = day 1; 2 = day 8; 3 = day 15; 4 = day 29; 5 = day 43; 6 = day 57) and the arrow indicates the direction of flow.

Fig. 2. Grand means (averaged across all six sampling dates) of total invertebrate densities, taxon richness, epilithic algal biomass and densities of the seven most common invertebrate taxa on experimental tiles in the disturbance and fish treatments. Error bars indicate standard errors. See Tables 1 and 2 for exact *P*-values.

Fig. 3. Temporal patterns of total invertebrate densities, taxon richness, epilithic algal biomass and densities of the seven most common invertebrate taxa in the three disturbance treatments (averaged across both fish treatments). Error bars indicate standard errors. See Tables 1 and 2 for exact *P*-values.

Fig. 4. Temporal patterns of densities of *Simulium* spp., *Sericostoma* spp. and *Agapetus* spp. in the two fish treatments (averaged across all three disturbance treatments). Error bars indicate standard errors. See Tables 1 and 2 for exact *P*-values.

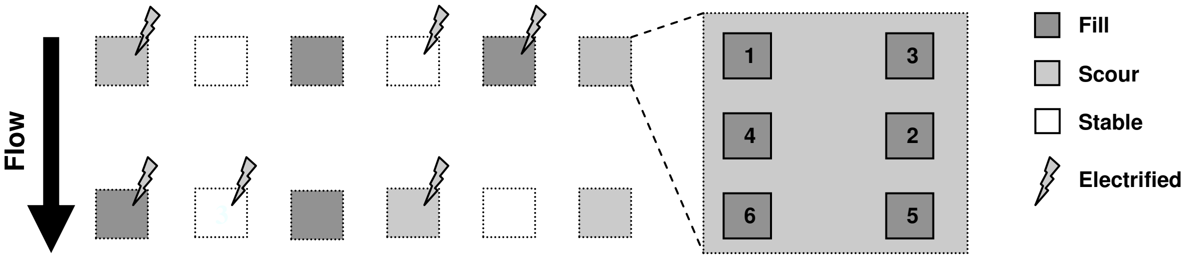


Fig. 1

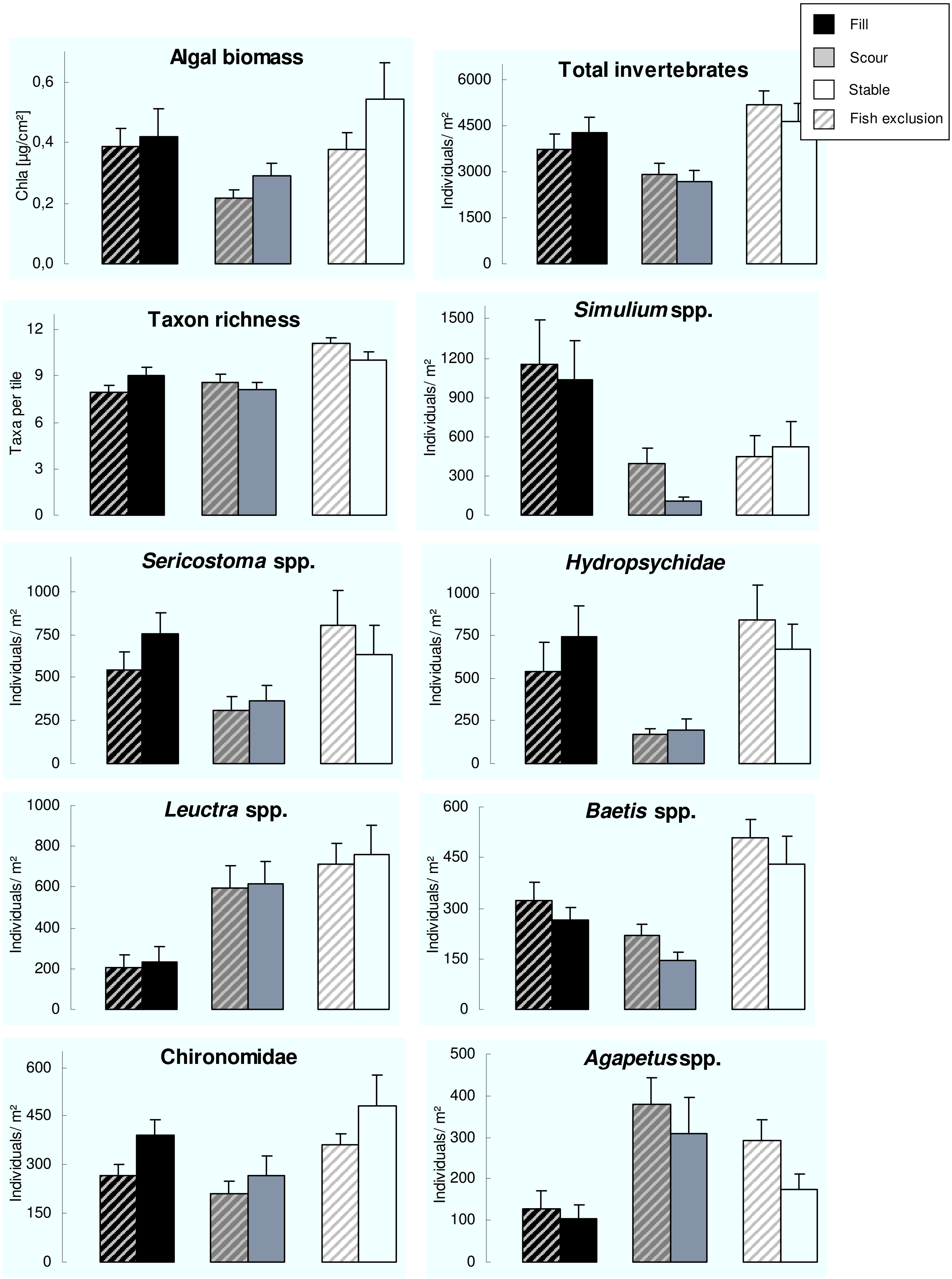

Fill
Scour
Stable
Fish exclusion
Algal biomass
Chla [µg/cm²]
0,0
0,2
0,4
0,6
Total invertebrates
Individuals/ m²
0
1500
3000
4500
6000
Taxon richness
Taxa per tile
0
3
6
9
12
Simulium spp.
Individuals/ m²
0
300
600
900
1200
1500
Sericostoma spp.
Individuals/ m²
0
250
500
750
1000
Hydropsychidae
Individuals/ m²
0
250
500
750
1000
Leuctra spp.
Individuals/ m²
0
200
400
600
800
1000
Baetis spp.
Individuals/ m²
0
150
300
450
600
Chironomidae
Individuals/ m²
0
150
300
450
600
Agapetus spp.
Individuals/ m²
0
100
200
300
400
500

Fig. 2

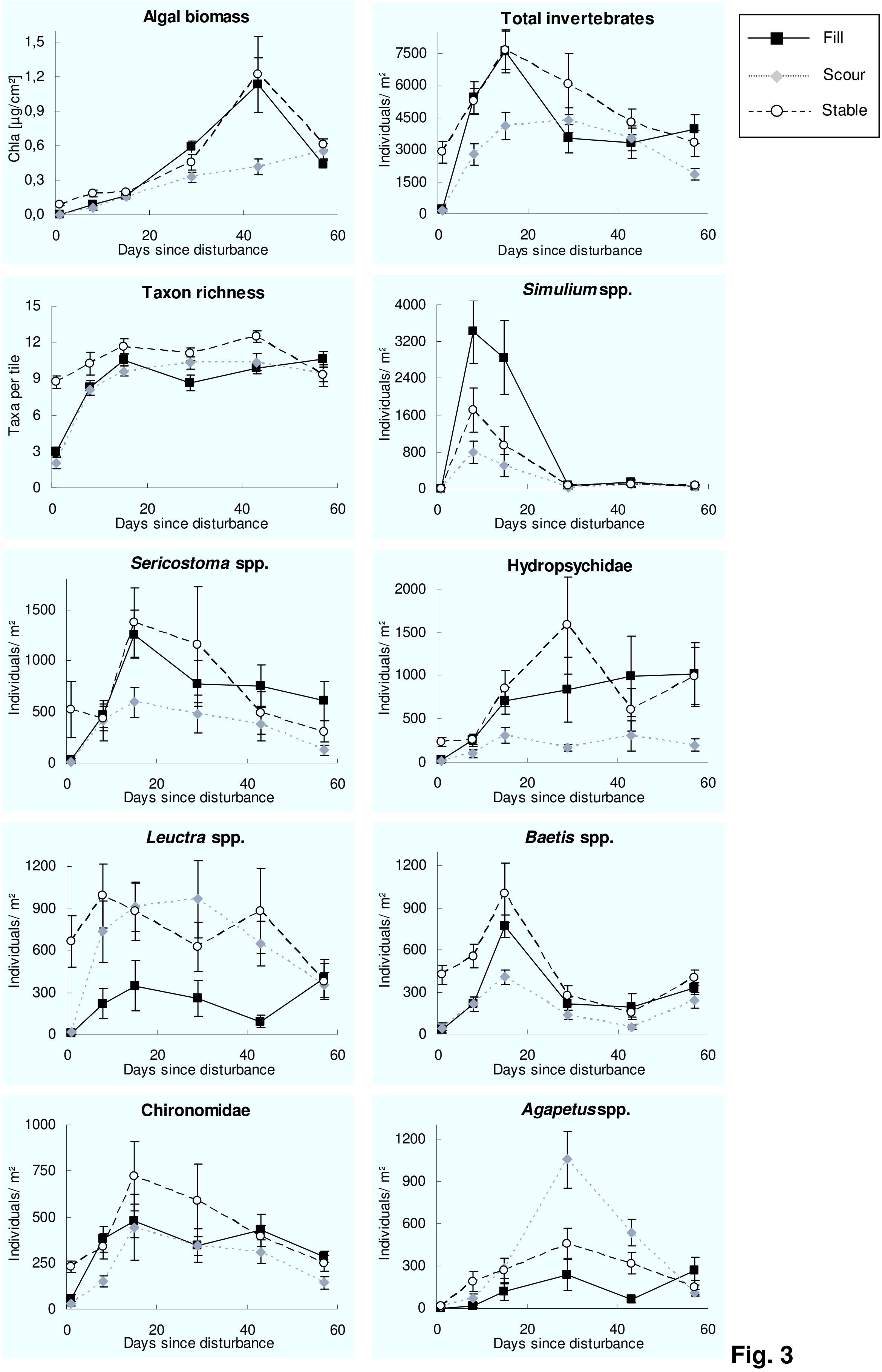
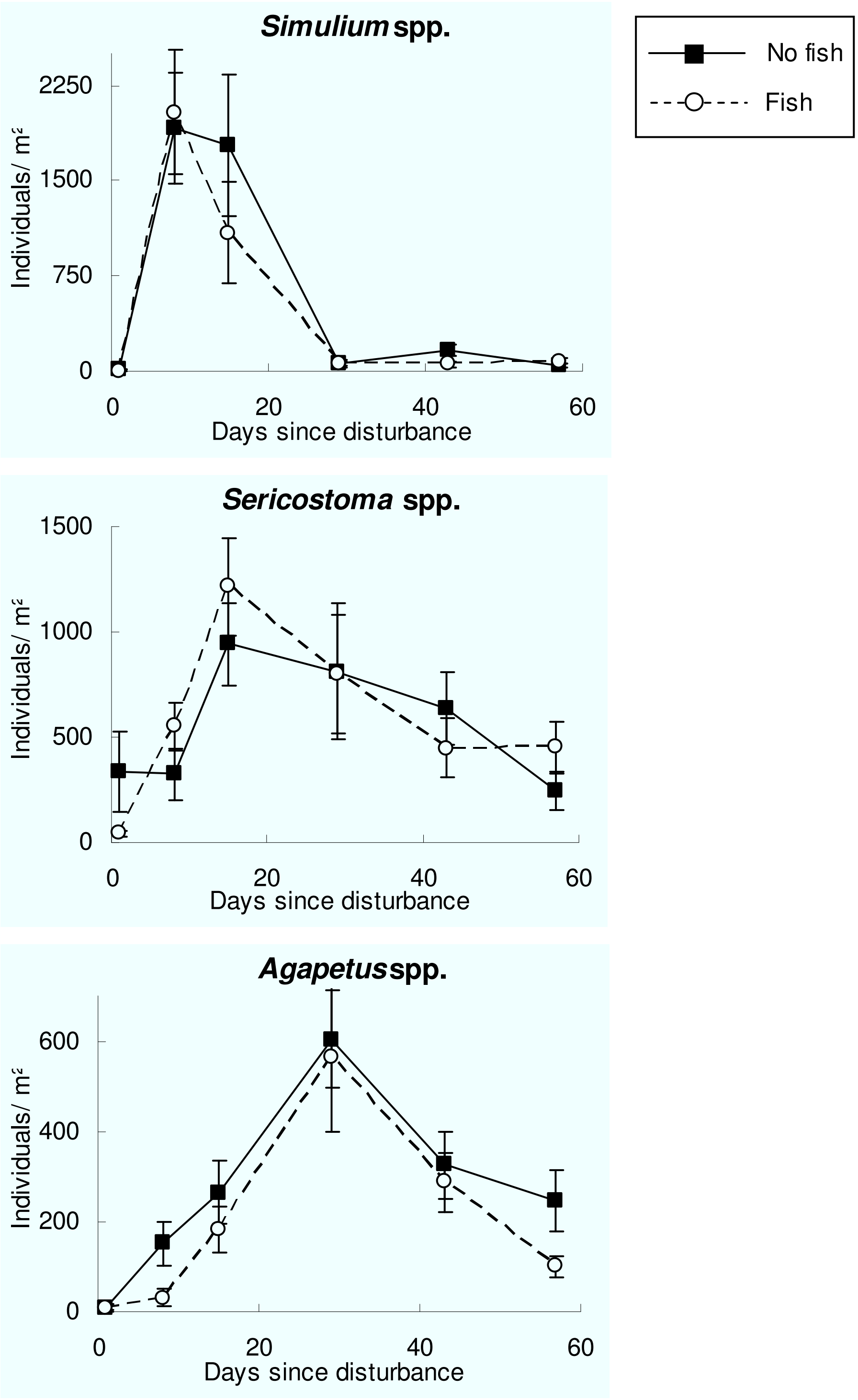

Algal biomass
Chla [µg/cm²]
1,5
1,2
0,9
0,6
0,3
0,0
Days since disturbance
0
20
40
60
Total invertebrates
Individuals/ m²
7500
6000
4500
3000
1500
0
Fill
Scour
Stable
Taxon richness
Taxa per tile
15
12
9
6
3
0
Simulium spp.
4000
3200
2400
1600
800
Sericostoma spp.
1500
1000
500
Hydropsychidae
2000
1500
1000
500
Leuctra spp.
1200
900
600
300
Baetis spp.
Chironomidae
1000
750
500
250
Agapetus spp.
1200
900
600
300

Fig. 3



Simulium spp.
Individuals/ m²
2250
1500
750
0
0
20
40
60
Days since disturbance
Sericostoma spp.
Individuals/ m²
1500
1000
500
0
0
20
40
60
Days since disturbance
Agapetus spp.
Individuals/ m²
600
400
200
0
0
20
40
60
Days since disturbance
No fish
Fish

Fig. 4

CONCLUSIONS, LIMITATIONS AND RESEARCH OUTLOOK

Observational and manipulative disturbance history research

In my thesis, I investigated the separate and interactive effects of flood disturbances and biotic interactions on benthic stream communities. In Chapter 1, I could show that local disturbance history clearly played an important role influencing the small-scale distribution of mobile invertebrates in two flood-prone streams, supporting conclusions from previous research (Matthaei *et al.* 2000, Matthaei & Townsend 2000). Additionally, benthic invertebrate distribution was correlated with several habitat parameters such as current velocity and substratum size. This observational study also supplied some first evidence that the longer-term effects (several weeks after a flood) of local disturbance history on benthic invertebrates may act ‘indirectly’ via disturbance history effects on those habitat parameters. Consequently, the results of Chapter 1 implied that a thorough understanding of the microdistribution of benthic invertebrates requires knowledge of disturbance history, as well as more readily measured habitat parameters such as current velocity or substratum size.

Even though the results from Chapter 1 and other previous research suggested that local disturbance history can be an important driver of the patchy microdistribution of stream organisms (Matthaei & Townsend 2000, Matthaei *et al.* 2003), little was known about the specific mechanisms through which disturbance history affects benthic communities. Moreover, the link between disturbance history and habitat parameters known to also influence the microdistribution of stream biota was not very clear. To my knowledge, the experiment described in Chapter 2 is the first manipulative study that specifically addressed 'indirect' effects of local disturbance history on benthic organisms. The findings of this experiment suggest that immediate, 'direct' effects of local disturbance on benthic invertebrates (mostly negative, i.e. density reductions in disturbed bed patches) are often in the longer term (several weeks after a flood) replaced by 'indirect' effects mediated via disturbance-induced changes in habitat parameters such as current velocity, substratum size and resource availability. In such a scenario, high mortality and emigration in scour and fill patches would be the driving forces for the microdistribution of invertebrates shortly after a flood. In the longer term, many mobile taxa may increasingly move from stable to scour and fill patches, where they may find microhabitat conditions that correspond better to their individual preferences.

It should be noted, however, that several effects of disturbance history remained significant towards the end of the experiment in spite of including the above habitat parameters in the statistical analysis. This result indicates that disturbance-driven changes in these habitat parameters could not explain all longer-term effects of disturbance history on the invertebrate community. Hence, it is possible that these unexplained long-term effects were caused by additional factors which had not been examined in the experiment (e.g. resource quality, competitors or predators). In streams, these biotic factors are most likely influenced by flood disturbances, as well, leading to patchy distributions of resources, competitors and predators of non-predatory benthic invertebrates (Townsend 1989).

It is well known, for example, that stable surface substrata can act as refugia for stream algae, one major food resource for benthic stream invertebrates, during floods (e.g. Power & Stewart 1987, Uehlinger 1991, Peterson *et al.* 1994, Matthaei *et al.* 2003). In our experiment (Chapter 2), algal biomass was also highest in stable patches shortly after the disturbance. Following floods, the successional stage and vitality of algal mats in stable patches is different from those in disturbed patches (see Peterson *et al.* 1990, Peterson 1996), with recently disturbed patches often containing more healthy algal cells than stable patches. Hence, algal mats in “aging” stable patches may be, due to their lower food quality or edibility, less attractive to invertebrate consumers than the “younger” algal mats in scour or fill patches. This reduced attractiveness of aging algal mats for invertebrate consumers may, in the longer term, lead to lower invertebrate densities in stable patches.

Another reason for the remaining unexplained longer-term differences between scour, fill and stable bed patches in Chapter 2 may lie in disturbance-induced changes in predator-prey interactions. According to consumer stress models (see Menge & Olson 1990), stress due to an environmental factor such as flood disturbance should reduce average predation rates per prey more than it reduces average growth rates (or immigration rates) of the prey population. For invertebrate communities in streams, this prediction could be true, because invertebrate predators are usually larger and may thus be more susceptible to flood disturbances because they offer more resistance to the current and cannot take shelter in the small interstitial spaces inside the stream bed. Consequently, one might expect lower predator densities and thus predation pressure in scour and fill patches compared to stable patches, leading to higher prey densities in the latter. Nevertheless, this potential explanation of the patterns in Chapter 2 has to remain tentative because predator-prey interactions were not investigated in this experiment. Competitive interactions between invertebrates were also not studied. To overcome these limitations, the remaining chapters of my thesis investigated the influence of these two key biotic processes combined with flood disturbance and habitat parameters on the microdistribution of benthic stream invertebrates (Chapters 3, 4 and 5).

Flood disturbance versus biotic processes

The experiment described in Chapter 3 examined the interplay between patchy bed disturbance (the mosaic of stable, scour and fill patches resulting from a simulated flood disturbance) and interspecific competition at the patch scale in determining the microdistribution of benthic invertebrates in a frequently disturbed stream. To my knowledge, this study is the first field experiment investigating this interplay. In contrast to the numerous and long-lasting effects of disturbance history (described in detail in Chapter 2), frequent removals of the numerically dominant invertebrate taxon (*Baetis* spp.) showed hardly any effects on the remaining invertebrate community and on benthic algae in spite of *Baetis* spp. being known as a strong competitor in competition experiments elsewhere (Kohler 1992, Kuhara *et al.* 1999). Interactions between disturbance and *Baetis* removal treatments also occurred in just a single case. These results thus confirm the importance of patchy disturbances for driving the microdistribution of stream invertebrates, whereas patchy removal of the numerically dominant taxon hardly influenced the invertebrate assemblages at the patch scale. Based on the findings of previous disturbance research in streams (see citations in General Introduction), we believe that the effects of an experimental manipulation of disturbance and species densities are likely to depend on the natural disturbance regime and resulting adaptations of the local community. Because all existing manipulative experiments investigating the interplay between bed disturbances and biotic interactions (including ours) were unreplicated at the stream level (owing to the prohibitive effort involved), more experiments with similar study designs are needed to examine the generality of the findings in Chapter 3.

To begin closing this knowledge gap, I examined the interplay between frequent abiotic disturbance and interspecific competition at the patch scale in determining benthic community composition in another two streams (Chapter 4). In this experiment, I repeatedly manipulated substrate stability and the densities of two common invertebrate taxa simultaneously in two study streams with contrasting flooding regimes (stable versus frequently disturbed). In the stable stream, the manipulated insect larvae were fairly sessile (a black fly and a caddis fly), whereas two highly mobile mayfly taxa were targeted in the frequently disturbed stream. In contrast to the results from Chapter 3, where I disturbed the stream bed only once at the beginning of the experiment by scouring or filling sediment, the interplay between the repeated disturbance and competition in shaping stream invertebrate communities was much stronger in Chapter 4.

As expected, the interplay between disturbance and competition in their influence on the benthic fauna also differed between our two study streams. Although the lack of replication at the stream level does not allow a rigorous comparison, a few striking patterns should be pointed out: In the stable stream, we found many (and exclusively negative) effects of disturbance on stream biota, and removal of one target taxon lead to higher densities of the other target taxon, regardless of disturbance treatment. In the flood-prone stream, we found negative effects of disturbance on the sedentary algae, but positive effects on the most common invertebrate taxa (which were all highly mobile). Moreover, positive effects of removal on non-target taxa were frequent, but only in undisturbed patches. There are at least two (non-exclusive) explanations for these differences in disturbance effects between streams. First, it seems plausible that the invertebrate community of a flood-prone stream is better adapted to fast recolonization of disturbed patches than the community of a stream with stable discharge. Second, negative effects of disturbance became more prevalent in the stable stream over the course of the experiment, suggesting that effects of repeated local disturbances in a matrix of surrounding undisturbed stream bed may accumulate over time, as it has been observed in a related experiment (Hemphill & Cooper 1983). In contrast, the flood-prone stream experienced a large-scale disturbance (a natural flood) after our first sampling date, forcing us to restart the experiment. Consequently, cumulative effects of our experimental disturbance could not develop in the flood-prone stream.

Compared to the experiments in Chapter 4, disturbance effects were much more frequent and longer-lasting in Chapter 3. Apparently the disturbance effect on invertebrates is different depending on whether the stream bed is scoured (resulting in removal of substratum) or filled (with substratum from elsewhere) at the beginning of an experiment (Chapter 3) or the same patch of stream bed is repeatedly disturbed every two weeks, without removing or adding substratum (Chapter 4). This difference could be due to the observed changes in habitat parameters originating from the experimental scouring or filling described in Chapter 3.

At first sight, the diverging results of our studies seem to contrast with the results of the few studies available for direct comparison (Hemphill & Cooper 1983, Hemphill 1991, McAuliffe 1984). Nevertheless, these three studies were all conducted in streams relatively near the stable end of the gradient of disturbance frequency and intensity occurring in natural streams (see Poff and Ward 1989, Poff 1996). Moreover, all three used more or less sessile organisms for their invertebrate removal treatments. As a result, all three studies concluded that competition between common invertebrate species played an important role in the investigated stream in question. This conclusion is paralleled by the findings from our hydrologically stable stream where we manipulated densities of two common sessile species and found several effects of this experimental removal on the invertebrate community (Chapter 4, stable stream). By contrast, in both experiments where we worked with highly mobile organisms in a stream closer to the frequently disturbed end of this gradient (Chapter 3, and frequently disturbed stream in Chapter 4), we found no or only weak evidence of competition between invertebrates. Collectively, the results from all six experiments (Hemphill & Cooper 1983, Hemphill 1991, McAuliffe 1984, our three experiments in Chapters 3 and 4) therefore conform with the predictions of Poff and Ward (1989) and Townsend (1989), according to which the importance of biotic interactions in shaping aquatic communities should decrease with increasing frequency or intensity of disturbance.

It should be noted, however, that the experimental removal of highly mobile invertebrate taxa was very challenging in both studies (Chapters 3 and 4) and thus had certain limitations. To my knowledge, no such manipulation has been attempted previously. In the flood-prone stream, the highly mobile target taxa (Chapter 3: *Baetis* spp.; Chapter 4: *Baetis* spp., heptageniid mayflies) were able to recolonize the relatively small removal patches from the surrounding, unmanipulated stream bed. Consequently, *Baetis* and Heptageniidae recolonized rapidly between consecutive removal dates and removal led only to temporary density reductions but not to persistent elimination in the corresponding treatments, in spite of the fact that intervals between consecutive removals were much shorter than in all previous related experiments (Hemphill & Cooper 1983, Hemphill 1991, McAuliffe 1984). This continuous recolonization between removals reduced the strength of the removal treatment. Therefore, our experimental removal may have underestimated the effects that a complete absence of the targeted common taxa would have had on the remaining invertebrate fauna. While the spatial scale of our disturbance manipulations is highly comparable to many situations after natural floods (Matthaei *et al.* 1999; Effenberger *et al.* 2006), it would have been desirable to manipulate invertebrate densities at larger spatial scales. Nevertheless, the high removal ratio in Chapter 3 indicates that *Baetis* removal was highly effective on the day of removal, resulting in intermittently reduced *Baetis* densities on the experimental substrata.

In the final experiment of my PhD research (Chapter 5), I examined the separate and interactive effects of patchy bed disturbance and fish predation on benthic invertebrates and algae in a field experiment. In this experiment, local disturbance history influenced all 10 investigated biological response variables, whereas exclusion of fish predators from the experimental patches affected five response variables. Most of the observed patterns for the disturbance history effects were in agreement with those found after natural floods and experimental disturbance in my previous thesis chapters. The results of Chapters 1, 2 and 5 are thus highly consistent, lending more weight to our contention that longer-term effects of local disturbance history occur mostly as consequences of disturbance-mediated changes in physical habitat parameters and food resources rather than as direct disturbance effects (see Chapter 2). The results from Chapter 5 emphasize the pervasive importance of patchy bed disturbances for the microdistribution of stream organisms and also indicate a notable, but less prevalent, influence of fish exclusion at the patch scale on this microdistribution. Disturbance and predation treatments interacted only once, suggesting that, where they occurred, predation effects were largely independent of local disturbance history. The combined findings from Chapters 2 and 5 imply that changes in habitat parameters (e.g. current velocity) induced by bed movement can be local cues for the active habitat choice of benthic invertebrates.

It is worth noting that the spatial scale of our experimental fish exclusion may have influenced the outcome of my final experiment. When choosing their preferred microhabitats, invertebrates may be less able to distinguish reliably between patches with reduced or sustained fish predation risk at a small spatial scale (0.5 m^2) when the surrounding water contains chemical cues of fish. Consequently, the effects of fish exclusion on the benthic community might have been stronger in an experiment in which fish had been excluded from entire stream reaches. Nevertheless, the effort for achieving adequate replication in such an experiment, especially in combination with an experimental disturbance in a full-factorial design, would have been prohibitive.

Possible directions for future research

The ability of our three manipulative experiments (Chapters 3, 4 and 5) to discriminate among the conceptual models of Poff and Ward (1989), Townsend (1989) and Chesson and Huntly (1997) was limited by the spatial and temporal scales of our experiments. We investigated effects of bed disturbances, invertebrate removals and fish exclusion occurring in a small-scale mosaic of patches, and the application of experimental treatments was limited to single stream reaches and periods of about 50 days in each case. Moreover, our experimental treatments were unavoidably embedded in a matrix of an unmanipulated stream bed. Fast exchange rates between patches and the matrix could thus have swamped responses of mobile organisms to patch-scale conditions (Cooper *et al.* 1990, Englund 1997). By contrast, the three abovementioned conceptual models compare different disturbance scenarios occurring at the spatial scale of entire ecosystems and the temporal scale of several generation times. However, these spatial and temporal scales are much less amenable to manipulative experimentation.

For future studies in streams that build on the findings of my PhD research there are, in my opinion, two necessarily complementary ways, which both have advantages and disadvantages in terms of experimental control and naturalness of experiments. For an optimal control of environmental conditions and interpretability of results, small-scale experiments in stream channels (laboratory or streamside) may be the most useful. Moreover, combining the findings of these small-scale experiments with simple mathematical models may be able to improve our understanding of large-scale processes. Patterns observed at large spatial scales might frequently emerge from and feed back on processes that occur at much smaller scales. While theoretical models suggest that the influence of spatial environmental variability on the distribution of drifting stream invertebrates cannot be inferred reliably from the resulting (lack of) empirical patterns, the reverse approach seems promising (Anderson *et al.* 2005, Diehl *et al.* 2008). Both local responses to the environment and the response length can be estimated from small-scale experiments. In principle, this information allows the prediction of population responses to arbitrary patterns of spatial environmental variability. Such theoretical models can incorporate spatially and temporally heterogeneous disturbances. Very small-scale habitat differences (on the scale on which organisms crawl), such as the ones we found in our experiment, cannot be solved in the present form of existing models (Anderson *et al.* 2005, Diehl *et al.* 2008). Hence, small-scale directional movements between microhabitats (e.g. per capita emigration rates) and demographic rates (e.g. per capita mortality rate) should be included in these models and should be parameterized by accordant small-scale studies. For example, studies of predator impacts on prey populations can quantify predator-induced changes in per capita emigration rates in addition to consumption rates (Englund *et al.* 2001). In addition, small- and medium-scale experiments can reveal the strength of density-dependent effects on emigration, consumption and recruitment rates (e.g. Kratz 1996, Diehl *et al.* 2000, Hildrew *et al.* 2004).

So which experiments could be done focusing on stream invertebrates? In laboratory channels and using only a single pair of invertebrate taxa that are potential competitors (for food or space), one could investigate the interactive effects of disturbance and biotic interactions on key life history parameters of these taxa. In streamside channels, which are a bit closer to the natural situation, the method and scale for manipulating competitive interactions between invertebrates that I used in my thesis would have to be modified. I have reached the conclusion that it is nearly impossible to substantially and consistently reduce densities of more or less mobile invertebrate taxa with in situ removals such as in previous research and in my own. Therefore, I propose excluding invertebrates with the electrified fences used for the exclusion of fish in Chapter 5. First attempts to exclude benthic insects with this technique have already been made and were at least partly successful (Brown *et al.* 2000, Opsahl *et al.* 2003). By reducing the intervals of electric pulses, relatively large invertebrates like hydropsychiid caddis flies or heptageniid mayflies could be prevented from colonising experimental channels or plots, thus altering the composition of the invertebrate community.

To increase naturalness of experiments investigating the interplay between flood disturbances and biotic interactions such as competition or predation, larger temporal and spatial scales should be attempted. Most experiments to date were small-scale studies conducted in single streams. In contrast, the existing ecological concepts predicting the interplay of disturbance and biotic interactions are mainly based on the assumption of large-scale disturbances. In streams, local dynamics of many mobile organisms are largely driven by migration and drift processes (e.g. Cooper *et al.* 1990, Sih & Wooster 1994, Englund 2005). Migration then often obscures the demographic effects of the local environment by swamping local demographic processes (see e.g. Flecker 1984). At small spatial scales, migration caused by local habitat preferences prevails, whereas at sufficiently large spatial scales demographic responses dominate. In this context, the definition of a “small” or “sufficiently large scale” depends on the migration behaviour of the investigated organisms (Englund 1997, Englund & Hambäck 2004). In addition, part of the invertebrate population dynamics (the part caused by birth and death of individuals), and hence community diversity, in streams strongly depends on the spatial scale of disturbance (Anderson *et al.* 2005). Only for disturbances that occur at a larger scale than the distance that its impacts can be detected downstream, birth and death rates (instead of emigration and immigration) dominate the development of an affected population. For stream invertebrates, this distance is usually correlated with the length they travel downstream during their lifetimes (e.g. 2 km for *Baetis* and 1.5 km for *Gammarus*; Anderson *et al.* 2005). Because disturbances are patchily distributed themselves (Matthaei & Townsend 2000, Effenberger *et al.* 2006), the responses of different organisms to these disturbances should depend strongly on the spatial scale of the patchiness in the distributions of each organism, and vice versa (Anderson *et al.* 2005). To detect such larger-scale population dynamics, small-scale disturbance experiments seem to be insufficient. Consequently, a first step towards larger-scale studies would be to verify the present results from small-scale experiments in comparative studies across different streams with contrasting disturbance regimes.

In such a cross-system approach, one could compare both intensity and relative importance of disturbance and predation relatively easily across the different streams by relating disturbance frequencies and predator densities (of fish and predatory invertebrates) to invertebrate diversities in the investigated streams. By contrast, determining the strength of competition would be somewhat harder. There is no way of measuring “competitor density”, because it is usually not known for most streams which invertebrate taxa compete with each other. Thus, the importance of competition could only be accomplished indirectly, via measuring invertebrate biodiversity. According to the Intermediate Disturbance Hypothesis (Connell 1978), the diversity of an ecosystem should reach its peak at intermediate levels of disturbance (Fig. 1A). At low disturbance levels, superior competitors should dominate and exclude weaker competitors, whereas at high disturbance levels only disturbance-adapted species should survive. Due to conceptual similarities between disturbance and predation (Chesson & Huntly 1997, Chase *et al.* 2002; see also General Introduction), the same hump-shaped relationship might be expected to exist between the intensity of predation and biodiversity. The key predictions of the Intermediate Disturbance Hypothesis have been confirmed in a number of studies in marine, terrestrial und freshwater ecosystems (e.g. Sousa 1979, Anderson *et al.* 2005, Svensson *et al.* 2007). Nevertheless, several other studies found no relationship between community diversity and disturbance frequency/intensity (e.g. Lake *et al.* 1989), or a monotonic positive or negative relationship (e.g. Death & Winterbourn 1995, Mackey & Currie 2001, Death 2002). One reason for these inconsistent results across different studies could lie in the specific productivity of a system, which can modify the relation between disturbance and diversity (productivity hypothesis; Rosenzweig & Abramsky 1993, Worm *et al.* 2002, Currie *et al.* 2004). According to the dynamic equilibrium model (Huston 1979), increased productivity means that higher levels of disturbance are necessary to prevent competitive exclusion of weak competitors (Fig.1B). Thus, the maximum of biodiversity at low productivity should be located at low disturbance levels (monotonic decline). At intermediate productivity, the curve should peak at intermediate disturbance levels (unimodal shape, as predicted in the Intermediate Disturbance Hypothesis). At high productivity, the peak should be at high disturbance levels (monotonic increase). Such patterns were actually observed in a number of studies ranging across different habitats (Mackey & Currie 2001, Worm *et al.* 2002, Kneitel & Chase 2004, Scholes *et al.* 2005). Consequently, including both disturbance and system productivity in a single conceptual model can help explain deviations from predictions of the original Intermediate Disturbance Hypothesis.

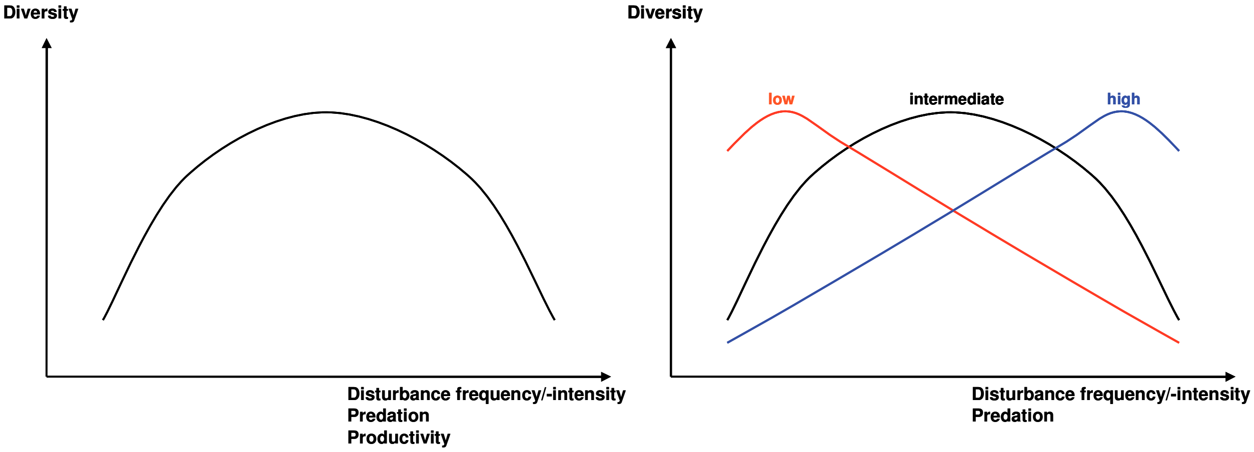


Fig. 1: A) Unimodal relationship between disturbance, predation, productivity and diversity (after Huston 1979, Sih *et al.* 1985, Rosenzweig & Abramsky 1993). B) Relationship between disturbance or predation and diversity at low, intermediate and high productivity levels.

To date it is still unclear how all three factors included in Fig. 1 – disturbance, predation and productivity – interact with each other when influencing biodiversity. Based on the predictions of the models described above, one could imagine that intermediate productivity leads to an ellipsoid-shaped pattern of biodiversity resulting from combining two unimodal curves (Fig. 2A), with maximum biodiversity occurring at intermediate levels of both disturbance and predation. At low productivity, low levels of both disturbance and predation pressure should lead to maximum biodiversity (Fig. 2B). At high productivity, by contrast, maximum biodiversity should be reached at higher levels of both disturbance and predation, thus moving the ellipsoid further away from the origin than at the two lower productivity levels (Fig. 2C).

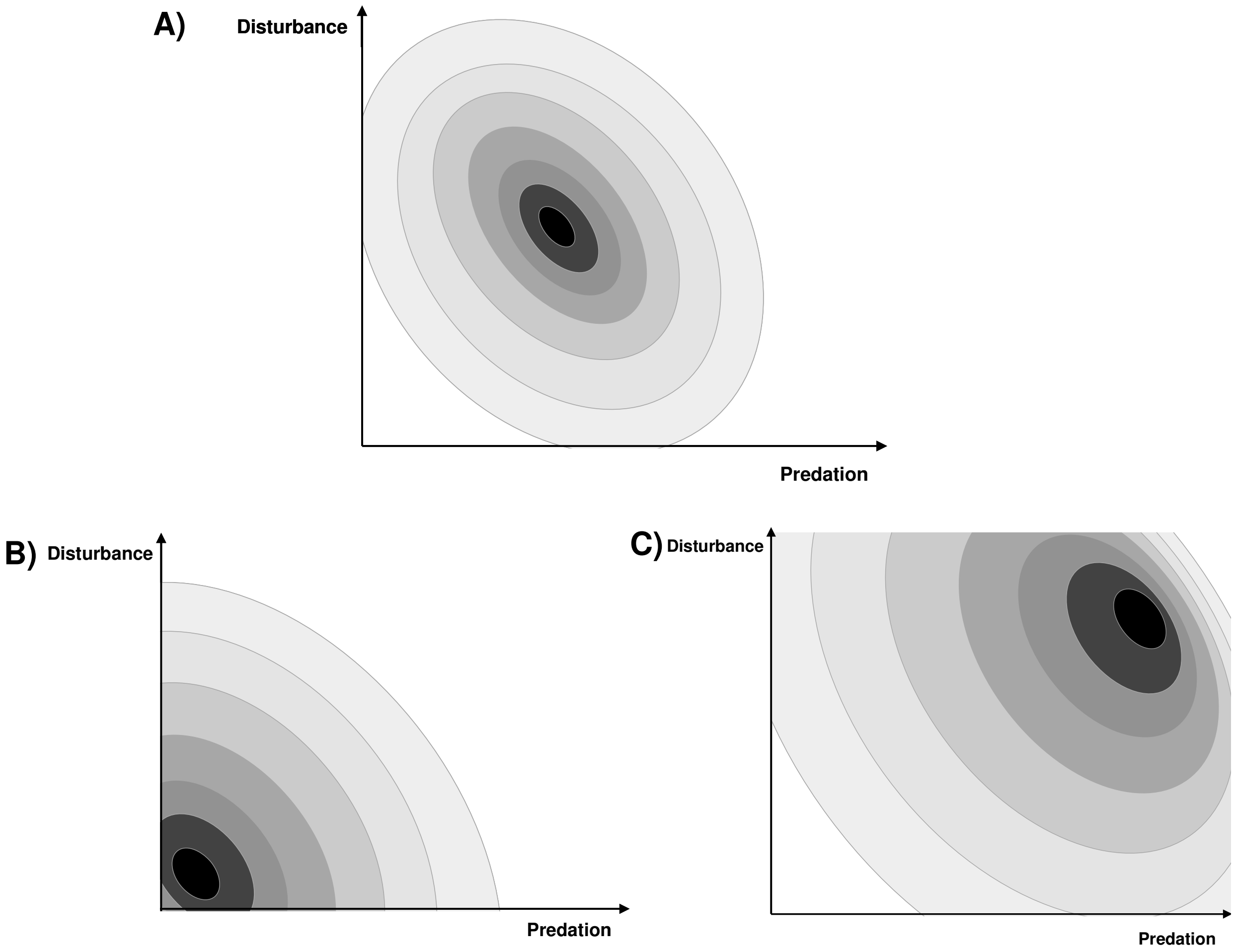


Fig. 2: Predicted relationship between disturbance, predation and relative biodiversity at (A) intermediate, (B) low and (C) high productivity. Relative biodiversity is displayed by grey shading (bright = low diversity, dark = high diversity).

The number of studies investigating the interplay of abiotic disturbances and biotic interactions in streams, regardless of their spatial scale, is still quite limited, leaving ample room for future research. The simultaneous investigation of multiple stressors on species interactions is still in its fledgling stages, not only in running waters but also in other ecosystems (Townsend *et al.* 2008). Field experiments that include just two factors which have the potential to influence the structure of benthic communities are fairly uncommon, and studies that include more than two are rare indeed. However, the combined findings of the few existing multiple-stressor studies imply that deeper insights in the mechanisms which regulate population fluctuations and the composition of communities may be gained by using this approach (Worm *et al.* 2002, Chase *et al.* 2002, Chase 2003a). For example, Sih *et al.* (2004) found strong, synergistic negative effects of pesticides (disturbance) and predators (biotic interaction) on some amphibian species. Similarly, Urban (2004) found that habitat permanence appeared to be a key factor shaping invertebrate community diversity, composition and trophic structure in freshwater ponds. Moreover, co-occurrences of invertebrate taxa did not deviate significantly from a random pattern, suggesting that competition was not an important driver of community composition. Besides, in more permanent ponds total predator diversity increased and these more diverse predator assemblages limited the abundance and composition of prey species. In a study of the simultaneous effects of disturbance, predation and resource availability on patterns of community composition, species richness and abundance in a protozoan and rotifer community, Kneitel & Chase (2004) found that richness in this community was altered by disturbance and predation. Species abundance was affected by all three manipulated factors (disturbance, predation, resources), and community composition was altered by each individual factor, plus by the two-way and three-way interactions between the manipulated factors. These results indicate that strong species sorting occurred in this community. Because no general patterns can be detected when comparing the findings of these few studies, a more general empirical framework that explicitly recognizes and predicts responses of communities to multiple factors and their interactions is required. Understanding these factors alone and in concert can provide valuable insights into the many complexities that underlie community structure and species composition.

Given that humans influence flow regimes of streams and rivers worldwide on an unprecedented scale through activities such as dam-building, water abstraction, river channelization and anthropogenic climate change (Poff 2002, Lytle & Poff 2004, Shea *et al.* 2004), we need to integrate disturbance and biotic interactions in a common conceptual framework if we want to understand the influences of altered flow regimes on stream communities (Power *et al.* 1995). Filling gaps in our knowledge of these topics will also help to tackle broader issues such as how to predict the response of lotic communities to major environmental changes (i.e. global climate change). Understanding the mechanisms of interactions between these multiple stressors will be crucial for applying ecological knowledge to solving environmental problems (Sih *et al.* 2004). Large-scale processes, such as climate, geomorphology, disturbance, and long-range dispersal can obscure patterns produced by processes operating at smaller scales. Thus, there is no correct scale at which to examine the factors affecting populations, communities, or ecosystems. We need to conduct more cross-scale studies to complement traditional approaches carried out at single scales of space, time, and organizational complexity (Levin 1992, Lancaster 1996, Peckarsky *et al.* 1997).

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CURRICULUM VITAE

Personal information

Name	Michael Effenberger
Date of birth	22.09.1976 in Augsburg, Germany
Marital status	married, one son
Citizenship	German
Address	Hinterer Lech 28, 86150 Augsburg, Germany

Education

September 1986 - June 1995	High school in Augsburg, Gymnasium bei St.Stephan Graduation: **Abitur**
September 1996 - July 2001	**Studies of biology** at the Ludwig-Maximilians-University (LMU) Munich Major subjects: Zoology, Ecology, Wildlife Biology, Landscape Management
August 2001 - May 2002	**Diploma Thesis** „The role of local disturbance history and habitat parameters for benthic invertebrate communities in a Bavarian mountain stream”
May 2002	Scientific degree: **Diploma Biologist** (equivalent to a MSc degree)
September 2002 - March 2003	**Master-Course** „Sustainable Resource Management“, Technical University (TU) Munich
April 2003 - present	**PHD studies** at the Department of Biology, LMU Munich Title: „Influence of flood disturbances and biotic interactions on the microdistribution of stream invertebrates.“

Teaching experience

Lecture „Introduction in limnology: lakes and streams“

One-week practical „Methods of stream ecology“

One-week practical „Biology and ecology of stream invertebrates“

Scholarships, grants and prizes

April 2002	Oskar-Karl-Forster scholarship, LMU Munich
April 2003 - December 2005	PhD Scholarship from the Episcopal Foundation (Cusanuswerk)
January 2006 - December 2007	2-year research grant from the German Research Foundation (DFG), title: “Disturbance, predation, and competitive interactions in streams: a multiple stressor study”
September 2008	Young academics award, German Limnological Society 2008

International experience

February - March 2005	Freshwater Ecology Group, University of Otago, Dunedin, New Zealand
December 2005 - March 2006	Freshwater Ecology Group, University of Otago, Dunedin, New Zealand

Internships

September 1999	Sewage treatment plant (Laboratory), Augsburg
October 1999	Beaver survey for the Environmental Protection Found (Bund Naturschutz), Deggendorf
October 2001	Bavarian Authority of Environmental Protection (Bayerisches Landesamt für Umweltschutz), Augsburg
June 2002	Bat survey for the Environmental Protection Found (Bund Naturschutz), Augsburg

Work experience

September 1996	Nurses assistant in a geriatric home (Kurzzeitpflege St.Georg), Augsburg
Februar 1998 - Mai 2000	Sales agent at a medical supplies agency (Sanitätshaus Limbächer), Augsburg
November 1999 - April 2008	Teaching assistant in various courses in Zoology and Ecology at the LMU Munich: • Limnology: streams and lakes (lecture) • Methods in stream ecology (practical) • Experimental stream ecology (practical) • Biology and ecology of stream invertebrates (practical)
July 2000 - March 2003	Research assistant in various research projects (stream restoration, experimental stream channels, stream disturbance), LMU Munich
January 2006 - February 2008	Research assistant in the Aquatic Ecology group, Department of Biology, LMU Munich
September 2007 – September 2008	Teacher (Biology) at the Peutinger Gymnasium, Augsburg
April 2008 – Juli 2008	Freelance biologist at BNGF, Pähl
August 2008 – present	Biologist at BNGF, Pähl

Skills

Languages	German (native), English (very good), Latin und ancient Greek (fair)
Computing skills	Microsoft Word, Excel and Powerpoint, SPSS, PAST (all very good); PRIMER, Sigmaplot, Jmp (good)

Publications

Effenberger M., Sailer G., Townsend C.R. & Matthaei C.D. (2006) Local disturbance history and habitat parameters influence the microdistribution of stream invertebrates. *Freshwater Biology* **51**, 312-332.

Effenberger M., Engel J., Diehl S. & Matthaei C.D. (2008) Disturbance history influences the distribution of stream invertebrates by altering microhabitat parameters: a field experiment. *Freshwater Biology*, **53**, 996-1011.

Effenberger M., Engel J., Diehl S. & Matthaei C.D. (2009a) Press removal of a dominant taxon following a pulsed disturbance: effects on the microdistribution of stream invertebrates. (Manuscript prepared for submission to *Journal of the North American Benthological Society*)

Effenberger M., Diehl S. & Matthaei C.D. (2009b) Flood disturbances alter interspecific interactions among stream invertebrates. (Manuscript prepared for submission to *Fundamental and Applied Limnology*)

Effenberger M., Gerth M., Diehl S. & Matthaei C.D. (2009c) Effects of experimental bed disturbance and fish exclusion on stream invertebrates and algae. (submitted to *Journal of Animal Ecology*)

Posters and presentations

Effenberger M., Sigl G. & Matthaei C.D. (2002) Die Bedeutung der kleinräumigen Sohlstabilität und lokaler Habitats-Parameter für die Besiedlung wirbelloser Tiere in einem bayerischen Wildbach. *DGL-Jahrestagung Braunschweig 2002*

Effenberger M., Herrmann P., Stadthagen T., Sigl G. & Matthaei C.D. (2003) Ein Vergleich der Bedeutung der kleinräumigen Sohlstabilität und lokaler Habitats-Parameter für wirbellose Tiere bei natürlichen und experimentellen Störungen. *DGL-Jahrestagung Köln 2003*

Effenberger M., Herrmann P., Sigl G., Stadthagen T. & Matthaei C.D. (2004) The roles of local disturbance history and habitat parameters for the microdistribution of stream organisms after natural and experimental disturbances: I. Invertebrates. *Jahrestagung der North American Benthological Society Vancouver 2004*

Effenberger M., Diehl S. & Matthaei C.D. (2005) The influence of disturbance on biotic interactions of macroinvertebrates in streams. *Jahrestagung der North American Benthological Society New Orleans 2005*

Effenberger M., Diehl S. & Matthaei C.D. (2005) Der Einfluss von Hochwasser-Störungen auf die interspezifische Konkurrenz zwischen Fließgewässer-Invertebraten. *DGL-Jahrestagung Karlsruhe 2005*

Herrmann, P.B., **Effenberger M.**, Sailer G., Stadthagen T.B. & Matthaei C.D. (2005) Local disturbance history and the microdistribution of benthic invertebrates in a flood-prone stream: a manipulative experiment. *Annual Meeting of the Freshwater Sciences Society of New Zealand Nelson 2005*

Effenberger M., Herrmann P., Winkelmann C., Diehl S. & Matthaei C.D. (2006) Störungen und biotische Interaktionen in Fließgewässern: Einfluss mehrerer Stressfaktoren. *DGL-Jahrestagung Dresden 2006*

Engel J., **Effenberger M.**, Diehl S. & Matthaei C.D. (2006) Einfluss der kleinräumigen Sohlstabilität auf die Besiedlung wirbelloser Tiere: Ein Freiland-Experiment. *DGL-Jahrestagung Dresden 2006*

Effenberger M., Herrmann P., Winkelmann C., Diehl S. & Matthaei C.D. (2007) Disturbance, predation, and competitive interactions in streams: a multiple-stressor study *SIL-Tagung Montreal 2007*

Effenberger M., Diehl S. & Matthaei C.D. (2008) Einfluss kleinräumiger Sohlstabilität und Prädation auf Fließgewässer-Invertebraten und Algen. *DGL-Jahrestagung Konstanz 2008*

Effenberger M. (2008) Einfluss von Hochwasser-Störungen und biotischen Interaktionen auf die kleinräumige Verteilung von Fließgewässer-Invertebraten. *DGL-Jahrestagung Konstanz 2008*

Matthaei C.D, Townsend C.R., Winkelmann C., Herrmann P. & **Effenberger M**. How disturbance, predation and competition interact in streams: a field experiment. *Annual Meeting of the Freshwater Sciences Society of New Zealand New Plymouth 2008*

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All chapters are mainly based on my personal work, but several Co-authors provided me with data, gave valuable comments or assisted me in the field. In the following, I describe their contributions to the single chapters:

Chapter 1:

Gabi Sailer was part of the field work crew and provided me with the data on algae. Colin Townsend gave valuable comments on an earlier version of this chapter.

Chapters 2 and 3:

During her diploma thesis Hanna Engel helped with the fieldwork and counted many of the invertebrate samples.

Chapter 5:

During his diploma thesis Max Gerth helped with the fieldwork and counted many of the invertebrate samples.

Sebastian Diehl (**Chapters 2-5**) and Christoph Matthäi (**Chapters 1-5**) helped with the conception of the experiments and supported me with comments on earlier drafts of the chapters.

EHRENWÖRTLICHE VERSICHERUNG UND ERKLÄRUNG

Diese Promotion wurde im Sinne des § 12 der Promotionsordnung von Prof. Dr. Sebastian Diehl betreut. Hiermit erkläre ich, dass die vorliegende Dissertation das Ergebnis meiner eigenständigen Arbeit ist und dass ich dieses Manuskript persönlich verfasst habe. Zudem habe ich keine anderen als die angegebenen Quellen und Hilfsmittel verwendet.

Ich versichere, dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

Augsburg, 12. März 2009

Michael Effenberger