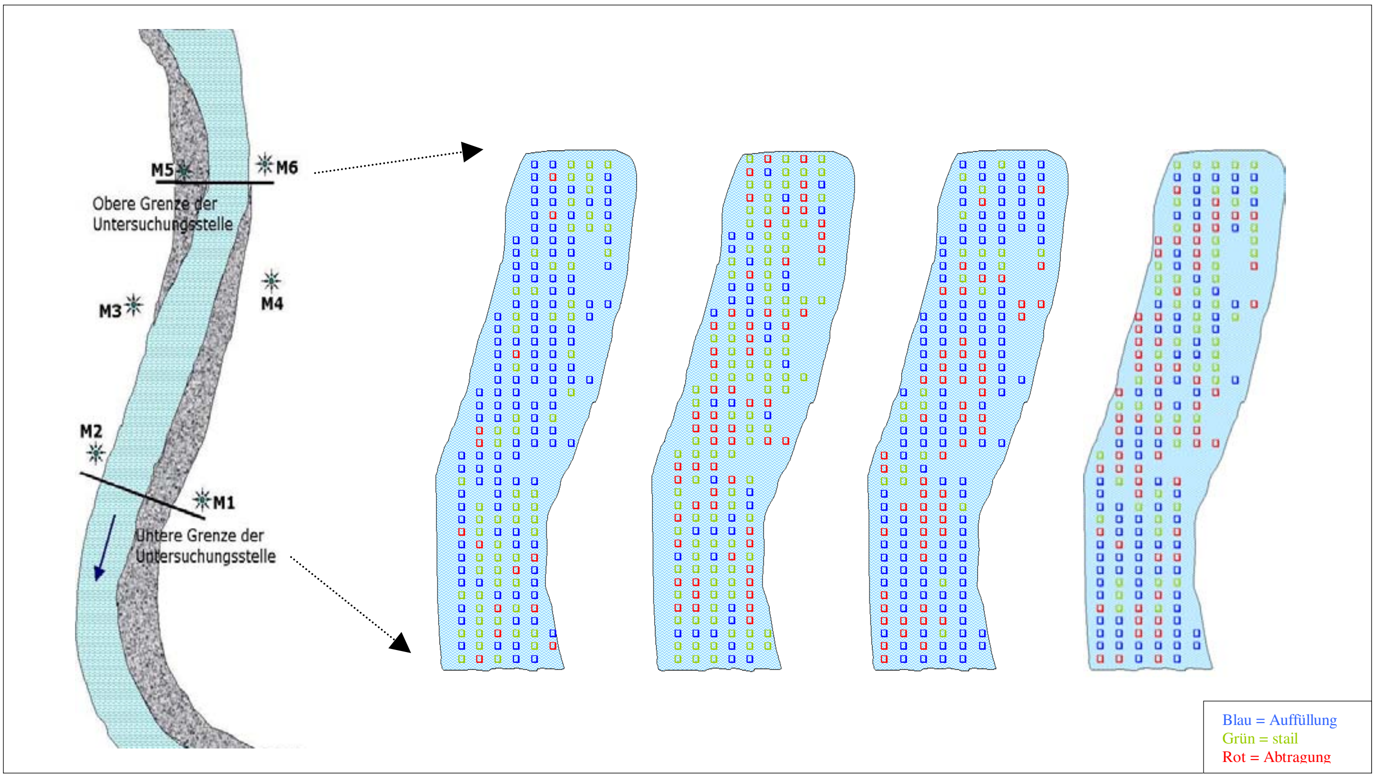
# The roles of local disturbance history and microhabitat parameters for stream biota



Dissertation

Gabriele Sailer

# The roles of local disturbance history and microhabitat parameters for stream biota

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# Die Rolle der lokalen Sohlstabilität und Mikrohabitatsparameter für Fließgewässerorganismen

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**Dissertation**

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## Summary

The identification of factors that cause the patchy distribution of organisms in space and time within natural ecosystems is a central concern in ecology. In running waters, disturbance by bed-moving flows has been recognized to contribute to this patchiness, but the mechanisms behind this process are still poorly understood. Recent research has revealed that most bed-moving spates and floods cause a small-scale mosaic of stream bed patches of different substratum stabilities (sediment scour, sediment deposition, and stable patches). The aim of the present research was to investigate the separate and combined roles of this "local disturbance history" and microhabitat parameters in determining the small-scale distributions of benthic stream organisms (bacteria, algae and invertebrates).

The first three chapters of my thesis investigate bacteria, algae and invertebrates after natural spates and floods in two gravel-bed streams, the Schmiedlaine in Bavaria, Germany, and the Kye Burn in the South Island of New Zealand. The final chapter describes a manipulative experiment in the Schmiedlaine in which the stream bed was disturbed manually to obtain a better understanding of how disturbance history affects stream organisms.

Local bed movement patterns during several natural disturbances were determined using metal-link scour chains. The same chains were also used as reference points when selecting stream bed patches for manipulation during the experimental disturbance. Quantitative samples were collected several times from random sites before each disturbance and from scour, fill and stable patches after each disturbance. In addition to sampling bacteria, algae and invertebrates, we measured primary production under controlled conditions in both streams and bacterial production in the Kye Burn. For each sampling site, we determined several abiotic and biotic microhabitat parameters that are known to influence the distributions of stream biota, e.g. water depth, substratum composition, near-bed current velocity and standing stock of particulate organic matter (POM).

The results of the correlative studies suggest that local disturbance history plays an important role in determining the small-scale distributions of stream bacteria, algae and invertebrates. Disturbance history was related to distributions of all three organism groups both directly and indirectly (via effects on habitat parameters) and significant habitat parameter effects revealed previously undetected history effects in several cases, indicating a strong interaction between disturbance history and the better explored habitat parameters.

Bacterial microdistribution was related directly to disturbance history at least as often as to any of the other nine studied habitat parameters (except for the surface area of the sampled stones in the Schmiedlaine). The relationships of local disturbance history with algal distributions were not quite as strong. In the flood-prone Schmiedlaine, substratum characteristics and current velocity were related to algal distribution at least as often as disturbance history. In the relatively more stable Kye Burn, there were no direct influences of disturbance history on the algae. Substratum characteristics, water depth, current velocity and POM were the habitat parameters with the highest numbers of significant relationships. However, disturbance history also influenced algal distribution indirectly in both streams, and this indirect influence was particularly strong in the Kye Burn. Primary production was always similar across bed stability types in both streams. Averaged across both streams, invertebrate distribution was related only to near-bed current velocity more often than to disturbance history. In the Kye Burn, disturbance history and water depth were the habitat parameters that were related most often to invertebrate distributions. Further important parameters for invertebrates were substratum size and epilithic algal biomass.

The observed relationships of benthic densities to the investigated habitat parameters were largely in accordance with previous microhabitat studies for benthic algae and invertebrates. These results also show that benthic bacteria in streams appear to be influenced by similar habitat parameters as benthic algae and invertebrates.

The findings of the experimental disturbance in the Schmiedlaine generally supported those of the correlative research, lending more weight to the generality of the results. Local disturbance history influenced directly algal microdistribution in the stream bed most often, followed by near-bed current velocity, total invertebrate density and the surface area of the sampled stone. Primary production was also always similar between the three bed stability types. In contrast to the benthic algae and the correlative study on bacteria, bacterial microdistribution in the experiment was influenced directly solely by stone surface area. However, disturbance history had a strong indirect influence via habitat parameters on bacterial distribution. For invertebrate distribution, disturbance history was the parameter with the second-highest number of significant relationships after current velocity. Indirect effects of disturbance history on the stream organisms were similarly common as in the correlative studies and significant habitat parameter effects revealed previously undetected history effects in several cases, confirming the strong interaction between disturbance history and the better-explored habitat parameters.

The combined findings of the present research provide substantial evidence that local disturbance history is an important, and previously unrecognised factor contributing to the patchy distribution of stream organisms in space and time.

## Zusammenfassung

In der Ökologie ist die Identifizierung von Faktoren, die eine kleinräumige Verteilung der Organismen örtlich und zeitlich bewirken, sehr wichtig. In Fließgewässern hat man erkannt, daß Störungen, hervorgerufen durch sohlumlagernde Hochwasser, zu dieser Kleinräumigkeit beitragen. Die Mechanismen dieses Prozesses sind aber noch sehr wenig verstanden. Neuere Forschungen haben belegt, dass die meisten sohlumlagernden Hochwasser ein kleinräumiges Muster des Substrates im Bachbett hinterlassen (Sedimentabtragung, -auffüllung oder stabile Bereiche). Das Ziel dieser Dissertation war die Erforschung der „lokalen Sohlstabilität“ (local disturbance history) und Mikrohabitatsparameter für sich alleine gesehen sowie im Kontext zueinander für die kleinräumige Verteilung von benthischen Fließwasserorganismen (Bakterien, Algen und Invertebraten).

Die ersten drei Kapitel dieser Doktorarbeit behandeln die Verteilung von Bakterien, Algen und Invertebraten nach natürlichen Hochwassern in zwei Bächen mit Kiesbett: die Schmiedlaine in Bayern, Deutschland und den Kye Burn auf der Südinsel Neuseelands. Das letzte Kapitel beschreibt ein manipulatives Experiment in der Schmiedlaine, deren Bachbett manuell gestört wurde, um Ursache und Wirkung der lokalen Sohlstabilität auf die Bachorganismen besser erkennen zu können.

Die lokalen Umlagerungsmuster des Bachbettes nach mehreren natürlichen Hochwassern wurden durch Metallketten bestimmt, die ins Bachbett eingebracht wurden. Die selben Ketten wurden als Referenzpunkte bei dem manipulativen Hochwasser genutzt. Vor den Hochwassern wurden quantitative Proben von zufällig ausgewählten Standorten entnommen, nach den Hochwassern von Abtragungs-, Auffüllungs- und stabilen Bereichen. Zusätzlich zu den Bakterien-, Algen- und Invertebratenproben wurde in beiden Bächen die Primärproduktion unter kontrollierten Bedingungen im Labor gemessen, sowie die bakterielle Produktion im Kye Burn. Für jede Probenahmestelle wurden verschiedene abiotische und biotische Mikrohabitatsparameter gemessen, die bekannt dafür sind, die Verteilung der Organismen im Fließgewässer zu beeinflussen, beispielsweise Wassertiefe, Substratzusammensetzung, sohlnahe Fließgeschwindigkeit und partikuläre organische Substanz (POM).

Die Ergebnisse der korrelativen Studie weisen darauf hin, daß die lokale Sohlstabilität eine wichtige Rolle bei der kleinräumigen Verteilung von Bakterien, Algen und Invertebraten in Fließgewässern spielt. Die Sohlstabilität beeinflusste die Verteilung aller drei Organismengruppen direkt und indirekt (über Effekte der Habitatsparameter), in einigen Fällen offenbarten signifikante Korrelationen der Habitatsparameter mit den Organismen

weitere Sohlstabilitätseffekte. Dies deutet darauf hin, dass es starke Wechselbeziehungen zwischen der lokalen Sohlstabilität und den besser untersuchten Mikrohabitatsparametern gibt.

Die kleinräumige Verteilung der Bakterien stand in direktem statistischen Zusammenhang mit der lokalen Sohlstabilität, und zwar mindestens genauso häufig wie mit den anderen neun untersuchten Habitatsparametern (mit Ausnahme der Oberfläche des beprobten Steines in der Schmiedlaine). Der Einfluss der lokalen Sohlstabilität auf die Algenverteilung war nicht so offensichtlich. In der Schmiedlaine, in der häufig Hochwasser vorkommen, waren Substratzusammensetzung und sohlnahe Fließgeschwindigkeit zusammen mit der Sohlstabilität am häufigsten mit den Algen korreliert. Im relativ stabileren Kye Burn wurden keine direkten Zusammenhänge der lokalen Sohlstabilität mit der Algenverteilung gefunden. Die meisten Korrelationen zeigten Substratzusammensetzung, Wassertiefe, Fließgeschwindigkeit und POM. Jedoch beeinflusste die Sohlstabilität in beiden Bächen die Verteilung der Algen indirekt, im Kye Burn sogar in hohem Maß. Bei der kleinräumigen Verteilung der Invertebraten zeigte, bei gemeinsamer Betrachtung beider Bäche, lediglich die sohlnahe Fließgeschwindigkeit mehr signifikante Zusammenhänge als die lokale Sohlstabilität. Im Kye Burn hatten Sohlstabilität und Wassertiefe den häufigsten Einfluß auf die Verteilung der Invertebraten. Weitere wichtige Parameter waren die Substratgröße und die epilithische Algenbiomasse.

Die in der vorliegenden Arbeit gefundenen Zusammenhänge der Bachorganismen mit den Habitatsparametern gingen meist mit den Ergebnissen vorausgegangener Mikrohabitatsstudien für benthische Algen und Invertebraten konform. Die Ergebnisse der vorliegenden Studie zeigen zudem, daß benthische Bakterien in Fließgewässern im wesentlichen von den selben Habitatsparametern beeinflusst werden wie Invertebraten und Algen.

Die Ergebnisse der experimentellen Störung in der Schmiedlaine unterstützen zumeist die der korrelativen Studie und stärken somit die Allgemeingültigkeit der wichtigsten Befunde. Die lokale Sohlstabilität beeinflusste die Verteilung der Algen am häufigsten, gefolgt von sohlnaher Fließgeschwindigkeit, Invertebratendichte und Oberfläche des beprobten Steins. Die Primärproduktion war in allen drei Sohlstabilitätskategorien stets sehr ähnlich. Im Gegensatz zu den Algen und der korrelativen Studie für Bakterien wurde die bakterielle Verteilung bei diesem Störungsexperiment direkt lediglich durch die Oberfläche des beprobten Steins beeinflusst. Zusätzlich waren indirekte Effekte der Sohlstabilität (über die Habitatsparameter) von großer Bedeutung. Für die Verteilung der Invertebraten im Störungsexperiment zeigte die lokale Sohlstabilität nach der sohlnahen Fließgeschwindigkeit die meisten signifikanten Zusammenhänge. Indirekte Effekte der lokalen Sohlstabilität waren genauso häufig wie in der korrelativen Studie, so daß die starken Wechselbeziehungen zwischen der lokalen Sohlstabilität und den Mikrohabitatsparametern bestätigt werden können.

Zusammenfassend liefert die vorliegende Arbeit umfangreiche Indizien und Belege dafür, dass die lokale Sohlstabilität ein wichtiger, jedoch bisher weitgehend unbeachteter Faktor ist, der die kleinräumige Verteilung von Fließgewässerorganismen in Raum und Zeit beeinflusst.

# Introduction

## Disturbance and the patch dynamic concept

The structure and function of ecological communities can be influenced by biotic and abiotic factors. Biotic interactions, such as predation (Paine 1966; Menge et al. 1986; Diehl et al. 2000), competition (e.g. McAuliffe 1984; Feminella & Resh 1991) or grazing (e.g. Power 1992; Biggs et al. 1998; Bergey 1999), have been shown to be very important determinants of community structure in many ecosystems. However, the role of disturbance in shaping living communities can be at least as important as that of biotic interactions (Resh et al. 1988; Lake 2000; White & Jentsch 2001), at least in certain ecosystems (see below).

Disturbance can be defined as ‘a discrete, punctuated killing, displacement, or damaging of one or more individuals that directly or indirectly creates an opportunity for new individuals to become established’ (Sousa 1985), or as ‘any relatively discrete event in time that removes organisms or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment’ (Begon et al. 1996). Likely consequences are the opening up of space or the freeing up of resources, both of which can be used by new individuals. Consequently, disturbances have negative as well as positive effects on ecosystems. Disturbances occur in virtually all ecosystems and affect all levels of biological organisation (White & Jentsch 2001). They include natural events such as fires, windstorms, landslides, flooding, burrowing animals and outbreak of pathogens, but also human landuses such as logging and grazing. In the past several decades, it has become clear that disturbance is an important factor in determining the abundance and diversity of species in ecological communities (e.g. Watt 1947; Connell 1978; Huston 1979; Pickett & White 1985; Vinson & Hawkins 1998). Disturbance is also a primary cause of spatial and temporal heterogeneity in ecosystems (e.g. Platt 1975; Peterson 1996; White & Jentsch 2001). As a consequence, disturbance features in influential ecological theories, namely the ‘intermediate disturbance hypothesis’ (Paine & Vadas 1969; Connell 1978; Sousa 1979) and the concept of ‘patch dynamics’ (Pickett & White 1985).

The patch dynamics concept views ecosystems as highly dynamic in four dimensions: the three spatial dimensions, and time. Patches are assumed to represent a multitude of different successional stages, from open space (created by disturbance) to a monoculture of the dominant competitor. The first patch dynamics research was conducted on terrestrial plants (Clements 1916; Watt 1947), in coral reefs (Connell 1978), and in marine tidal zones (Sousa 1979). Since then, patch dynamics have been studied in organisms as diverse as annual grasses (e.g. Wu & Levin 1994), seagrasses (Marba & Duarte 1995), forest herbs (Collins et al. 1985), woody plants (Frelich & Reich 1995), marine nematodes (Lambshead & Hodda 1994), mussels (Denny 1995), zooplankton (Folt & Burns 1999), terrestrial insects (Schowalter 1985) and vertebrates (Bunnell 1995). It is only relatively recently that the concept have been applied to streams and rivers (Ward & Stanford 1983; Pringle et al. 1988; Frid & Townsend 1989; Townsend 1989).

The influence of disturbance on running water ecosystems is particularly strong (Resh et al. 1988; Lake 2000), because disturbances tend to occur more often and be more severe than in most other ecosystems. The most common type of natural disturbance in running waters are spates (smaller high-flow events with peak flows below bankfull discharge, i.e. the river does not overflow its banks) and floods (larger events with peak flows above bankfull discharge that indundate the floodplain; Matthaei et al. 2004). However, several other types of disturbance can also affect running water communities, such as droughts, lack of oxygen, increased sedimentation of fine particles and extreme water temperatures (e.g. Steinman & McIntire 1990; Wallace 1990; Wood & Armitage 1997; Lake 2000; Humphries & Baldwin 2003).

Spates and floods have been identified as a major reset mechanism for community dynamics, initiating new cycles of all stages of succession (Fisher et al. 1982; Pringle et al. 1988; Townsend 1989; Poff & Ward 1990). Hydrologic disturbances can also modify population, community and ecosystem processes (Townsend 1989; Mackay 1992; Townsend & Hildrew 1994). For example, compared to more stable sites more intensely disturbed stream sites in the Taieri River catchment in New Zealand had invertebrate communities with a significantly higher percentage of insects possessing ‘flood-adapted’ traits (Townsend et al. 1997a), i.e. small size, high adult mobility, habitat generalist (predicted to confer resilience in response to bed disturbance), ability to cling to substratum, streamlined/flattened, and with two or more life stages outside the stream (predicted to confer resistance in the face of disturbance). Further, maximum invertebrate taxon richness coincided with intermediate levels of disturbance (Townsend et al. 1997b), giving a dome-shaped relationship between richness and intensity of disturbance as predicted by the intermediate disturbance hypothesis. Finally, the structure of benthic food webs in a subset of ten of the Taieri streams was related to the disturbance regime, with a smaller number of dietary links per species in disturbed sites (Townsend et al. 1998). For benthic algal communities in running waters, the frequency of flood disturbances seems to be the decisive factor determining algal biomass and taxonomic richness (Biggs 1996; Biggs et al. 1998).

## Flood refugia in running waters

Recovery of communities after spates and floods is often rapid (e.g. Fisher et al. 1982; Mackay 1992; Matthaei et al. 1997). Therefore, ecologists have predicted that refugia which lessen the impacts of hydrologic disturbances on stream organisms should occur at several spatial and temporal scales (Townsend & Hildrew 1994; Lancaster & Belyea 1997). Explicit testing of these different refugium hypotheses has only begun in the last two decades. Proposed local, short-term refugia include lateral stream margins (Bishop 1973), large, immobile surface particles (Townsend 1989; Biggs et al. 1997), dead zones where shear stresses on the bed are always low (Lancaster & Hildrew 1993a), inundated floodplain sediments (Badri et al. 1987), and the hyporheic zone (Williams & Hynes 1974). Examples of proposed larger-scale and/or longer-term mechanisms of re-colonization are invertebrate drift from upstream areas (Scarsbrook & Townsend 1993) and adults flying in from adjacent tributaries (Townsend 1989).

For stream invertebrates, the first flood refugia studies provided evidence that inundated floodplain vegetation (Badri et al. 1987) and areas of permanently low shear stress (Lancaster & Hildrew 1993b; Robertson et al. 1995; Winterbottom et al. 1997) served as invertebrate refugia in two small, sluggish streams. Prévot & Prévot (1986) found the same for inundated floodplain gravels in the lateral river margins and for a calm, hyporheically-fed side arm of a French river. In a sandy-bottomed Virginia river, invertebrates associated with woody debris dams were more resistant to floods than the fauna in the sandy mid-channel (Palmer et al. 1996).

High-flows can directly influence communities of organisms that dwell primarily in the water column (Poff & Allan 1995). On the other hand, whether or not a high-flow event represents a disturbance for the benthic community depends largely on to what extent the stream bed has been moved (Poff 1992; Townsend et al. 1997c). Consequently, the search for local flood refugia is closely linked to quantifying bed movement patterns in streams and rivers. Many researchers have studied community recovery after severe floods (e.g. Fisher et al. 1982; Smock et al. 1994; Matthaei et al. 1997) that had caused obvious, large-scale bed movements. By contrast, the impact of smaller high-flow events is much more difficult to assess. This is unfortunate because such events may be more important for the spatio-temporal dynamics of the benthic community than large floods simply because they occur more frequently (Matthaei et al. 1996, 1997).

Townsend & Hildrew (1976) were the first to speculate that invertebrate recolonization after smaller high-flow events in gravel-bed streams might represent a redistribution rather than ‘true’ colonization from distant sources, if the event does not disturb the whole stream bed. However, they did not test their hypothesis in the field. Several years later, patches of stream bed where algae had been removed from surface stones led ecologists to consider the possibility of ‘patchy’ bed movements during smaller high-flow events (e.g. Doeg et al. 1989; Matthaei et al. 1996). Eventually, Matthaei et al (1999a) determined the spatial patterns of bed movements in the Kye Burn, a gravel-bed stream in New Zealand, using arrays of several hundred *in-situ* marked surface stones and monitoring their stability during several high-flow events. Simultaneously, arrays of metal-link scour chains were installed at contiguous sites to determine the three-dimensional patterns of sediment scour and fill (Matthaei et al. 1999b). Both marked stones and scour chains showed that bed movement patterns were highly heterogeneous in space. Bed patches that experienced scour were often located very close (≤ 1 m) to patches that had experienced sediment deposition (fill patches), or to patches that had remained undisturbed (stable patches), and there were similar patterns for stable and unstable surface stones. Matthaei & Townsend (2000) later defined this small-scale mosaic of scoured, depositional and stable bed patches as ‘local disturbance history’ (see next subchapter). During five below-bankfull events, 18 - 70 % of the chain locations or marked stones remained stable. All these bed patches or stones were potential refugia for benthic organisms. Only an above-bankfull event left few marked patches or stones undisturbed (generally 15 % or less), indicating that potential surface refugia were scarce during this large flood. Matthaei & Huber (2002) found a similar lack of surface refugia during a large flood in a flood-prone Bavarian stream. Further, scour in the Kye Burn affected only the uppermost 15 cm of the bed at most of the chain locations, even during the largest event. Consequently, most of the deeper sediment layers in the hyporheic zone could also have been used as refugia by mobile stream invertebrates.

A follow-up study in the Kye Burn (Matthaei et al. 2000) showed that surface refugia for benthic invertebrates can exist during high-flow events in gravel-bed streams. During this investigation, replicated stable and unstable surface stones were sampled shortly before a bed-moving spate, during the declining limb of the spate, and two weeks after flow had receded to normal. Before the spate, total invertebrate densities were similar on subsequently stable and unstable stones. During the receding limb of the spate, by contrast, invertebrate densities on *in-situ*-marked, stable stones were significantly higher than on stones that had been disturbed during this spate. This result was paralleled by the mean number of invertebrate taxa per sampled stone and densities of all five of the most common taxa. Invertebrate densities on stable and unstable stones were similar again two weeks later, indicating that the effect of stone stability on the microdistribution of the invertebrates was relatively short-lived.

While the above mentioned refugium types for benthic stream invertebrates appear fairly well-documented, convincing evidence that stable sediments in the hyporheic zone can act as invertebrate refugia is still lacking (see Palmer et al. 1992; Schmid-Araya 1994; Dole-Olivier et al. 1997). The only two rigorous field tests of this hypothesis, conducted on the meiofauna in a sandy-bottomed river in Virginia (Palmer et al. 1992) and the macroinvertebrate fauna in the Kye Burn in New Zealand (Olsen & Townsend 2005), both yielded negative results.

The responses of benthic algae to physical disturbance during high-flow events have been investigated in numerous studies (see reviews by Fisher 1990; Steinman & McIntire 1990; Peterson 1996). Investigated factors influencing the resistance and resilience of algae to scour include substratum size and surface irregularity, nutrients and grazing, community physiognomy and taxomonic composition, algal senescence, and contribution of persistent cells or new immigrants to recovery (see various references and conceptual models in Peterson 1996; Biggs et al. 1998; Mulholland et al. 1991; Bergey 1999). Substrata unlikely to be moved by increased flow (e.g. boulders and bedrock patches) have been reported to act as refugia for periphyton during high-flow events (Douglas 1958: Power & Stewart 1987; Uehlinger 1991; Peterson et al. 1994; Francoeur et al. 1998).

Because microbial ecology in running waters is a relatively young discipline (Ward & Johnson 1996), few studies have investigated effects of high-flow events on lotic bacteria (e.g. Holmes et al. 1998; Marxsen 1999, 2001). To my knowledge, studies investigating potential flood refugia for benthic bacteria do not exist.

### The role of local disturbance history

Ecologists are starting to realise that local disturbance history can affect benthic communities in streams and rivers in several ways that go beyond creating potential flood refugia in stable bed patches. It is well known that the small-scale distributions of both benthic invertebrates and algae in running waters are influenced by abiotic factors, including shear stress, water depth and substratum size, and by biotic factors including predation, competition and food (see e.g Peckarsky et al. 1990; Hearnden & Pearson 1991; Kohler 1992; Holomuzki & Messier 1993; Ruse 1994; Stevenson 1996; Biggs et al. 1998; Passy 2001). By contrast, the role of hydrological disturbance in generating patchy distributions is less well understood, probably because of the difficulty of mapping the local effects of specific spates and floods.

After quantifying the three-dimensional bed movement patterns in the Kye Burn (Matthaei et al. 1999b, see above), Matthaei & Townsend (2000) showed that local disturbance history can have long-term effects on the small-scale distribution of benthic invertebrates in this stream, with higher densities in fill or scour patches two months after a disturbance. 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, but in fill patches three months after another flood. Although the response of benthic algae to physical disturbance during high-flow events has been investigated in numerous studies (see studies cited above), the effect of small-scale patchiness in bed movements on benthic algae had not been addressed prior to the study of Matthaei et al. (2003), especially the distinction between scoured and depositional bed patches.

## Objectives of this PhD research

Despite the fact that much of the patch dynamics research in streams has focussed on benthic invertebrates (see above), these organisms make up just a small fraction of the total amount of organic carbon in lotic ecosystems. By comparison, the amount of organic carbon contained in benthic algae or bacteria is much greater (Allan 1995). Benthic algae are regarded as the most important primary producers in mid-sized streams (Minshall 1978; Vannote et al. 1980; Stevenson 1996; Lock et al. 1984; Mulholland 1996). Moreover, stream ecologists know very little about factors driving the patchiness of benthic bacteria. Due to their abundance (Haack & McFeters 1982; Stock & Ward 1989) and productivity (Marxsen 1996, 1999), benthic bacteria play an important role in the carbon dynamics of streams and rivers (Meyer 1990; Ward & Johnson 1996; Hall & Meyer 1998). Clearly, benthic algae and bacteria need to be included in a comprehensive picture of the effects of local disturbance history on stream communities.

While showing convincingly that disturbance history can affect benthic organisms, the first disturbance history studies (Matthaei et al. 2000; Matthaei et al. 2003) also had certain limitations. Thus, invertebrates were sampled only once after a single high-flow event in Matthaei & Townsend (2000) and neither physical habitat parameters nor invertebrate food resources were quantified. In Matthaei et al. (2003), algae were collected at widely set intervals (up to two months) and only three 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. Furthermore, the effects of disturbance history on important ecosystem processes, for example primary production, were not examined. Finally, all disturbance history research to date consists of correlative studies. While such studies allow the description of existing patterns, they cannot determine true causes and effects and need to be complemented by manipulative experiments (Townsend 1989).

The objectives of the thesis were therefore

(1) to describe the relationships among local disturbance history, microhabitat parameters and the microdistributions of stream bacteria, algae and invertebrates, bacterial secondary production, and on algal community structure and primary production during extended periods following several high-flow events in two gravel bed streams,

(2) to investigate the same relationships after experimentally creating a mosaic of bed patches with different disturbance histories.

The overall objective was to search for patterns of direct and indirect (via changes in microhabitat parameters) influences of local disturbance history on the distribution and patchiness of bacteria, algae and invertebrates, and resulting consequences for ecosystem processes such as bacterial and primary production.

## The Project

To achieve the first objective, two different streams in two different hemispheres, the Schmiedlaine in Germany and the Kye Burn in New Zealand, were investigated between May 2001 and March 2002. In both streams, at least two series of pre-flood samples and multiple post-flood samples were collected. Both streams have natural channel morphologies, cold, nutrient-poor waters and unstable stream beds due to high sediment input from the catchment. However, bed-moving high-flow events are not quite as frequent in the Kye Burn as in the Schmiedlaine because rainfall is lower in the Kye Burn catchment and catchment topography is less steep. Due to logistical constraints, experimental manipulations of disturbance history (Objective 2) were performed only in the Schmiedlaine (in June/July 2002).

### *The scour chain method*

Scour chains (Nawa & Frissell 1993) were of crucial importance to the project because they allowed detailed quantification of bed movement patterns after each high-flow event that occurred during the field research. Therefore, the method is described in some detail here. Each scour chain unit consisted of a given number of galvanised chain links that had been fixed to a hollow metal head with a steel tip (link size 3 x 1.7 cm, head length 15.5 cm, head diameter 4 cm, total chain length about 60 cm, total weight about 750g). A 0.85m piece of bright yellow nylon rope was attached to the top link of each chain to facilitate re-location after a high-flow event. The devices were inserted vertically in the stream bed using a hollow metal standpipe (outer diameter 7 cm) and a 20 kg metal fencepost driver. After installation, only the top one or two links were exposed on the bed surface. Scouring events expose additional chain links, whereas fill can be measured by the thickness of the sediment layer deposited on top of the originally exposed links. Note that the chains can also detect and quantify scour-before-fill, when a location in the stream bed is scoured during some stage of a high-flow event (exposing some links that come to lie horizontally), but this is followed by sediment deposition during a later stage of the same event, so that the net result is fill or no change. For more details of the method see Nawa & Frissell (1993) and Leopold et al. (1964).

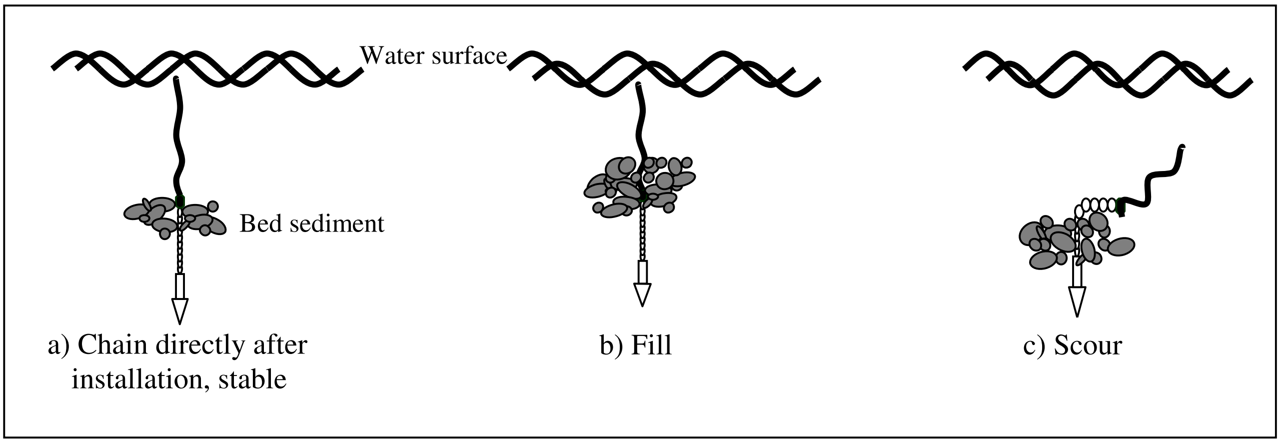

**Fig. 1** Schematic design of a scour chain in the stream bed, (a) directly after installation or in a stable bed patch, (b) after sediment deposition (fill), (c) after sediment scour.

The results for the three different organism groups and the manipulative experiment are presented separately in the following publications: (1) bacteria, (2) algae, (3) invertebrates and (4) experimental disturbance.

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# Local disturbance history, microhabitat parameters and the microdistribution of benthic bacteria in streams

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## Abstract

We investigated the relationships between local disturbance history and habitat parameters (abiotic and biotic) and the microdistribution of benthic bacteria during several high-flow events 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 event, bacterial samples were collected from surface stones and fine sediment in replicate patches that had experienced scour, fill or remained stable. In the Kye Burn, we also measured production of the sediment bacteria. Patterns of bacterial densities in the different bed stability types varied considerably between high-flow events, sampling dates and streams, and the response of sediment bacteria often differed from epilithic bacteria. In the Schmiedlaine, only stone surface area was related to bacterial microdistribution more often than disturbance history. In the Kye Burn, disturbance history influenced bacterial distribution and production most often, followed by water depth. A thorough understanding of the microdistribution of benthic bacteria requires knowledge of disturbance history, as well as more readily measured habitat parameters such as sediment size or water depth.

## 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 in general (Pickett and White 1985) and stream ecology in particular (Townsend 1989; Downes 1990; Poff and Ward 1990; Townsend and Hildrew 1994).

It is well known that the microdistributions of both benthic macroinvertebrates and algae in streams are correlated with abiotic factors, including shear stress, water depth and substratum size, and with biotic factors including predation, competition and food (see for example, Peckarsky et al. 1990; Hearnden and Pearson 1991; Kohler 1992; Holomuzki and Messier 1993; Ruse 1994; Stevenson 1996; Biggs et al. 1998; Passy 2001). By contrast, the potential importance of hydrological disturbance in generating patchy distributions has received much less attention, probably because of the difficulty of mapping the local effects of specific disturbance events. To address this deficiency, 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 high-flow events caused a complex mosaic of small (≤ 1 $m^2$) bed patches that had experienced scour, sediment deposition (fill) or remained undisturbed. This "local disturbance history" (Matthaei and Townsend 2000) had long-term effects on the microdistribution of macroinvertebrates, with higher densities in fill or scour patches two months after a disturbance (Matthaei and Townsend 2000). 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, but in fill patches three months after another flood.

While clearly showing that disturbance history can affect benthic organisms, these first disturbance history studies also had certain limitations. Thus, invertebrates were sampled only once after a single high-flow event in Matthaei and 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 three 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. Moreover, in comparison to macroinvertebrates and algae, stream ecologists know much less about factors driving the patchiness of benthic bacteria, despite their abundance ($10^{10}$-$10^{12}$ cells $m^{-2}$; Haack and McFeters 1982; Stock and Ward 1989), productivity (Marxsen 1996, 1999) and important role in carbon dynamics (Meyer 1990; Ward and Johnson 1996; Hall and Meyer 1998). Clearly, benthic bacteria need to be included if the patch dynamics perspective is to be extended to the entire lotic ecosystem. Because microbial ecology in running waters is a relatively young discipline (Ward and Johnson 1996), few studies have investigated effects of high-flow events on lotic bacteria (e.g. Holmes et al. 1998; Marxsen 1999, 2001) or the effects of habitat parameters on bacterial microdistribution (Marxsen 1996; Fischer et al. 2002, 2003). To our knowledge, studies investigating effects of local disturbance history (as defined by Matthaei and Townsend 2000, see above) on benthic bacteria do not exist.

The objectives of the present research were to investigate

(1) short- and long-term effects of disturbance history on the microdistributions of stream bacteria and their secondary production,

(2) the relative contributions of disturbance history, physical habitat parameters and food resources to bacterial distribution, and

(3) effects of disturbance history on the habitat parameters (which could cause indirect effects of disturbance history on bacterial distribution).

# Material and methods

## Study sites

Our study was conducted in the northern and austral springs and summers of 2001/2002 in two streams, the Schmiedlaine in Germany (70 km south of the city of Munich; 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). Thus, this study, whose logistics would have taken two years to undertake in a single hemisphere, was completed in a single year. Our study was not designed to compare Northern and Southern Hemisphere stream ecology.

The Schmiedlaine is a prealpine stream with a steep catchment (area 9.4 km², altitude 750-1800 m a.s.l.; de Jong and Ergenzinger 1995) that lies in a high rainfall zone at the northern edge of the Alps (annual rainfall in the catchment is 1500-2150 mm; Felix et al. 1988; Becht and Wetzel 1989). It has a harsh discharge regime with frequent high-flow events (Ergenzinger and de Jong 1997; Matthaei and Huber 2002), a mean flow of about 0.54 $m^3 s^{-1}$ and a baseflow of about 0.12 $m^3 s^{-1}$ (Wagner 1987; de Jong and Ergenzinger 1995). The catchment lacks agricultural development and about 75% of its area is covered by forest.

Vegetation in the Kye Burn catchment (area ca. 25 km², altitude 600-1600 m a.s.l.) is mainly indigenous tussock grassland lightly grazed by sheep. Annual rainfall is 600-1000 mm (Otago Catchment Board 1983), and the relief is not quite as steep as the Schmiedlaine. Therefore, the Kye Burn has a more moderate discharge regime (in terms of frequency and severity of high-flow events) than the Schmiedlaine (Matthaei et al. 1999a; 1999b). Mean annual flow at the study reach is 1.1 $m^3 s^{-1}$ and baseflow about 0.4 $m^3 s^{-1}$ (National Institute of Water and Atmospheric Research, unpublished data). Apart from their different flow regimes, the two streams share several similar characteristics: stream width at baseflow is about 5-10 m, flow regime and stream channel are natural, the water is cold (<13°C in summer in the Schmiedlaine and <16°C in the Kye Burn; G. Sailer, unpublished data) and nutrient-poor (Bavarian Water Management Authority [Wasserwirtschaftsamt] Weilheim, unpublished data; Niyogi et al. 2003). The stream beds consist mainly of cobbles (particle width 64-256 mm; Schmiedlaine) or cobbles and gravels (width 2-64 mm; Kye Burn) interspersed with small and medium boulders (256-1024 mm), the latter especially in the Schmiedlaine. The Schmiedlaine runs through a narrow, v-shaped valley with steep slopes about 200 m high; the studied reach of the Kye Burn is located in a small, steep canyon (wall height about 15-25 m) and has a tightly confined channel.

Sediment supply into both streams is high because of the presence of steep, unstable scree areas (Matthaei et al. 1999a; Matthaei and Huber 2002), resulting in unstable stream beds that are easily moved at high flow. In each stream, we selected a single study site of about 40 m length. The site in the Kye Burn included ‘Site 2’ used for monitoring patterns of scour and fill in Matthaei et al. (1999a) and ‘Site 2’ used for stone monitoring in Matthaei et al. (1999b).

### Quantification of bed movement

Bed movement patterns were quantified using metal-link scour chains (Matthaei et al. 1999a). The chains (each about 0.5 m long) were installed vertically in the bed (using a 15-kg metal fencepost driver and a hollow steel standpipe, outer diameter 5 cm), with only the top one or two chain links exposed. Scour during a high-flow event exposes additional chain links, whereas fill can be measured by the thickness of the sediment layer deposited on top of the originally exposed links (for more details see 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 about 1 m between chains and transects. Most transects contained five chains. The exact location of each chain in the stream bed was determined by measuring distances to three pairs of permanently-marked points on the banks that were situated at least 1.5 m above the water line. All chains were equipped with magnetic tracers (Ergenzinger and Conrady 1982) to facilitate re-location with a magnetic locator (model GA-52B, Schonstedt, Virginia) after high-flow events. In addition, we used a theodolite (Tachymeter SET 3, Sokkisha/SOKKIA, Tokio; leveling unit Ni 2, Zeiss, Jena) to measure the positions of all chains relative to another permanently marked point on the true left bank (2 m above the water line) on 16 May. These measurements ensured that, in case of a very large flood, we would still be able to determine net changes for chain locations which might experience 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 (see Table 1), and finally 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 this would not be necessary (Matthaei et al. 1999a; Matthaei and Townsend 2000).

**Table 1.** Bed-moving high-flow events and sampling occasions in the **Schmiedlaine** and in the **Kye Burn** from May 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 | 3 x 5 |
| | | 5 June | After Event 1<br>(=Before Event 2) | Fill, Stable, Random | 3 x 5 |
| | **Event 2 (10 / 11 June)** | | | | |
| | | 13 June | After Event 2<br>(=Before Event 3) | Scour, Fill, Stable | 3 x 5 |
| | **Event 3 (18 - 20 June)** | | | | |
| | | 25 June | After Event 3 | Scour, Fill, Stable | 3 x 5 |
| | | 11 July | After Event 3 | Scour, Fill, Stable | 3 x 5 |
| | | 24 July | After Event 3 | Scour, Fill, Stable | 3 x 5 |
| | | 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 | 3 x 5 |
| | | 26 September | After Event 4 | Scour, Fill, Stable | 3 x 5 |
| | | 9 October | After Event 4 | Scour, Fill, Stable | 3 x 5 |
| Kye Burn | | 21 November | Before Event 1 | Random | 8 |
| | | 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 | 3 x 5 |
| | | 27 December | After Event 1<br>(=Before Event 2) | Scour, Fill, Stable | 3 x 5 |
| | **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 |

### Studied high-flow events and biological sampling

We investigated all bed-moving high-flow events that occurred during a six-month period in each stream, four in the flood-prone Schmiedlaine and two in the relatively more stable Kye

Burn. Whenever possible, samples were taken before and three times after each event (shortly after, about 2-3 weeks after, and about one month after; see Table 1 for exact sampling dates).

Our focus was on densities of epilithic bacteria and of bacteria in fine surface sediments. However, we also determined the biomass of epilithic algae for use as a covariate in our analysis (see Publication 2). A parallel study (Effenberger et al. in press, see Publication 3) investigated densities of benthic invertebrates and standing stocks of particulate organic matter (POM) using a Surber sampler (area 0.0625 m², mesh size 200 µm). These two parameters were used as additional covariates in our analysis. The Surber samples also served as sampling units in the present study. On each sampling date after a high-flow event, 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 was taken in the immediate vicinity of the focal chain (with at least one side of the frame of the sampler touching the chain). A marked screwdriver fixed a sampling depth of 10 cm. Densities of epilithic bacteria and algal biomass 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%) in the field and stored on ice in the dark. Sediment bacteria were studied by collecting a sample of 4-10 ml from the uppermost 1-2 cm of fine sediment patches within the frame of the Surber sampler using a plastic syringe (diameter 2 cm; Marxsen 1996).

For each Surber sample, we determined water depth and near-bed current velocity (≈3 cm above the substratum) with a propeller flow meter (Hoentzsch GmbH, Waiblingen, Germany; propeller diameter 2 cm). We also determined substratum composition by eye as the averaged b-diameter (particle width) of the first- to third-most common substratum size classes inside the Surber sampler. These size classes were identified using a modified Wentworth scale (Harrelson et al. 1994), which uses the half-phi scale (e.g. 16-22 mm, 22-32 mm, 32-45 mm, 45-64 mm, 64-90 mm, 90-128 mm etc.). All particles smaller than 8 mm were combined in a single category. The four habitat parameters were used as additional covariates in our analysis.

We started biological sampling in the Schmiedlaine 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, based on field observations during a scour chain study in another prealpine river (Matthaei et al. 2003), we expected epilithic algae and bacteria to recover quickly from the disturbance caused by chain installation.

On 9 and 15 May, we collected eight random pre-disturbance samples in our study reach. In the evening and night of 15 May, a brief high-flow event occurred that was caused by a single hour of heavy rain (Event 1; see Table 1). This event had a moderate peak discharge and brought about a patchy mosaic of predominantly shallow fill (range 2-15 cm, mostly <10 cm), some shallow scour (2-10 cm), and 30% stable patches in our study reach (Table 2). Post-disturbance sampling (as described above) started seven days after Event 1 and continued 14 days later on 5 June. On this day, we took five random samples in addition to the samples from fill and stable patches because no patches with ≥5 cm of scour were left. Four days later, this sampling phase was truncated by Event 2, another moderate event that left more than half of the chains undisturbed, caused shallow scour at one third of the chains (range 2-16 cm, mostly <10 cm), and also some shallow fill (range 2-9 cm).

Post-disturbance sampling after Event 2 was possible only once because Event 3, the largest flood recorded during our field work in the Schmiedlaine, occurred seven days later (Table 1). This flood deposited up to 40 cm of (mostly relatively fine) sediment at the majority of chain locations, caused scour of up to 30 cm at almost one third of the chains and also left some stable patches (Table 2). For this event, 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 with a peak flow of $\approx 6\ m^3\ s^{-1}$ occurred on 20-21 July. However, this spate caused shallow scour or fill at only a few chain locations, which we avoided on the third sampling date. No further bed movements occurred from 21 July to 5 September.

After completing the post-flood series for Event 3, we ran out of stable bed patches to sample. Therefore, we returned to taking random samples on 14 and 30 August. Six days after the latter date, a cold front with considerable rainfall led to Event 4, another sizeable flood which had two separate flow peaks on 5-6 and 8-9 September (Table 1). This event caused scour of up to 45 cm at 38% of the chains and removed much of the fine sediment deposited by Event 3 from the site. It also resulted in fill (up to 22 cm, but mainly around 10 cm) at 28% of the chains and left about one third of the chains undisturbed (Table 2). Post-flood sampling started two days after Event 4 and continued on 26 September. Between these two sampling dates, another brief flow peak of $\approx 6.5\ m^3\ s^{-1}$ occurred on 15 September. However, data from 30 randomly chosen chains relocated on 26 September indicated that this spate caused hardly any bed movement. A final field day on 9 October completed a second series of two pre- and three post-flood sampling dates.

The first of the two high-flow events in the Kye Burn occurred on 5-6 December 2001, about four weeks after chain installation was completed (Table 1). This moderate event caused fill (2-20 cm, but mostly ≤10 cm) at 62% of the chain locations, some shallow scour at 12% of all chains (mostly around 5 cm, maximum 11 cm), and left 26% of the chains undisturbed (Table 2). Before Event 1, we had taken three weekly sets of random pre-disturbance samples. After the event, we collected two sets of post-disturbance samples.

On the day we intended to take a third set of post-disturbance samples, a major flood began that lasted from 9-21 January 2002 (with four distinct flow peaks) and had a return period of about five years (Tables 1 & 2). This caused sediment deposition (of up to at least 39 cm) at all 208 chain locations, with more than 20 cm of fill at the majority of locations. Patches that experienced net scour, or stable patches, did not exist. Because we expected bacteria recovery to be very slow after this rare and unusual flood, we decided to collect four sets of eight post-flood samples chosen randomly from fill patches to monitor bacterial recovery (see Table 1). No further bed movements occurred until the end of this second sampling series.

**Table 2.** Event magnitudes and percentages of scoured, depositional and stable bed patches caused by the four high-flow events in the **Schmiedlaine** between May and September 2001 and the two events in the **Kye Burn** between November 2001 and March 2002.

| | **Schmiedlaine** | | | | **Kye Burn** | |
|---|---|---|---|---|---|---|
| **High-flow event** | **Event 1** | **Event 2** | **Event 3** | **Event 4** | **Event 1** | **Event 2** |
| **Peak flow** [m$^3$/s] | 7.5 | 9.5 | 25 | 14.5 | 4.7 | 20.7 |
| **Duration** [days] | < 1 | 1-2 | 2-3 | 3-4 | ~ 1 | ~ 12 |
| **Return period** [years] | ≤ 0,5 | 0.5-0.75 | 2-3 | 1 | ~ 0.4 | ~ 5 |
| **Bed movements:** | | | | | | |
| **fill** [% of all chains] | 63 | 19 | 61 | 27 | 62 | 100 |
| **stable** [%] | 30 | 51 | 11 | 34 | 26 | 0 |
| **scour** [%] | 7 | 31 | 28 | 39 | 12 | 0 |

## Sample processing and bacterial production

We collected 344 samples of bacterial abundance and algal biomass in the Schmiedlaine and 176 in the Kye Burn, plus 86 samples of bacterial production in the Kye Burn. In the parallel study (Effenberger et al. in press, see Publication 3), 167 invertebrate and POM samples were collected in the Schmiedlaine, and 78 in the Kye Burn. Ten percent of the POM samples from the Schmiedlaine were lost during processing (13 June: 3 replicates from each patch type; 25 June: 2 from each type; 9 October: 1 from each type). Each surface stone sample was divided into four equal parts in the laboratory. One quarter was used for quantitative counts of bacteria with the 4´, 6-diamidino-2-phenylindol (DAPI) staining method (Porter and Feig 1980; Ward and Johnson 1996). Because most of the bacterial samples contained many detrital and mineral particles even after dilution, we used a combination of the "standard" technique and a modification described by Schallenberg et al. (1989). This technique removed most of the larger detritus particles from the filtrate and thus made it easier to count the bacteria. All DAPI samples were counted using a fluorescence microscope (Leitz Laborlux D with phase-contrast objective; Wetzlar, Germany) at 1000 x magnification under immersion oil. For each bacterial sample, a volume of 0.1 µl was DAPI-stained, and the bacterial cells in 20 random subsamples (microscope viewing fields) of this volume were counted, adding up to a total of at least 400 cells (Ward and Johnson 1996). We distinguished between coccoid and rod-shaped bacteria during counting.

The remaining three quarters of each surface stone sample were used to determine algal biomass as chlorophyll a, algal cell densities and ash free dry mass (AFDM) of the epilithic biofilm in a related study (Sailer et al. submitted, see Publication 2). The AFDM data were excluded from the statistical analysis because this parameter includes both epilithic algae and bacteria and we investigated these two variables separately in our experiment. The surface area of each stone was determined by wrapping stones in aluminum foil and weighing the foil (Townsend et al. 1997), and bacterial counts were converted to densities per $cm^2$ of stone surface area. Further, stone surface area was used as a covariate for epilithic bacterial densities in our analysis, because this parameter influenced densities of epilithic algae in a previous study (Matthaei et al. 2003).

The bacteria in the fine sediment samples were also counted using the DAPI method. Bacterial production in the Kye Burn was measured with the leucine incorporation technique (Tulonen 1993; Marxsen 1996). We determined the dry mass of each fine sediment sample, and both bacterial counts and production estimates were converted to values per g of fine sediment. We also determined the overall mean of the first- to third-most common grain sizes in each sediment sample in a Petri dish set on graph paper, using four different size classes (particle width >3 mm, 2-3 mm, 1-2 mm, and <1 mm). The resulting mean particle size was used as a covariate for the sediment bacteria in our analysis.

Some bacterial samples from the Kye Burn had to be discarded because the Seral water used to dilute them during preparation for the DAPI counts proved to be contaminated with bacteria. This contamination affected the random samples collected on the three dates before Event 1 (all samples on 21 and 28 November, plus 3 epilithic samples and 5 sediment samples on 4 December), and the sediment bacteria on 11 December (3 samples from scour patches, 3 from stable and 4 from fill patches lost).

## Data analysis

To determine the overall initial effect of each high-flow event on the bacterial community, we compared the last pre-disturbance sampling date with the first post-disturbance date, using one-way analysis of variance (ANOVA). For this analysis, all three disturbance history categories on the first post-disturbance date were combined. Comparisons between disturbance history categories were conducted using one-way ANOVAs and one-way analysis of covariance (ANCOVA), with ’patch type’ as factor and the studied habitat parameters as covariates. Exploratory correlation matrices for both streams (all samples combined in each stream) had revealed that none of the eight covariates were strongly correlated with each other ($r_p$-values were <0.40 in 139 of 144 cases and the highest $r_p$-value was 0.61, well below the threshold of 0.8 for strong collinearity; see Lewis-Beck 1980).

Dependent variables were total densities of epilithic and sediment bacteria, densities of coccoid bacteria on stones and in the sediment, and densities of rod-shaped bacteria on stones and in the sediment. In the Kye Burn, we also analysed bacterial production. Three of the nine habitat parameters were used as covariates only in combination with the dependent variables they were relevant for. Thus, ANCOVAs with ’grain size of fine sediment’ were calculated only for sediment bacteria, and ANCOVAs with ’stone surface area’ or ’epilithic algal biomass’ were calculated only for epilithic bacteria. Direct effects of disturbance history on the habitat parameters themselves were also assessed using one-way ANOVAs. After exploratory analysis, data were $\log_{10}$ transformed where necessary to improve normality and homoscedasticity.

Based on our previous results for stream invertebrates (Matthaei et al. 2000; Matthaei and Townsend 2000), we expected the effects of disturbance history to change with time since the last high-flow event. 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 and Keough 2002). If a significant factor x covariate interaction was found, we verified the reliability of the estimated marginal means for each patch type. This test was performed by comparing the actual adjusted means for each patch type (determined using the individual regression lines of the dependent variable against the covariate) with the estimated marginal means calculated by the ANCOVA (see Matthaei and Huber 2002). Only covariates with significant effects on the dependent variable are discussed. In cases where no covariate had a significant effect, all covariates were dropped from the analysis and a simple one-way ANOVA was calculated. An effect of disturbance history was only considered as valid if it was detected in at least 50% of all ANCOVAs with significant covariate effects (or in the ANOVA, if none of the covariates had a significant effect on the dependent variable).

The type-I error rate of the main analysis was controlled for each variable and sampling date, so there was no need to adjust $\alpha$ (Rice 1989). Because of 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 and Townsend 2000; $n = 8$-$15$), we set $\alpha$ at 0.1 in all patch-specific analyses. Comparisons between sampling dates (in which all samples collected on each date were combined) were conducted with $\alpha$ 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 and Quinn 1989). With the ANOVAs, we used Tukey-HSD tests, except in cases of persisting heteroscedasticity (results of Levene´s test still significant after transformation, see Quinn and Keough 2002), where we performed Games-Howell tests which do not assume equal variances between groups (Quinn and 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 calculated in SPSS® version 11.0 (SPSS Inc., Chicago). For graphical illustration of the results, the unadjusted means were used instead of the estimated marginal means calculated in the ANCOVAs because none of the covariates consistently had a significant effect on the dependent variables (see Tables 4 & 6). All differences between patch types summarized in the Results section were significant (unless stated otherwise in the text).

## Results

**Schmiedlaine**. Density patterns for total epilithic bacteria, coccoid epilithic bacteria and rod-shaped epilithic bacteria were generally quite similar (Fig. 1). Total epilithic bacteria were reduced significantly by Event 2 (p=0.02) and Event 4 (p=0.003) in comparison to the respective pre-disturbance densities. On 13 June (shortly after Event 2) and on 9 October (five weeks after Event 4), epilithic bacteria were more abundant in fill than in scour patches (Table 3). By contrast, density of epilithic bacteria was higher in stable patches than in scour or fill patches on 25 June, shortly after Event 3. Epilithic bacterial densities were correlated with most of the covariates (except for water depth and total invertebrates) on at least one of the sampling dates (Table 4), with stone surface area having the highest number of significant (and always negative) correlations.

Coccoid epilithic bacteria also showed significant reductions in overall densities after Event 2 (p=0.03) and Event 4 (p<0.001). On 13 June and on 9 October, coccoid bacteria were more common in fill than in scour patches, and on 25 June they were more common in stable than in scour or fill patches (Table 3). The significant covariate x factor-interaction for the covariate stone surface area on 13 June reduced the difference between mean densities of coccoid bacteria in fill and scour patches by only 4%; therefore, the result of this ANCOVA was valid. Coccoid epilithic bacteria were correlated with all covariates except for total invertebrates on at least one sampling date each (Table 4). Again stone surface area showed the highest number of significant (and negative) correlations.

Density of rod-shaped epilithic bacteria was reduced significantly after Event 2 (p=0.02). On 13 June, rod-shaped bacteria were more common in fill than in scour patches (Table 3). The significant covariate x factor-interactions for the covariate near-bed current velocity on this date increased the difference between mean densities of rod-shaped bacteria in fill and scour patches by 4%. Consequently, the result of this ANCOVA was valid. On 25 June, rod-shaped epilithic bacteria were more abundant in stable than in fill patches. By contrast, their densities were higher in scour and fill patches than in stable patches on 9 October. Rod-shaped bacteria were correlated with all covariates except for total invertebrates on at least one sampling date each (Table 4). As for the other epilithic bacteria, stone surface area showed the highest number of significant, negative correlations.

Density patterns for total sediment bacteria, coccoid sediment bacteria and rod-shaped sediment bacteria were generally similar (Fig. 2). Total sediment bacteria were not reduced significantly by any of the high-flow events (p>0.43) but were more common in scour than in fill patches on 13 June, shortly after Event 2 (Table 3). Densities of total sediment bacteria were correlated with all covariates (except for total invertebrates) on one or two sampling dates each (Table 4).

Densities of coccoid sediment bacteria were not affected by any event (p>0.27) and never differed significantly between the three bed stability types (Table 3). Coccoid bacteria were correlated with water depth, near-bed current velocity and grain size of fine sediment on one or two sampling dates each (Table 4).

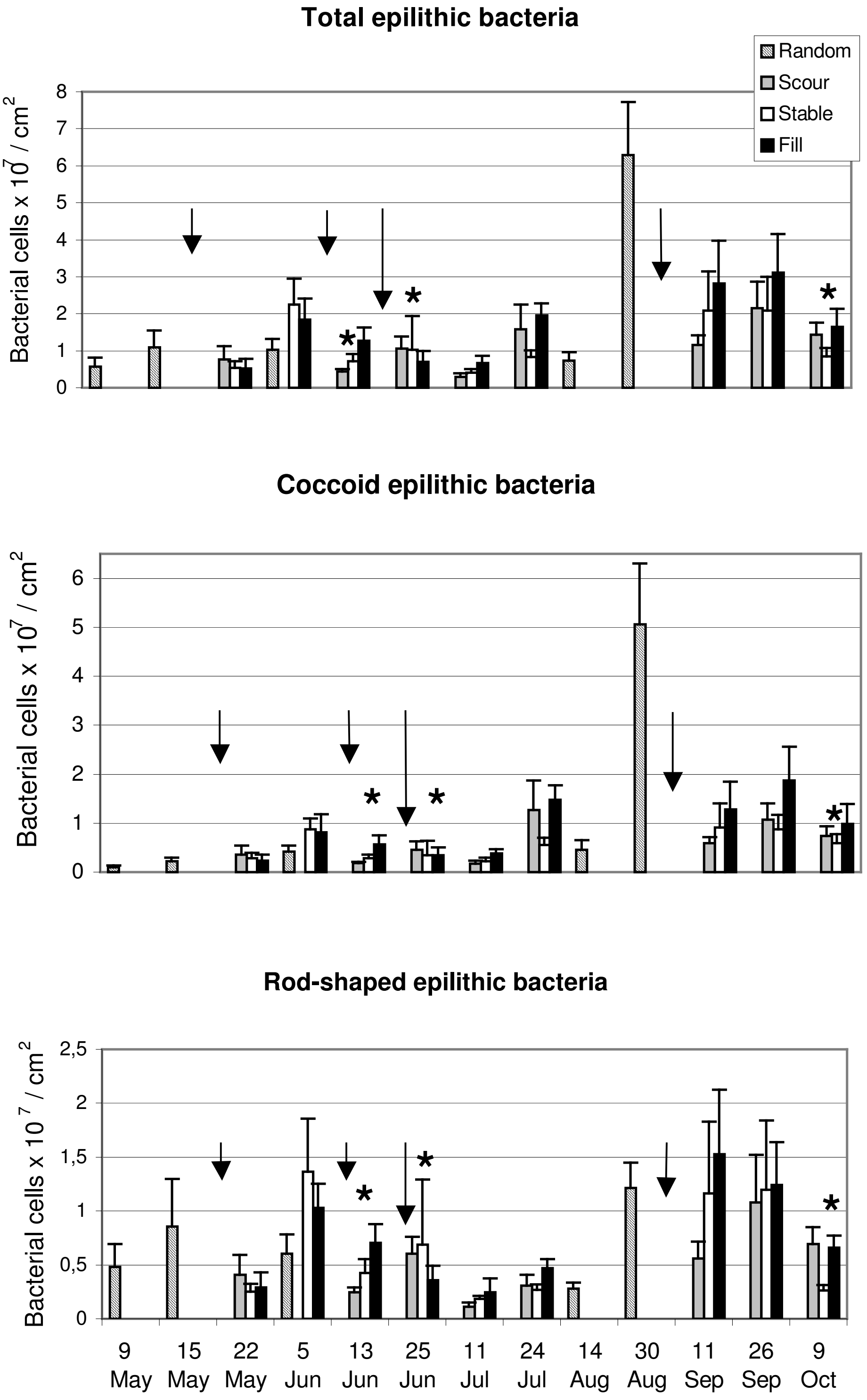
Similarly, overall densities of rod-shaped sediment bacteria were not reduced by any event (p>0.60). Nevertheless, rod-shaped bacteria were more common in fill patches than in random patches three weeks after Event 1 (Table 3). Shortly after Event 3 and shortly after Event 4, their densities were higher in stable and scour patches than in fill patches. Densities of rod-shaped sediment bacteria were correlated with water depth and POM on two sampling dates each (Table 4).

**Table 3.** Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing bacterial densities in scour, fill and stable patches in the **Schmiedlaine**. Prior to final analysis, data were log-transformed where necessary and potential factor x covariate interactions explored (see column 4). Only covariates with significant effects on the dependent variables are included, and only ANCOVAs resulting in significant differences between disturbance categories are shown (for a complete list of all covariate effects see Table 4). $\alpha = 0.1$.

| **Date and dependent variable** | **Covariate in ANCOVA** | **Covariate** | **Inter-action** | **Factor** | **Ranking** |
|---|---|---|---|---|---|
| **22 May** | | | | | |
| **5 June** | | | | | |
| Rod-shaped sediment bacteria | Water depth | 0.06 | 0.71 | 0.08 | Fill > random |
| **13 June** | | | | | |
| Total epilithic bacteria | - | - | - | 0.07 | Fill > scour |
| | Stone surface area | 0.003 | 0.24 | 0.02 | Fill > scour |
| Coccoid epilithic bacteria | Near-bed velocity | 0.08 | 0.25 | 0.05 | Fill > scour |
| | Stone surface area | 0.005 | 0.07 | 0.08 | Fill > scour |
| Rod-shaped epilithic bacteria | - | - | - | 0.05 | Fill > scour |
| | Near-bed velocity | 0.02 | 0.04 | 0.02 | Fill > scour |
| | Stone surface area | 0.01 | 0.48 | 0.02 | Fill > scour |
| Total sediment bacteria | Near-bed velocity | 0.04 | 0.71 | 0.07 | Scour > fill |
| **25 June** | | | | | |
| Total epilithic bacteria | Stone surface area | < 0.001 | 0.16 | 0.003 | Stable > (scour = fill) |
| Coccoid epilithic bacteria | Stone surface area | 0.002 | 0.86 | 0.06 | Stable > (scour = fill) |
| Rod-shaped epilithic bacteria | Stone surface area | < 0.001 | 0.75 | 0.05 | Stable > fill |
| Rod-shaped sediment bacteria | POM | 0.01 | 0.22 | 0.004 | (Stable = scour) > fill |
| **11 July** | | | | | |
| **24 July** | | | | | |
| **11 September** | | | | | |
| Rod-shaped sediment bacteria | - | - | - | 0.02 | (Stable = scour) > fill |
| **26 September** | | | | | |
| **9 October** | | | | | |
| Total epilithic bacteria | POM | 0.001 | 0.60 | 0.06 | Fill > scour |
| Coccoid epilithic bacteria | POM | 0.003 | 0.53 | 0.08 | Fill > scour |
| Rod-shaped epilithic bacteria | - | - | - | 0.02 | (Scour = fill) > stable |
| | Stone surface area | 0.02 | 0.27 | 0.02 | (Scour = fill) > stable |
| | Chlorophyll a | 0.02 | 0.34 | 0.02 | (Scour = fill) > stable |
| | POM | 0.02 | 0.59 | 0.03 | Fill > stable |

**Table 4.** Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing bacterial densities in scour, fill and stable patches in the **Schmiedlaine** (for factor effects see Table 3). Only significant results are shown; blanks indicate non-significant results. * P < 0.10; ** P <0.01; *** P <0.001; + positive correlation; - negative correlation. Note that some of the covariates were not calculated for all of the dependent variables (for details see text).

| **Covariate and dependent variable** | **22 May** | **5 June** | **13 June** | **25 June** | **11 July** | **24 July** | **11 Sept** | **26 Sept** | **9 Oct** |
|---|---|---|---|---|---|---|---|---|---|
| **Water depth** | | | | | | | | | |
| Coccoid epilithic bacteria | * (-) | | | | | | | | |
| Rod-shaped epilithic bacteria | | * (-) | | | | | | | |
| Total sediment bacteria | * (+) | | | | | | | | |
| Coccoid sediment bacteria | * (-) | | | | | | | | |
| Rod-shaped sediment bacteria | * (-) | * (+) | | | | | | | |
| **Near-bed current velocity** | | | | | | | | | |
| Total epilithic bacteria | | | | | | * (+) | | | |
| Coccoid epilithic bacteria | | | * (+) | | | * (+) | | | |
| Rod-shaped epilithic bacteria | | | * (+) | | | * (+) | | | |
| Total sediment bacteria | * (-) | | * (+) | | | | | | |
| Rod-shaped sediment bacteria | | | | | | | | * (+) | |
| **Substratum size** | | | | | | | | | |
| Total epilithic bacteria | | * (-) | | * (-) | * (-) | | | | |
| Coccoid epilithic bacteria | | * (-) | | * (-) | * (-) | | | | |
| Rod-shaped epilithic bacteria | | * (-) | | * (-) | * (-) | | | | |
| Total sediment bacteria | | | | | | | | * (+) | |
| **Grain size fine sediment** | | | | | | | | | |
| Total sediment bacteria | | | | | | | | * (+) | |
| Coccoid sediment bacteria | | | | * (-) | | | | * (-) | |
| Rod-shaped sediment bacteria | | | | | | | | * (-) | |
| **Stone surface area** | | | | | | | | | |
| Total epilithic bacteria | | ** (-) | ** (-) | *** (-) | | | *** (-) | ** (-) | * (-) |
| Coccoid epilithic bacteria | | ** (-) | ** (-) | ** (-) | | | *** (-) | ** (-) | * (-) |
| Rod-shaped epilithic bacteria | | ** (-) | * (-) | *** (-) | | | ** (-) | ** (-) | * (-) |
| **Algal biomass (Chl a)** | | | | | | | | | |
| Total epilithic bacteria | * (+) | | | | | | | | |
| Coccoid epilithic bacteria | * (+) | | | | | | | | |
| Rod-shaped epilithic bacteria | * (+) | | | | | | | | * (+) |
| **POM** | | | | | | | | | |
| Total epilithic bacteria | | | | | | | | * (-) | ** (-) |
| Coccoid epilithic bacteria | * (+) | | | | | | | * (-) | ** (-) |
| Rod-shaped epilithic bacteria | | | | | * (-) | | | * (-) | * (-) |
| Total sediment bacteria | * (+) | | | | | * (+) | | | |
| Rod-shaped sediment bacteria | | | | ** (-) | | * (+) | | | |
| **Total invertebrates (Surber)** | | | | | | | | | |


Total epilithic bacteria

Coccoid epilithic bacteria

Rod-shaped epilithic bacteria

**Fig. 1.** Total bacterial densities and densities of coccoid and rod-shaped bacteria on surface stones collected in random, scour, stable and fill patches in the **Schmiedlaine**. The arrows indicate timing and magnitudes (arrow length) of the high-flow events (for details see text). Significant differences between patch types in the ANOVAs or ANCOVAs are shown by asterisks above the mean values. Error bars indicate standard errors. See Table 3 for *P*-values of all comparisons between patch types. *P<0.10; **P<0.01; ***P<0.001.

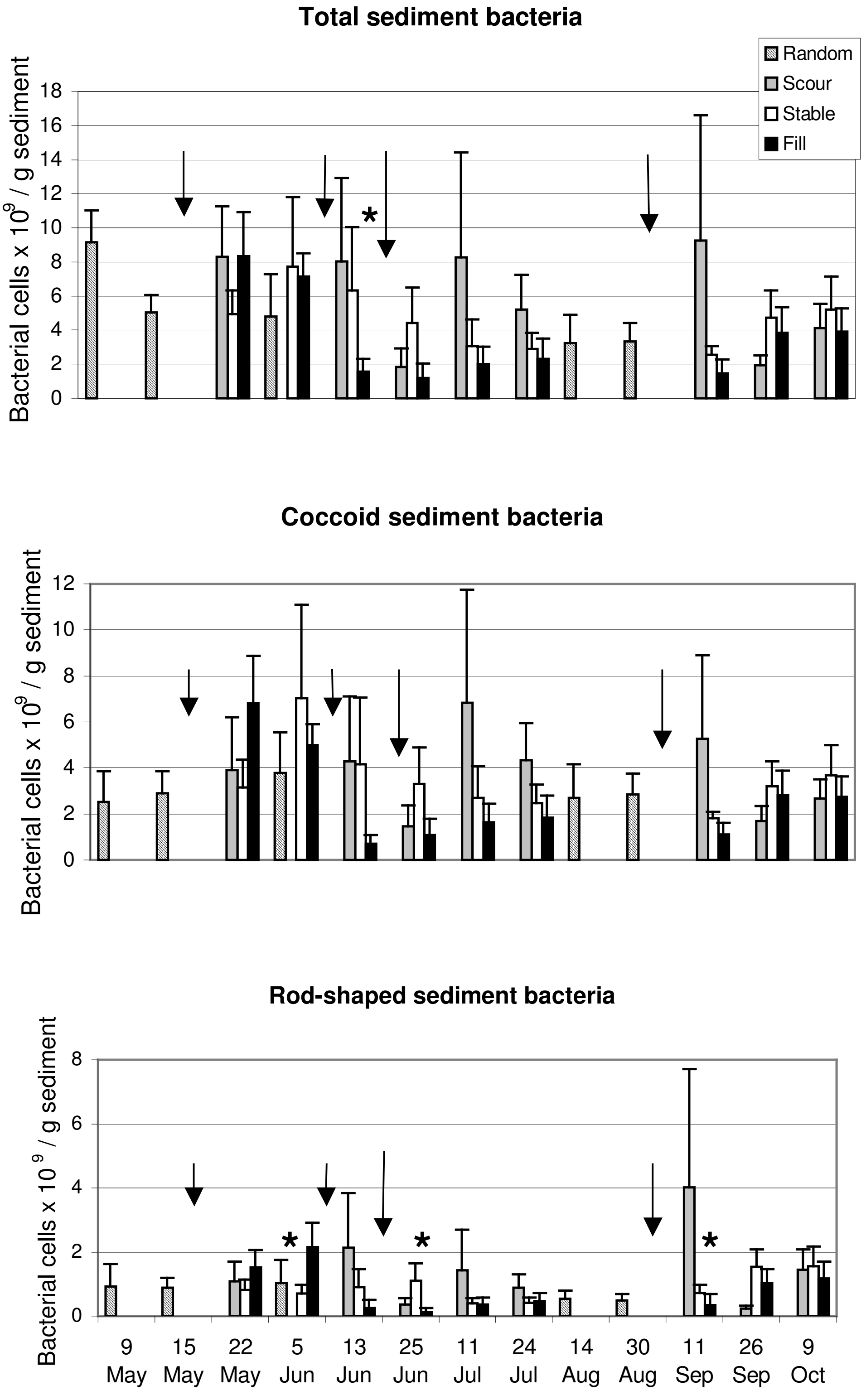


**Fig. 2.** Total bacterial densities and densities of coccoid and rod-shaped bacteria in fine surface sediments collected in random, scour, stable and fill patches in the **Schmiedlaine**. See Fig. 1 for further details.

**Kye Burn.** Density patterns for total epilithic bacteria and rod-shaped epilithic bacteria were generally similar, whereas coccoid epilithic bacteria showed a somewhat different pattern after Event 2 (Fig. 3). Total epilithic bacteria decreased significantly after Event 1 in comparison to pre-disturbance densities ($p<0.05$). Shortly after Event 1, epilithic bacteria were more abundant in fill patches than in scour or stable patches (Table 5). Epilithic bacteria were correlated positively with water depth and POM on this date (Table 6). The significant covariate x factor-interaction for POM increased the respective differences between mean densities of total epilithic bacteria in fill versus scour patches and in fill versus stable patches by more than 20%. Consequently, the results of the ANCOVA were valid.

Overall densities of coccoid epilithic bacteria were lower after Event 1, but this effect was not quite significant ($p=0.06$, power=0.49). Shortly after Event 1, coccoid bacteria were more abundant in fill patches than in scour or stable patches (Table 5). Densities of coccoid epilithic bacteria were correlated significantly with none of the covariates (Table 6).

Densities of rod-shaped epilithic bacteria were not affected by the two events ($p>0.31$) and were similar in the three bed stability types on both dates after Event 1 (Table 5). Rod-shaped bacteria were correlated significantly with water depth on 11 December (Table 6).

Density patterns for total sediment bacteria, coccoid sediment bacteria and rod-shaped sediment bacteria were generally similar, while bacterial production showed a different pattern after Event 2 (Fig. 4). Densities of total sediment bacteria decreased significantly after Event 2 in comparison to their average densities in the pre-flood samples collected on 27 December ($p=0.001$). Sediment bacteria had recovered to pre-flood densities by 7 February ($p=0.26$). Shortly after Event 1, sediment bacteria were most abundant in fill patches and least abundant in scour patches, with intermediate densities in stable patches (Table 5). Total sediment bacteria were correlated negatively with near-bed current velocity on 11 December (Table 6).

Densities of both coccoid and rod-shaped sediment bacteria were also reduced by Event 2 ($p=0.001$ in both cases). Both groups of bacteria had recovered to pre-flood densities by 7 February (coccoid: $p=0.18$; rod-shaped: $p=0.57$). After Event 1, densities of both groups were similar in the three bed stability types on the two sampling dates (Table 5). Coccoid sediment bacteria were correlated with none of the covariates, whereas densities of rod-shaped sediment bacteria were correlated negatively with the grain size of the fine sediment on 27 December (Table 6).

Bacterial production was reduced by Events 1 and 2 in comparison to the mean values in the respective pre-disturbance samples ($p<0.001$ in both cases). After Event 2, production remained significantly lower than pre-flood levels on all four post-flood sampling dates ($p<0.001$ in each case). Production values were similar across patch types on both sampling dates after Event 1 (Table 5). On 27 December, bacterial production was correlated positively with substratum size in the Surber samples (Table 6).

**Table 5.** Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing bacterial densities in scour, fill and stable patches in the **Kye Burn**. Prior to final analysis, data were log-transformed where necessary and potential factor x covariate interactions were explored (see column 4). Only covariates with significant effects on the dependent variables are include, and only ANCOVAs resulting in significant factor effects are shown (for a complete list of all covariate effects see Table 6). $\alpha = 0.1$.

| Date and dependent variable | Covariate in ANCOVA | Covariate | Inter-action | Factor | Ranking |
|---|---|---|---|---|---|
| **11 December** | | | | | |
| Total epilithic bacteria | - | - | - | 0.04 | Fill > stable |
| | POM | 0.09 | 0.07 | 0.02 | Fill > (stable = scour) |
| Coccoid epilithic bacteria | - | - | - | 0.02 | Fill > (stable = scour) |
| Total sediment bacteria | near-bed velocity | 0.03 | 0.12 | 0.03 | Fill > stable > scour |
| **27 December** | | | | | |

**Table 6.** Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing bacterial densities in scour, fill and stable patches in the **Kye Burn** (for factor effects see Table 5). Only significant results are shown; blanks indicate non-significant results. * P<0.1; ** P<0.01; *** P<0.001; + positive correlation; - negative correlation. Note that some of the covariates were calculated not for all of the dependent variables (for details see text).

| Covariate and dependent variable | 11 December | 27 December |
|---|---|---|
| **Water depth** | | |
| Total epilithic bacteria | * (+) | |
| Rod-shaped epilithic bacteria | * (+) | |
| **Near-bed current velocity** | | |
| Total sediment bacteria | * (-) | |
| **Substratum size** | | |
| Bacterial production | | * (+) |
| **Grain size fine sediment** | | |
| Rod-shaped sediment bacteria | | * (-) |
| **Stone surface area** | | |
| **Algal biomass (Chl a)** | | |
| **POM** | | |
| Total epilithic bacteria | * (+) | |
| **Total invertebrates (Surber)** | | |

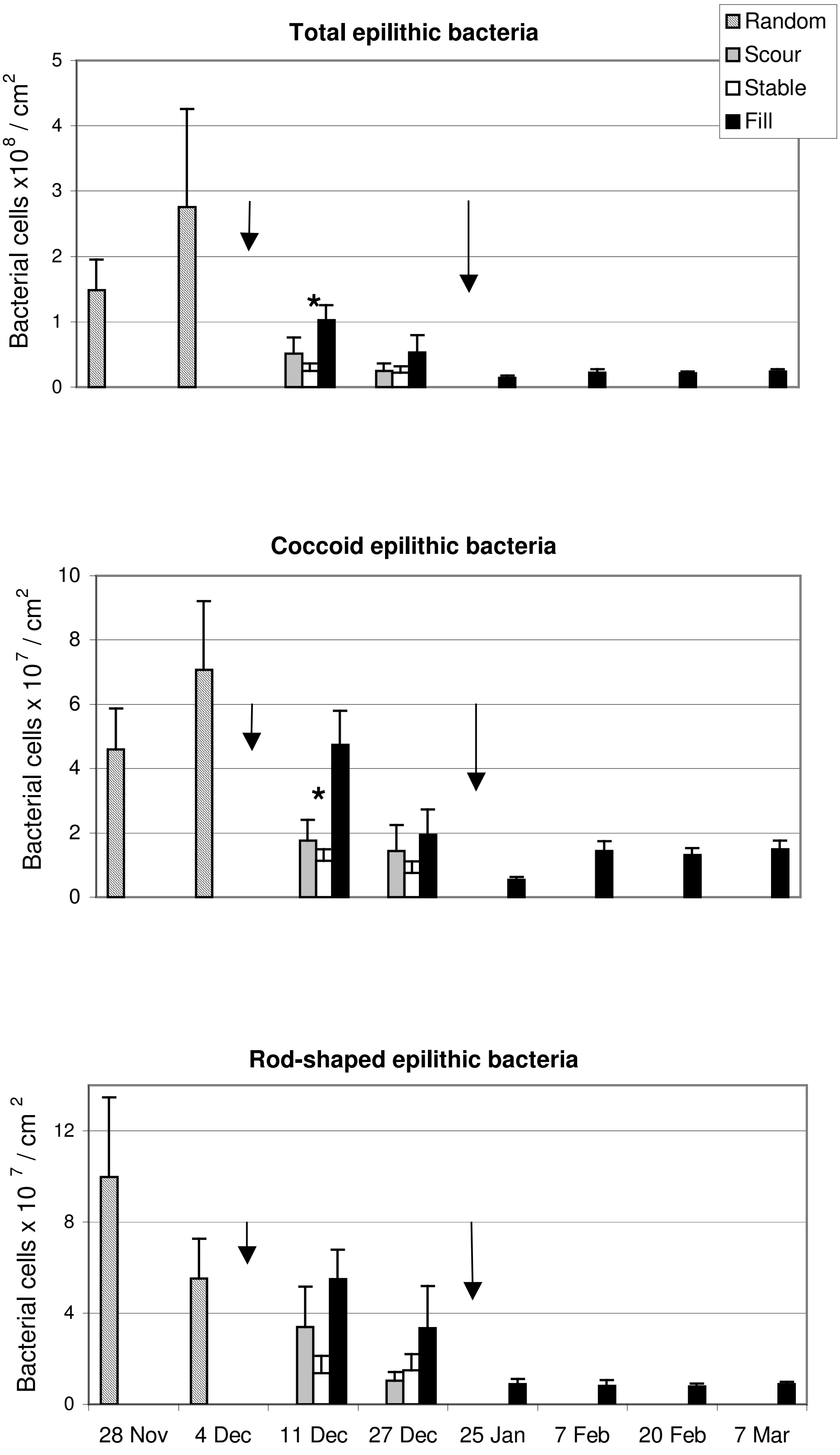


**Fig. 3.** Total bacterial densities and densities of coccoid and rod-shaped bacteria on surface stones collected in random, scour, stable and fill patches in the **Kye Burn**. See Fig. 1 for further details.

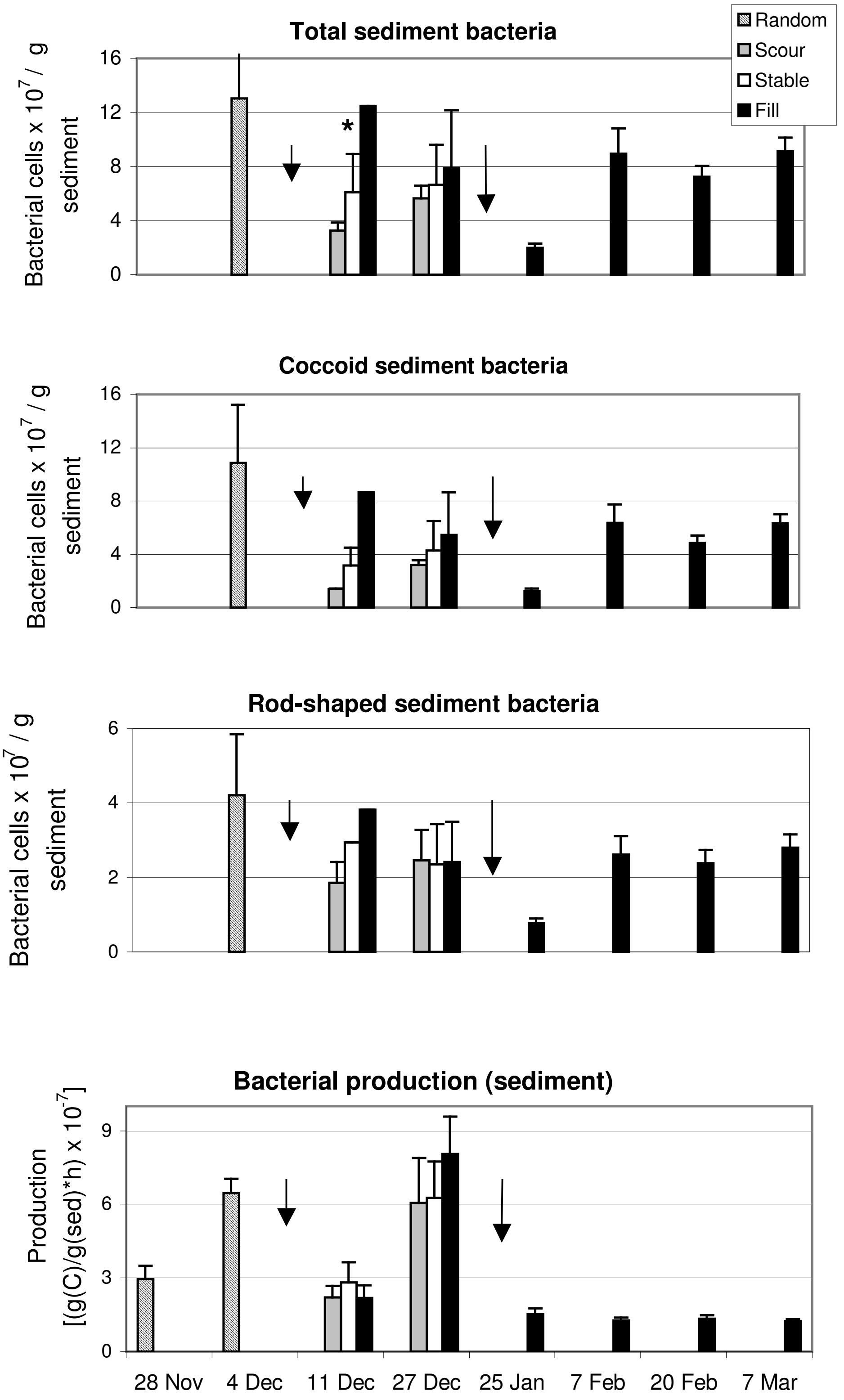


**Fig. 4.** Total bacterial densities, densities of coccoid and rod-shaped bacteria, and bacterial production in fine surface sediments collected in random, scour, stable and fill patches in the **Kye Burn**. All samples of bacterial density on 28 November were lost, also several on 4 December (n=3) and 11 December (n=2 each in scour and stable patches, n=1 in fill patches; for details see text). See Fig. 1 for further details.

### Summary of relationships with disturbance history and habitat parameters

In the Schmiedlaine, we analysed patch-specific patterns of bacterial densities for the nine dates when samples had been collected after bed-moving high-flow events. A total of 54 cases was analysed for the factor disturbance history and six of the eight covariates (9 dates x 6 bacterial groups). For the covariates stone surface area and epilithic algal biomass, we analysed 27 cases because these parameters were not relevant for sediment bacteria (see Methods). Similarly, we analysed 27 cases for ‘grain size of fine sediment’ because this parameter was not relevant for epilithic bacteria. Stone surface area was related to bacterial microdistribution most often (in 67% of all cases analysed), followed by disturbance history (24%), POM (22%), substratum size in Surber samples (19%), near-bed velocity, algal biomass and grain size of fine sediment (all 15% each), and water depth (11%). Total invertebrate densities in Surber samples was not related at all to bacterial distribution.

In the Kye Burn, analyses of patch-specific patterns of bacterial density were possible only for the two sampling dates after Event 1. A total of 14 cases was analysed for six covariates (6 bacterial groups plus bacterial production x 2 dates). Six cases each were analysed for stone surface area and epilithic algal biomass, and eight cases for grain size of fine sediment (three sediment bacteria groups plus production of sediment bacteria x two dates). Disturbance history was related to bacterial distribution most often (in 21% of all cases analysed), followed by water depth (14%), grain size of fine sediment (13%), and near-bed velocity, substratum size in Surber samples and POM (all 7% each). Stone surface area, epilithic algal biomass or total invertebrates in Surber samples did not affect bacterial microdistribution in the Kye Burn.

In all cases where a relationship of disturbance history with bacterial distribution in the ANOVA occurred simultaneously with a correlation of a habitat parameter with bacterial distribution in the ANCOVAs, the relationship with disturbance history remained valid (compare Tables 3 & 4 and Tables 5 & 6). In addition, there were several cases when significant correlations with habitat parameter revealed relationships with disturbance history that had remained undetected in the ANOVAs (see Tables 3 & 5).

### Disturbance history effects on habitat parameters and indirect effects on stream biota

Values for the studied habitat parameters differed between the three disturbance history categories in 6% of 81 cases analysed (9 parameters x 9 dates) in the Schmiedlaine and in 22% of 18 cases (9 parameters x 2 dates) in the Kye Burn. These differences may indicate that disturbance history influenced certain habitat parameters, although the reverse relationship cannot be ruled out (see Discussion).

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 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), and the surface area of the sampled stones was larger in stable (929 ± 84 $cm^2$) than in scour patches (194 ± 34 $cm^2$) on 25 June (p=0.04).

One or two of these habitat parameters were, in turn, correlated with the distributions of coccoid epilithic bacteria and all three sediment bacteria parameters on 22 May (water depth) and all three epilithic bacteria parameters on 25 June (substratum size and stone surface area; see Table 4). Consequently, the correlations of the habitat parameters with bacterial densities in these seven cases (13% of 54 possible cases) can be seen as *indirect* effects of disturbance history on these stream biota. Note that the three epilithic bacteria parameters were also influenced directly by disturbance history on 25 June (see Table 3).

In the Kye Burn on 11 December, the water was deeper in fill than in stable patches (40 ± 2 versus 28 ± 4 cm; p=0.09), substratum size was twice as large in stable than in scour patches (63 ± 13 versus 34 ± 7 mm; p=0.06), and standing stock of POM was higher in stable (3.8 ± 1.1 $g{\cdot}m^{-2}$) than in fill patches (0.8 ± 0.3 $g{\cdot}m^{-2}$; p=0.08). Water depth and POM also influenced the distributions of total and rod-shaped epilithic bacteria on this date (Table 6), resulting in two indirect effects of disturbance history on stream bacteria. Both bacterial parameters were also influenced directly by disturbance history (Table 5).

On 27 December, near-bed current velocity was three times faster in fill than in scour patches (11 ± 5 versus 33 ± 7 $cm{\cdot}s^{-1}$; $P = 0.04$). This parameter was correlated with the distribution of total sediment bacteria on this date (Table 6). Altogether, bacteria were thus influenced indirectly by disturbance history in three cases (21% of 38 possible cases) in the Kye Burn.

## Discussion

Our first objective was to investigate short- and long-term relationships of local disturbance history to the microdistributions of stream bacteria and their secondary production. We found convincing evidence for such relationships. Bacterial densities differed significantly between patch history types on five of nine patch-specific sampling dates in the Schmiedlaine and one of two such sampling dates in the Kye Burn. Further, disturbance history was related to bacterial microdistribution at least as often as any of the nine studied habitat parameters (except for stone surface area in the Schmiedlaine). History was related to bacterial distributions directly and indirectly (via effects on habitat parameters) and significant habitat parameter correlations revealed previously undetected relationships with history in several cases, indicating a strong interaction between disturbance history and the better-explored habitat parameters. To our knowledge, this is the first study documenting that disturbance history can influence benthic stream bacteria. In the only related study known to us (Fischer et al. 2003), the movement speed of different layers of sand affected bacterial activity in a moving sand dune in a German lowland river, with activity being higher in the faster-moving upper layer than in the slower-moving deeper layer. Our study is also one of the first to investigate the influence of local habitat parameters on benthic stream bacteria.

Based on our previous results for stream invertebrates (Matthaei et al. 2000; Matthaei and Townsend 2000) and river algae (Matthaei et al. 2003), we expected stable bed patches to act as refugia for benthic bacteria during the high-flow events. With increasing time since each event, however, bacterial densities might become highest in areas of scour or fill, rather than in stable patches, as did invertebrate and algal densities in our earlier research. These expectations were only partly supported by our data.

Epilithic bacteria were most abundant in stable bed patches on 25 June, shortly after the largest flood in the Schmiedlaine. Rod-shaped sediment bacteria were more common in stable than in fill patches on this date and also on 11 September, shortly after the second-largest flood. By contrast, bacterial densities were similar across all three patch types after the first of the two smaller high-flow events in this stream, and higher in fill than in scour patches after the second smaller event. In the Kye Burn, densities of total epilithic, coccoid epilithic and total sediment bacteria were highest in fill patches shortly after another relatively small event on 5-6 December, and bacterial production was similar across all patch types. Consequently, stable bed patches apparently served as refugia for benthic bacteria during two large floods but not during three smaller high-flow events. This result cannot be readily explained by the magnitudes of these five events, because two of the smaller events (Event 2 in the

Schmiedlaine and Event 1 in the Kye Burn) reduced overall bacterial densities significantly but did not result in a refugium effect of stable bed patches. In the Kye Burn, stable surface stones served as refugia for invertebrates during another smaller event (Matthaei et al. 2000). The results of this earlier study suggested that benthic invertebrates (which are mostly highly mobile) may actively seek out stable stones during smaller high-flow events, when surface refugia are abundant (see Matthaei et al. 1999a, 1999b). This option is not available to the sessile bacteria, a difference which may explain why there was no refugium effect of stable bed patches for these organisms during the smaller event in the Kye Burn.

We now turn our attention to the long-term influence of disturbance history on bacterial distributions. Densities of epilithic bacteria were generally highest in fill patches on 9 October, four weeks after Event 4 in the Schmiedlaine. However, only densities of rod-shaped epilithic bacteria were actually higher than in stable patches, as we had observed for benthic invertebrates and algae (Matthaei and Townsend 2000; Matthaei et al. 2003). Small cocci are usually the dominant component of bacterial communities in oligotrophic aquatic environments (Rheinheimer 1985) but rods and other larger bacteria are generally more active. Thus, cultured bacteria that undergo nutrient starvation and pass into dormancy become small cocci whereas during recovery from dormancy and starvation they develop into larger cells, especially rods, but also other forms such as vibrios, or large cocci (e.g. Amy and Morita 1983; Amy et al. 1983). In natural environments too, such as groundwater habitat close to the surface, it was mainly rods and larger bacteria that were active (respiring) whereas little respiratory activity could be detected among small cocci (Marxsen 1988a). Therefore, the increased densities of rod-shaped bacteria can be regarded as indicative of a more active community recovering from disturbance. Moreover, the larger proportion of rods in epilithic than sediment habitats agrees with earlier findings from streams that bacterial biofilm communities on rocks are more active (per substratum surface area) than those in fine grained sediments (Marxsen and Witzel 1991; Marxsen 2001).

Further, bacterial densities were always similar across all three patch types on the remaining four dates when samples were collected at least 17 days after a bed-moving high-flow event. In the Kye Burn, bacterial densities and production were also similar across bed stability types 21 days after Event 1. Thus, disturbance history had fewer, and often different, long-term effects on bacteria than on invertebrates and algae in our previous research. This result can be explained only partly by differences or similarities between the three groups of organisms. Bacteria experience bed-moving disturbance at a different spatial scale than the much larger and mobile invertebrates. They are also capable of population recovery through rapid growth rates (with generations times of less than a day to a few days - Marxsen 1988b; Wetzel 2001) of surviving cells that are always present after a disturbance. In contrast, the much longer-lived invertebrates depend on recolonisation via drift, or from nearby refugia or as a result of oviposition by adults. On the other hand, benthic algae are small, sessile and have short generation times (closer in these characteristics to bacteria) and yet the long-term effects of disturbance history on these algae were different from those on bacteria.

### Recovery of stream bacteria after a purely depositional flood

The complexity of disturbance history patterns and their effects on benthic organisms is illustrated further by the large flood (duration 13 days, return period about five years) which occurred in January 2002 in the Kye Burn, disturbing our entire study site and resulting in substantial net sediment deposition at all 208 scour chain locations. Out of 14 high-flow events investigated in three different rivers using scour chains (Matthaei et al. 1999a; Matthaei et al. 2003; present study), this was the only one to produce such a uniform pattern of bed disturbance. We expected recovery of the benthic bacteria to be very slow after this flood because of the lack of surface refugia and the fact that the uppermost 15-40 cm of the stream bed at our site consisted entirely of newly deposited sediment. In agreement with these expectations, bacterial production in the fine surface sediment was strongly reduced by the flood and had still not reached pre-flood levels more than six weeks after the flood (Fig. 4). However, densities of fine sediment bacteria recovered to pre-flood levels within 17 days, and densities of epilithic bacteria were not even reduced significantly by the flood. The latter result may be mainly due to the fact that epilithic bacteria had been already affected by the first high-flow event in early December 2001. On 27 December, the last sampling date prior to the large flood in January, densities were still quite low in comparison to values on the dates before the first event (Fig. 3). This interpretation is strengthened by the fact that total densities of total and rod-shaped epilithic bacteria hardly increased at all from 25 January to 7 March (Fig. 3). Nevertheless, the sediment bacteria did recover remarkebly fast after the large flood, especially for such a cool and nutrient-poor stream as the Kye Burn. By comparison, Holmes et al. (1998) found that bacterial numbers at the stream-parafluvial interface needed 60 days to recover to pre-flood values after a flash flood in a desert stream, and Marxsen (2001) observed that bacterial production recovered within 30 days after a spring spate in a small German stream. Overall, the above results suggest that even a large flood causing very unusual bed movement patterns does not necessarily lead to a slow recovery of the entire bacterial community.

### Relationships between habitat parameters and bacterial distribution

Our second aim was to investigate the role of physical habitat parameters and potential food resources for the microdistribution of benthic stream bacteria. We found several relationships of these parameters with bacterial distribution in both streams. In the Schmiedlaine, the habitat parameter with the most consistent influence on epilithic bacteria was clearly the surface area of the sampled stones. Large stones tend to be more stable than smaller ones at high flow (Downes et al. 1998; Matthaei et al. 1999b), and this stability of individual particles may have affected bacterial density in all three patch types. We observed a similar effect of stone surface area on the microdistribution of epilithic algae in one of our previous studies (Matthaei et al. 2003). Interestingly, stone surface area was not correlated at all with densities of epilithic bacteria in the Kye Burn. This difference between streams may be linked to the fact that the substratum in the Schmiedlaine is far more heterogeneous than that in the Kye Burn. Therefore, the stability of individual surface particles is likely to differ more markedly in the former than in the latter, and dissimilarities in particle stability within the Kye Burn may not be substantial enough to affect bacterial densities.

While stone surface area affected the epilithic bacteria, the grain size of the sampled fine sediment influenced the distribution of the sediment bacteria, and substratum size in the Surber samples influenced both groups of bacteria. Water depth, near-bed current velocity were also relevant for bacterial distribution. In addition to these physical parameters, POM and epilithic algal biomass influenced bacterial distribution. Both POM (Sander and Kalff 1993; Ward and Johnson 1996; Findlay and Sobczak 2000) and epilithic algae (Chappell and Goulder 1994; Romaní and Sabater 2000) are important sources of organic carbon for benthic bacteria in running waters. Except for stone surface area (see above) and algal biomass, bacterial distribution in the Kye Burn was related to the same habitat parameters as in the Schmiedlaine.

Altogether, these results imply that the small-scale distribution of benthic bacteria in streams is affected by similar physical and biological habitat parameters as benthic invertebrates (see e.g. Ulfstrand 1967; Barmuta 1989; Peckarsky et al. 1990) or benthic algae (see e.g. Stevenson 1996; Biggs et al. 1998; Passy 2001). In addition to these parameters, the occurrence of hyporheic flow (Findlay 1995; Brunke and Gonser 1997), its velocity (Marxsen 1996) or its direction (upwelling/downwelling; Hendricks 1996) have been found to influence bacterial distributions.

### Disturbance history effects versus habitat parameters effects

Our next objective was to compare the relative contributions of local disturbance history, physical habitat parameters and potential food resources to bacterial microdistribution. Based on the results of our previous study for benthic algae (Matthaei et al. 2003), we expected disturbance history to be one of the most important parameters. This expectation was supported. In the Schmiedlaine, only stone surface area was related to bacterial distribution more often than disturbance history. In the Kye Burn, local disturbance history was the parameter with the most consistent influence on bacteria, followed by water depth and grain size of fine sediment.

None of the observed relationships of disturbance history with bacterial densities could be explained by a correlation of one of the habitat parameters with the bacteria, and significant correlations with habitat parameters revealed previously undetected history effects in several cases. These results suggest that local disturbance history is an additional, and previously unknown, parameter influencing the microdistribution of benthic bacteria. One might argue that our chosen statistical analysis caused inflated effect frequencies for disturbance history relative to those for the eight habitat parameters, because up to eight ANCOVAs that included the factor disturbance history were calculated for each dependent variable on each sampling date, whereas only a single ANCOVA was calculated for each of the nine covariates (see Methods). However, our main reason for including the habitat parameters in our analysis was to find out if ‘apparent’ relationships between disturbance history and bacterial distributions were actually caused by correlations between certain habitat parameters and bacterial densities (as we had determined for one of the 11 disturbance history effects on benthic algae found in Matthaei et al. (2003)). Consequently, the likelihood that a significant disturbance history effect would remain 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 ANCOVAs for a single factor. As a further safeguard, we only considered disturbance history effect as valid that were detected in at least 50% of all ANCOVAs with significant covariate effects (or in the ANOVA, if none of the covariates had a significant correlation with the dependent variable). Therefore, we believe that our chosen analysis is reliable, and that the above interpretation of our results is justified.

### Direct versus indirect effects and concluding remarks

Our final objective was to determine if disturbance history contributed to the small-scale patchiness of physical habitat parameters and food resources for the benthic bacteria, and whether such relationships with habitat parameters caused indirect effects of disturbance history on bacterial distribution.

We found that the values for certain habitat parameters differed between the three disturbance history categories. Theoretically, this result could mean that these habitat parameters influenced the small-scale patterns of bed stability. However, our previous scour chain research in the Kye Burn (Matthaei et al. 1999a) had shown that the spatial mosaic of scour, fill and stable patches was largely independent of habitat parameters such as water depth and substratum size. Consequently, we believe that it is more likely that disturbance history influenced the habitat parameters in our present study than vice versa.

In the Schmiedlaine, disturbance history affected water depth, substratum size in Surber samples and the surface area of the sampled stones on some of the sampling dates, although altogether less often than disturbance history affected the bacteria themselves. In the Kye Burn, the relative frequencies of history relationships with habitat parameters (water depth, substratum size, POM, and near-bed velocity) and bacteria were quite similar. The influence of disturbance history on these habitat parameters led to several indirect effects of disturbance history on bacterial distribution in both streams. Consequently, habitat parameters and disturbance history interacted with each other when influencing bacterial distributions. In earlier research on benthic river algae (Matthaei *et al.*, 2003), by contrast, disturbance history and habitat parameters had been largely independent of each other.

Matthaei and Townsend (2000) speculated that indirect effects of disturbance history on physical habitat parameters and food resources of benthic organisms are more likely to be responsible for long-term differences (several weeks after disturbance) in densities between patch history types. Our present results provide little support for this idea, at least not for bacteria and the 8 studied habitat parameters, because 9 out of 10 indirect effects of disturbance history (data from both streams combined) were found within 7 days after disturbance.

The habitat parameters investigated in the present research represent most of the factors known to influence microdistributions of stream organisms, except for competition and predation. A challenge for future researchers is to include biotic factors in disturbance history studies, and to investigate the interplay between abiotic and biotic factors in determining the patchy distributions of organisms in running waters.

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# Local disturbance history, habitat parameters and the microdistributions of stream algae and primary production

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## Summary

1. We investigated the relationships between local disturbance history and habitat parameters (abiotic and biotic) and the microdistribution of benthic algae and their primary production during several high-flow events in two streams, the Schmiedlaine in Germany (four events) and the Kye Burn in New Zealand (two events).
2. Bed movement patterns were quantified using metal-link scour chains. Before and after each event, algal samples were collected from surface stones in replicate patches that experienced scour, fill or remained stable. Primary production in each sampled patch was measured under controlled conditions in the laboratory. Algal biomass and cell densities were determined per substratum area.
3. Patterns of algal densities in the different bed stability types varied considerably between high-flow events, sampling dates and streams, but densities were highest in stable patches and fill patches somewhat more often than in scour patches. Stable bed patches acted as refugia for benthic algae during the two largest floods in the Schmiedlaine.
4. In the Schmiedlaine, disturbance history played a significant role in determining algal distribution, although substratum characteristics, surface area of the sampled stone and near-bed current velocity influenced algal distribution even more often. In the Kye Burn, the surface area of the sampled stones and water depth had the strongest influence on algal distribution, disturbance history was relatively unimportant.
5. A thorough understanding of the microdistribution of benthic algae requires knowledge of disturbance history, as well as more readily measured habitat parameters such as substratum size, current velocity or water depth.

## Introduction

The patchy distribution of organisms in space and time is a pervading feature of natural ecosystems. Consequently, the identification of factors that cause this patchiness is a central concern of ecology in general (Pickett & White, 1985) and stream ecology in particular (Townsend, 1989; Downes, 1990; Poff & Ward, 1990; Townsend & Hildrew, 1994).

It is well known that the small-scale distributions of both benthic invertebrates and algae in streams are influenced by abiotic factors, including shear stress, water depth and substratum size, and by biotic factors including predation, competition and food (see for example Peckarsky *et al*., 1990; Hearnden & Pearson, 1991; Kohler, 1992; Holomuzki & Messier, 1993; Ruse, 1994; Stevenson, 1996; Biggs, Stevenson & Lowe, 1998; Passy, 2001). By contrast, the role of hydrological disturbance in generating patchy distributions is less well understood, probably because of the difficulty of mapping the local effects of specific spates and floods. To address this deficiency, Matthaei *et al.* (1999a) used arrays of buried scour chains to investigate the three-dimensional bed movement patterns in the Kye Burn, a New Zealand stream, and found that most high-flow events caused a complex mosaic of small ($\leq 1$ $m^2$) bed patches that had experienced scour, sediment deposition (fill) or remained undisturbed. This ’local disturbance history’ (Matthaei & Townsend, 2000) had long-term effects on the microdistribution of macroinvertebrates, with higher densities in fill or scour patches two months after a disturbance (Matthaei & Townsend, 2000).

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, but in fill patches three months after another flood. Although the response of benthic algae to physical disturbance during high-flow events has been investigated in numerous studies (see reviews or conceptual models by Fisher, 1990; Steinman & McIntire, 1990; Mulholland *et al*., 1991; Peterson, 1996; Biggs *et al*., 1998), the effect of small-scale patchiness in bed movements on benthic algae had not been addressed prior to the study of Matthaei et al. (2003), especially the distinction between scoured and depositional bed patches.

While clearly showing that disturbance history can affect benthic organisms, the first disturbance history studies also had certain limitations. Thus, invertebrates were sampled only once after a single high-flow event in 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 three 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. Furthermore, the effects of disturbance history on important ecosystem processes, for example primary production, were not examined.

The objectives of the present research were to investigate

(1) short- and long-term effects of disturbance history on the microdistributions of stream algae and their primary production during several high-flow events,

(2) the relative contributions of disturbance history, physical habitat parameters and food resources to algal distribution, and

(3) effects of disturbance history on the habitat parameters (which could cause indirect effects of disturbance history on algal distribution).

## Materials and methods

### Study sites

We investigated 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). Thus, this study, whose logistics would have taken two years to undertake in a single hemisphere, was completed in a single year. However, our study was not designed to compare Northern and Southern Hemisphere stream ecology. Detailed descriptions of both study streams are given in Matthaei *et al.* (1999a) and Matthaei & Huber (2002). In each stream, we selected a single study site of about 40 m length.

The Schmiedlaine has a steep, predominantly forested catchment (altitude 750-1800 m a.s.l.) that lies in a high rainfall zone at the northern edge of the Alps (annual rainfall 1500-2150 mm; Felix *et al.*, 1988). Consequently, 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). Annual rainfall in the tussock grassland catchment of the Kye Burn (altitude 600-1600 m a.s.l.) is only 600-1000 mm (Otago Catchment Board, 1983), and the relief is not quite as steep as in the catchment of the Schmiedlaine. Therefore, 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, unpublished data). Both streams are 5-10 m wide at baseflow, the flow regimes and stream channels are natural, the water is cold (<13°C in summer in the Schmiedlaine and <16°C in the Kye Burn; G. Sailer, unpublished data) and nutrient-poor (Water Management Authority Weilheim, unpublished data; Niyogi, Simon & Townsend, 2003). The stream beds consist mainly of cobbles (particle width 64-256 mm; Schmiedlaine) or cobbles and gravels (2-64 mm; Kye Burn) interspersed with boulders (256-1024 mm), the latter especially in the Schmiedlaine. The Schmiedlaine runs through a narrow, v-shaped valley; the studied reach of the Kye Burn is located in a small, steep canyon. Sediment supply to the two streams is high because of the presence of several steep, unstable scree slopes in both catchments, resulting in unstable stream beds that are easily moved by floods.

### Quantification of bed movement

Bed movement patterns were quantified using metal-link scour chains (Matthaei *et al.*, 1999a). The chains (each about 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 links exposed. Scour during a high-flow event exposes additional chain links, whereas fill can be measured by the thickness of the sediment layer deposited on top of the originally exposed links (for more details see 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 about 1 m between chains and transects. Most transects contained five chains. The exact location of each chain in the stream bed was determined by measuring distances to three pairs of permanently-marked points on the banks that were situated at least 1.5 m above the water line. All chains were equipped with magnetic tracers (Ergenzinger & Conrady, 1982) to facilitate re-location with a magnetic locator (model GA-52B, Schonstedt, Virginia) after high-flow events. In addition, we used a theodolite (Tachymeter SET 3, Sokkisha/SOKKIA, Tokio; leveling unit Ni 2, Zeiss, Jena) to measure the positions of all chains relative to another permanently marked point on the true left bank (2 m above the water line) on 16 May. These measurements ensured that, in case of a very large flood, we would still be able to determine net changes for chain locations which might experience 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 (see Table 1), and finally 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 this would not be necessary (Matthaei *et al*., 1999a; Matthaei & Townsend, 2000).

### Studied high-flow events and biological sampling

We investigated all bed-moving high-flow events that occurred during a six-month period in each stream, four in the Schmiedlaine and two in the Kye Burn. Whenever possible, samples were taken before and three times after each event (shortly after, about 2-3 weeks after, and about one month after; see Table 1 for exact sampling dates).

Our focus was on densities of epilithic algae and their primary production. However, we also determined the densities of epilithic bacteria (Sailer *et al.*, submitted, see Publication 1) for use as a covariate in our analysis (see Publication 1). A parallel study (Effenberger *et al.*, submitted, see Publication 3) investigated densities of benthic invertebrates and standing stocks of particulate organic matter (POM) using a Surber sampler (area 0.0625 m², mesh size 200 µm). These two parameters were used as additional covariates in our analysis. The Surber samples also served as sampling units in the present study. On sampling dates before a high-flow event, we collected eight pre-disturbance samples randomly because did not know the local disturbance history patterns caused by the previous (unstudied) flood. On each post-disturbance 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 patch, a Surber sample was taken in the immediate vicinity of the focal chain (with at least one side of the frame of the sampler touching the chain). A marked screwdriver fixed a sampling depth of 10 cm. Densities of algal biomass and epilithic bacteria 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 algae and bacteria 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%) in the field and stored on ice in the dark. A second surface stone was used to determine epilithic primary production in the laboratory (see below). These stones were transported in separate 5-litre buckets filled with stream water and transferred into individual production chambers directly after arrival in the laboratory.

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

**Schmiedlaine.** We started biological sampling on 9 May 2001, four days after completing chain installation. The installation causes little damage to the sediment structure within the stream bed (Matthaei *et al.*, 1999a) and, based on field observations during a scour chain study in another prealpine river (Matthaei *et al.*, 2003), we expected epilithic algae and bacteria to recover quickly from the disturbance caused by chain installation.

On 9 and 15 May, we collected pre-disturbance samples in our study reach. In the evening of 15 May, a brief high-flow event occurred (Event 1; see Table 1). This event had a moderate peak discharge and brought about a patchy mosaic of predominantly shallow fill (range 2-15 cm, mostly < 10 cm), some shallow scour (2-10 cm), and 30% stable patches (Table 2). Post-disturbance sampling (as described above) started seven days after Event 1 and continued 14 days later on 5 June. On this day, we took five random samples in addition to the samples from fill and stable patches because no patches with ≥ 5 cm of scour were left. Four days later, this sampling phase was truncated by Event 2, another moderate event that left more than half of the chains undisturbed, caused shallow scour at one third of the chains (range 2-16 cm, mostly < 10 cm), and also some shallow fill (range 2-9 cm).

Post-disturbance sampling after Event 2 was possible only once because Event 3, the largest flood recorded during our field work in the Schmiedlaine, occurred seven days later (Table 1). This flood deposited up to 40 cm of sediment at the majority of chain locations, caused scour of up to 30 cm at almost one third of the chains and also left some stable patches (Table 2). For this event, 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 with a peak flow of ≈ 6 $m^3 s^{-1}$ occurred on 20-21 July. However, this spate caused shallow scour or fill at only a few chain locations, which we avoided on the third sampling date. No further bed movements occurred from 21 July to 5 September.

After completing the post-flood series for Event 3, we ran out of stable bed patches to sample. Therefore, we returned to taking random samples on 14 and 30 August. Six days after the latter date another sizeable flood which had two separate flow peaks on 5-6 and 8-9 September occurred (Event 4, Table 1). This event caused scour of up to 45 cm at 38% of the chains. It also resulted in fill (up to 22 cm, but mainly around 10 cm) at 28% of the chains and left about one third of the chains undisturbed (Table 2). Post-flood sampling started two days after Event 4 and continued on 26 September. Between these two sampling dates, another brief flow peak of ≈ 6.5 $m^3 s^{-1}$ occurred on 15 September. However, data from 30 randomly chosen chains relocated on 26 September indicated that this spate caused hardly any bed movement. A final field day on 9 October completed a second series of two pre- and three post-flood sampling dates.

**Kye Burn.** The first of the two high-flow events occurred on 5-6 December 2001, about four weeks after chain installation was completed (Table 1). This moderate event caused fill (2-20 cm, but mostly ≤ 10 cm) at 62% of the chain locations, some shallow scour at 12% of all chains (mostly around 5 cm, maximum 11 cm), and left 26% of the chains undisturbed (Table 2). Before Event 1, we had taken three weekly sets of random pre-disturbance samples. After the event, we collected two sets of post-disturbance samples.

On the day we intended to take a third set of post-disturbance samples, a major flood began that lasted from 9-21 January 2002 (with four distinct flow peaks) and had a return period of about five years (Tables 1 & 2). This caused sediment deposition (of up to at least 39 cm) at all 208 chain locations, with more than 20 cm of fill at the majority of locations. Patches that experienced net scour, or stable patches, did not exist. Because we expected algal recovery to be very slow after this rare and unusual flood, we collected four sets of eight post-flood samples chosen randomly from fill patches to monitor recovery (see Table 1). No further bed movements occurred until the end of this second sampling series.

**Table 1.** Bed-moving high-flow events and sampling occasions in the **Schmiedlaine** (May to October 2001) and in the **Kye Burn** (November 2001 to March 2002).

| | 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 | 3 x 5 |
| | | 5 June | After Event 1 (=Before Event 2) | Fill, Stable, Random | 3 x 5 |
| | **Event 2 (10 / 11 June)** | | | | |
| | | 13 June | After Event 2 (=Before Event 3) | Scour, Fill, Stable | 3 x 5 |
| | **Event 3 (18 - 20 June)** | | | | |
| | | 25 June | After Event 3 | Scour, Fill, Stable | 3 x 5 |
| | | 11 July | After Event 3 | Scour, Fill, Stable | 3 x 5 |
| | | 24 July | After Event 3 | Scour, Fill, Stable | 3 x 5 |
| | | 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 | 3 x 5 |
| | | 26 September | After Event 4 | Scour, Fill, Stable | 3 x 5 |
| | | 9 October | After Event 4 | Scour, Fill, Stable | 3 x 5 |
| **Kye Burn** | | 21 November | Before Event 1 | Random | 8 |
| | | 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 | 3 x 5 |
| | | 27 December | After Event 1 (=Before Event 2) | Scour, Fill, Stable | 3 x 5 |
| | **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 |

### Sample processing and primary production measurements

We collected 167 samples of algal abundance in the Schmiedlaine, and 86 in the Kye Burn. We were unable to measure primary production accurately on the first three sampling dates in each stream due to problems with the equipment. Ten percent of the POM samples from the Schmiedlaine were lost during processing (13 June: 3 replicates from each patch type; 25 June: 2 from each type; 9 October: 1 from each type). Each surface stone sample was divided into four equal subsamples in the laboratory. Three quarters were used to determine quantitative counts of algal cells, algal biomass as chlorophyll a, and biomass of the epilithic biofilm as ash free dry mass (AFDM). The AFDM data were excluded from the statistical analysis because biofilm biomass in both streams was often too small to obtain reliable results with this method. The remaining quarter was used for quantitative counts of bacteria in a related study (Sailer *et al.*, submitted, see Publication 1). The surface area of each stone was determined by wrapping stones in aluminum foil and weighing the foil (Townsend *et al.*, 1997), and algal counts were converted to densities per $cm^2$ of stone surface area. Further, stone surface area was used as a covariate in our analysis, because this parameter influenced densities of epilithic algae in a previous study (Matthaei *et al*., 2003).

Algal cells were counted in a nanoplankton counting chamber (Neubauer 'improved', volume 0.9µl; VWR International, Darmstadt, Germany) at a magnification of 400x under a Leitz Laborlux K microscope. Cox (1996) and Dillard (1999), keys to identify algae from live or formalin-preserved material, were used to make a list of the common genera. The genera *Amphora* spp., *Cymbella* spp. and *Encyonema* spp. were combined into a single taxon because the keys did not allow us to distinguish reliably between them. For each sample, 5-20 random subsamples of 0.1 µl each were counted, adding up to a total of at least 400 algal cells (Schwoerbel, 1994). In the Schmiedlaine, we found a total of 26 algal taxa and analysed taxon-specific density patterns for the 12 taxa that occurred regularly in the samples. The corresponding figures for the Kye Burn were 24 and 12 algal taxa. The analysed taxa represented 99% of the total number of algal cells found in all samples in each stream.

Primary production and respiration of epilithic biofilms were measured in transparent respiration chambers made from acrylic glass (dimensions 40 cm x 18 cm x 13.5 cm, volume = 8 L). Each chamber was equipped with a pump to circulate the water (Universal 1060, capacity 38 l/min, Eheim GmbH, Deizisau, Germany) and an oxygen probe with a thermistor. This probe was fitted to an oxygen meter (Oxi 340, WTW, Weilheim, Germany) with the capacity to log oxygen concentration and temperature data. Fifteen chambers (five for each bed stability category) were deployed in a climate chamber at a temperature of 16 °C.

One day after each sampling date, each chamber was loaded with one stone and filled with stream water from the study site. For each chamber run in the Schmiedlaine, we applied the following light-dark regime (in $\mu E\ m^{-2}\ sec^{-1}$): 0 (darkness), 49.2, 71.1, 107.1, 228.3, and once again 0. In the Kye Burn, the corresponding figures were 0, 51.3, 73.3, 102.2, 157.9 and 0 $\mu E\ m^{-2}\ sec^{-1}$. Each dark and light period lasted 100 minutes. Temperature (T) and dissolved oxygen ($O_2$) were recorded twice per minute. Average net oxygen production rates ($\beta$) during each light or dark period were obtained by linear regressions of $O_2$-concentration against time. Because chamber temperatures increased during the incubations (on average from 11 to 25°C), $\beta$ was normalized on 20°C using the equation $\beta(20°C) = \beta(T)/1.072^{(T-20°C)}$ for oxygen saturation of water at an air pressure of 712.1 mm Hg. In this equation, $\beta$ is the net oxygen production rate (mg $O_2L^{-1}h^{-1}$) and T the average chamber temperature during a light or dark period (Uehlinger *et al.*, 2000).

Calculations of the metabolic parameters respiration and gross primary production rates (gpp) were based on $\beta(20°C)$. Dark respiration ($r_D$) was calculated by averaging $\beta(20°C)$ of the two dark periods. Respiration rates during the light periods ($r_L$) were assumed to equal $r_D$., GPP was computed as mean of all light intensities ($R_L$) and the corresponding $\beta(20°C)$, the ratio of P/R as GPP/$R_L$. Rates of gross primary production and dark respiration were normalized on stone surface area. Algal biomass and stone volume were determined at the conclusion of each metabolism run.

**Table 2.** Event magnitudes and percentages of scoured, depositional and stable bed patches caused by four high-flow events in the **Schmiedlaine** and two events in the **Kye Burn**.

| | **Schmiedlaine** | | | | **Kye Burn** | |
|---|---|---|---|---|---|---|
| | **Event 1** | **Event 2** | **Event 3** | **Event 4** | **Event 1** | **Event 2** |
| **Peak flow** [$m^3/s$] | 7.5 | 9.5 | 25 | 14.5 | 4.7 | 20.7 |
| **Duration** [days] | < 1 | 1-2 | 2-3 | 3-4 | ~ 1 | ~ 12 |
| **Return period** [years] | ≤ 0,5 | 0.5-0.75 | 2-3 | 1 | ~ 0.4 | ~ 5 |
| **Bed movements** [% of all chains]**:** | | | | | | |
| **fill** | 63 | 19 | 61 | 27 | 62 | 100 |
| **stable** | 30 | 51 | 11 | 34 | 26 | 0 |
| **scour** | 7 | 31 | 28 | 39 | 12 | 0 |

## Data analysis

To determine the overall initial effect of each high-flow event on the algal community, we compared the last pre-disturbance sampling date with the first post-disturbance date, using one-way analysis of variance (ANOVA). For this analysis, all three disturbance history categories on the first post-disturbance date were combined. Comparisons between disturbance history categories were conducted using one-way ANOVAs and one-way analysis of covariance (ANCOVA), with ‘patch type’ as factor and the studied habitat parameters as covariates. Exploratory correlation matrices (all samples combined in each stream) had shown that none of the seven covariates were strongly correlated with each other. Values for $r_p$ were $< 0.40$ in most cases and the highest $r_p$-value was 0.61, well below the threshold of 0.8 for strong collinearity (see Lewis-Beck, 1980).

Dependent variables were total density of epilithic algae, algal taxon richness, living algal biomass (Chl a), periphyton vitality (living / total algal cells), ratio of Chl a to phaeophytin (Peterson, Hoagland & Stevenson, 1990), gross primary production (GPP), ratio of primary production to respiration (P / R), and the densities of each common algal taxon. ANCOVAs with the habitat parameter 'total bacterial density' were not calculated for the primary production parameters because the latter had been measured using a different surface stone (see above). Direct effects of disturbance history on the 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 algae (Matthaei *et al.*, 2003), we expected the effects of disturbance history change strongly with time since the last previous disturbance. 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 x covariate interaction was found, we verified the reliability of the estimated marginal means for each patch type, and all ANCOVAs with unreliable results were excluded (see Table 3). This reliability test was performed by comparing the actual adjusted means for each patch type (determined using the individual regression lines of the dependent variable against the covariate) with the estimated marginal means calculated by the ANCOVA (see Matthaei & Huber, 2002).

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 variable and sampling date, so there was no need to adjust α (Rice, 1989). Because of 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. 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 which do not assume equal variances between groups (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). Here we selected the ranking that had been determined in the majority of these tests.

All analyses were calculated in SPSS® version 11.0 (SPSS Inc., Chicago). For graphical illustration of the results, the unadjusted means were used instead of the estimated marginal means calculated in the ANCOVAs because none of the covariates consistently had a significant effect on the dependent variables (see Tables 4 & 6). All differences between patch types summarized in the Results section were significant (unless stated otherwise in the text).

## Results

### Summary of disturbance history and habitat parameter effects

In the Schmiedlaine, we analysed patch-specific patterns of algal densities for the nine post-disturbance sampling dates. A total of 166 cases was analysed for the factor disturbance history with seven covariates (9 sampling dates x 19 dependent variables minus two cases of missing primary production variables and three cases where *Diatoma* spp. (25 June and 11 September) or *Fragilaria* spp. (25 June) were absent). The covariate total epilithic bacteria was not relevant for the two primary production variables in both streams because the latter had been measured using a different surface stone (see Methods). Substratum size in the Surber samples was related to algal microdistribution in the stream bed most often (in 25% of all analysed cases), followed by the surface area of the sampled stone (21%), near-bed current velocity (20%), local disturbance history (18%), epilithic bacteria, total invertebrates and POM (13% each), and water depth (11%).

In the Kye Burn, analyses of patch-specific patterns of all variables were possible only for the two sampling dates after Event 1. A total of 38 cases was analysed (2 sampling dates x 19 dependent variables). Stone surface area was related to algal microdistribution most often (in 32% of all analysed cases), followed by water depth (24%), near-bed current velocity, POM and substratum size in the Surber samples (all 16% each), epilithic bacteria and total invertebrates (11% each), and local disturbance history (5%).

**Specific relationships of algae with disturbance history and habitat parameters**

**Schmiedlaine.** Total algal density (all patch types combined) was reduced by Event 4 (P=0.002) in comparison to the respective pre-disturbance densities (Fig. 1). Algal density was higher in random than in stable patches on 5 June (after Event 1; Table 3), in fill than in scour patches on 11 July (after Event 2), and in stable than in scour or fill patches on 11 September (shortly after Event 4). Algal density was correlated with all covariates on at least one sampling date each (Table 4). Water depth, substratum size in Surber samples and stone surface area showed the highest numbers of significant correlations.

Algal taxon richness was reduced by Event 3 (P<0.0001) and Event 4 (P=0.002). Taxon richness was greater in fill than in stable patches on 22 May (Table 3), in random than in fill patches on 5 June, in stable than in fill patches on 25 June, in fill than in scour patches on 11 July and in stable than in fill patches on 9 October. Taxon richness was correlated with most of the covariates at least once (except for water depth and total invertebrate density; Table 4). Substratum size in Surber samples had the highest number of significant correlations.

Living algal biomass (measured as Chl *a*) was also reduced by Event 3 (*P*<0.0001) and Event 4 (*P*=0.009). Algal biomass never differed significantly between the three patch types (Table 3) and was correlated with all covariates at least once, except for water depth (Table 4). Near-bed current velocity had the highest number of significant correlations.

Periphyton vitality (living / total algal cells; Fig. 2) was generally high and did not decrease after any of the high-flow events (*P*>0.74). Vitality was higher in scour than in stable patches on 24 July (Table 3) and was correlated with all covariates on at least one sampling date each, except for POM and bacterial density (Table 4). Near-bed current velocity and stone surface area showed the highest number of correlations with vitality.

The ratio of Chl a to phaeophytin was quite low on most sampling dates. This ratio was reduced by Event 1 (*P*<0.0001) and Event 3 (*P*=0.04) but was always similar across patch types (Table 3). Chl a / phaeophytin was correlated with near-bed velocity and stone surface area on at least one sampling date each (Table 4).

Gross primary production was reduced by Event 2 (*P*=0.001; Fig. 2), as was the ratio of primary production to respiration (P/R; *P*=0.004). Primary production and P/R were always similar across patch types. Gross primary production was correlated with all covariates once or twice, except for total invertebrates and epilithic bacteria (Table 4). P/R was correlated with water depth, substratum size in Surber samples, stone surface area and POM (Table 4). Substratum size showed the highest number of significant correlations with P/R.

Densities of the common algal genera were generally reduced by only one of the four high-flow events, and some taxa were reduced by none of the events. *Achnanthes* spp. was reduced by Event 4 ($P$=0.01) and was more common in scour than in fill patches on 25 June (Fig 3; Table 3). *Achnanthes* density was correlated with all covariates at least once, except for water depth and total invertebrates (Table 4). Substratum size in Surber samples showed the highest number of significant correlations.

*Cocconeis* spp. showed a higher density in stable than in fill patches on 9 October (Table 3) and was correlated with all covariates on one or two sampling dates each, except for water depth (Table 4).

*Cymbella/Encyonema/Amphora* spp. were reduced by Event 4 ($P$<0.001) and were more abundant in fill than in scour patches on 11 July. This taxon-group was correlated with all covariates once or twice, except for near-bed velocity (Table 4).

*Fragilaria* spp. was reduced by Event 4 ($P$=0.01) and was more common in fill than in scour patches on 22 May, in random than in stable patches on 5 June, and in stable than in disturbed patches on 11 July (Table 3). *Fragilaria* was correlated with every covariate on one sampling date each, except for near-bed velocity and epilithic bacteria (Table 4).

*Gomphonema* spp. and *Meridion* spp. were both reduced by Event 4 ($P$=0.01 and <0.001, respectively). *Gomphonema* was more common in stable than in disturbed patches on 25 June (Table 3). Density of *Gomphonema* was correlated with all covariates at least once, except for water depth (Table 4). Substratum size in Surber samples showed the highest number of significant (and mainly negative) correlations. *Meridion* density was greater in scour than in stable patches on 11 July and in fill than in scour patches on 26 September (Table 3). *Meridion* was correlated with all covariates on one or two sampling dates each, except for stone surface area (Table 4).

*Navicula* spp. was in two of three cases less abundant in scour than in stable or fill patches on 11 July (Fig. 4; Table 3). Density of this taxon was correlated with every covariate at least once (Table 4).

*Nitzschia* spp. was more common in fill than in scour (or stable) patches on 11 July and on 11 September, and in stable than in scour patches on 26 September (Table 3). This taxon was correlated with all covariates once or twice each, except for substratum size (Table 4).

Filamentous Cyanophyta were reduced by Event 4 ($P$=0.04), more abundant in random than in stable patches on 5 June, and less abundant in scour than in fill or stable patches on 11 July (Table 3). This taxon was correlated with all covariates at least once, except for epilithic bacteria (Table 4). Substratum size (in Surber samples) showed the highest number of significant correlations.

Density of coccoid Cyanophyta was reduced by Event 2 ($P$=0.03), was higher in fill than in scour patches on 11 July, in stable than in scour patches on 11 September, in scour than in stable patches on 26 September, and in fill than in scour patches on 9 October (Table 3). Coccoid Cyanophyta were correlated with all covariates on one to three sampling dates each (Table 4).

Density of filamentous Chlorophyta was higher in random than in stable or fill patches on 5 June (Table 3). Filamentous Chlorophyta were correlated with all covariates on one to three dates each, except for POM, total invertebrates and epilithic bacteria (Table 4).

Non-filamentous Chlorophyta were more common in scour than in fill or stable patches on 13 June, in fill than in scour patches on 11 July and in stable than in scour patches on 11 September (Table 3). Non-filamentous Chlorophyta were correlated with all covariates at least once, except for substratum size (Table 4). The surface area of the sampled stone showed the highest number of significant correlations.

**Table 3.** Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing the algal communities in scour, fill and stable patches in the **Schmiedlaine**. Prior to final analysis, data were log-transformed where necessary and factor x covariate interactions explored (see column 4). Three ANCOVAs with unreliable results due to significant interactions were excluded (see Methods). The significant interactions included in column 4 did not affect the reliability of the respective 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 covariate effects see Table 4). α=0.10; ♦ invalid result (detected in <50% of all ANCOVAs with significant covariate effects).

| Date and dependent variable | Covariate in ANCOVA | Covariate | Inter-action | Factor | Ranking |
|---|---|---|---|---|---|
| **22 May** | | | | | |
| Algal taxon richness | - | - | - | 0.04 | Fill > stable |
| | POM | 0.06 | 0.08 | 0.06 | Fill > stable |
| *Fragilaria.* spp. | - | - | - | 0.09 | Fill > scour |
| **5 June** | | | | | |
| Total algal density | Substratum size | 0.06 | 0.07 | 0.02 | Random > stable |
| Algal taxon richness | POM | 0.03 | 0.24 | 0.05 | Random > fill |
| *Fragilaria.* spp. | - | - | - | 0.08 | Random > stable |
| Filamentous Cyanophyta | - | - | - | 0.097 | Random > stable |
| | Substratum size | 0.05 | 0.53 | 0.08 | Random > stable |
| Filamentous Chlorophyta | Water depth | 0.07 | 0.52 | 0.096 | Random > (stable/fill) |
| **13 June** | | | | | |
| Non-filamentous Chlorophyta | - | - | - | 0.04 | Scour > fill |
| | Epilithic bacteria | 0.01 | 0.02 | 0.07 | Scour > (stable/fill) |
| **25 June** | | | | | |
| Algal taxon richness | - | - | - | 0.095 | Stable > fill |
| | Near-bed velocity | 0.08 | 0.11 | 0.02 | Stable > fill |
| *Achnanthes* spp. | Epilithic bacteria | 0.034 | 0.21 | 0.01 | Scour > fill |
| *Gomphonema* spp. | - | - | - | 0.02 | Stable > (scour/fill) |
| | Stone surface area | <0.001 | 0.42 | <0.001 | Stable > (scour/fill) |
| | Epilithic bacteria | <0.001 | 0.15 | 0.02 | Stable > (scour/fill) |
| **11 July** | | | | | |
| Total algal density | - | - | - | 0.07 | Fill > scour |
| Algal taxon richness | - | - | - | 0.07 | Stable > scour |
| | Substratum size | 0.04 | 0.99 | 0.08 | Fill > scour |
| *Cymbella/Encyonema/Amphora* spp. | - | - | - | 0.09 | Fill > scour |
| | Epilithic bacteria | 0.03 | 0.36 | 0.098 | Fill > scour |
| *Fragilaria.* spp. | - | - | - | <0.001 | Stable > (scour/fill) |
| | Water depth | <0.001 | 0.48 | <0.001 | Stable > (scour/fill) |
| | Total invertebrates | <0.001 | 0.03 | 0.096 | Stable > (scour/fill) |

Table 3 (continued)

| **Date and dependent variable** | **Covariate in ANCOVA** | **Covariate** | **Inter-action** | **Factor** | **Ranking** |
|---|---|---|---|---|---|
| **11 July** (continued) | | | | | |
| *Meridion* spp. | Epilithic bacteria | 0.099 | 0.85 | 0.07 | Scour > stable |
| *Navicula* spp. | - | - | - | 0.05 | Scour > (stable/fill) |
| | Epilithic bacteria | 0.01 | 0.86 | 0.08 | (Stable/fill) > scour |
| | POM | 0.03 | 0.09 | 0.09 | (Stable/fill) > scour |
| *Nitzschia* spp. | - | - | - | 0.08 | Fill > scour |
| | POM | 0.03 | 0.19 | 0.05 | Fill > (scour/stable) |
| Filamentous Cyanophyta | - | - | - | 0.02 | (Stable/fill) > scour |
| | Near-bed velocity | 0.01 | 0.32 | 0.02 | (Stable/fill) > scour |
| Coccoid Cyanophyta | Near-bed velocity | 0.06 | 0.05 | 0.03 | Fill > scour |
| | Total invertebrates | 0.03 | 0.07 | 0.04 | Fill > scour |
| Non-filamentous Chlorophyta | - | - | - | 0.02 | Fill > scour |
| **24 July** | | | | | |
| Periphyton vitality | Substratum size | 0.09 | 0.27 | 0.09 | Scour > stable |
| **11 September** | | | | | |
| Total algal density | Stone surface area ♦ | 0.02 | 0.07 | <0.001 | Stable > (scour/fill) |
| *Nitzschia* spp. | Epilithic bacteria | 0.04 | 0.19 | 0.08 | Fill > (scour/stable) |
| Coccoid Cyanophyta | Stone surface area | 0.06 | 0.55 | <0.001 | Stable > scour |
| Non-filamentous Chlorophyta | - | - | - | 0.04 | Stable > scour |
| | Near-bed velocity | 0.08 | 0.06 | 0.099 | Stable > scour |
| | Stone surface area | 0.02 | 0.02 | 0.08 | Stable > (scour/fill) |
| | Total invertebrates | 0.04 | 0.50 | 0.06 | Stable > scour |
| **26 September** | | | | | |
| *Meridion* spp. | - | - | - | 0.09 | Fill > scour |
| *Nitzschia* spp. | Stone surface area | 0.03 | 0.14 | 0.01 | Stable > scour |
| | Epilithic bacteria | 0.04 | 0.26 | 0.01 | (Stable/fill) > scour |
| Coccoid Cyanophyta | Total invertebrates | 0.06 | 0.45 | 0.01 | Scour > stable |
| **9 October** | | | | | |
| Algal taxon richness | - | - | - | 0.05 | Stable > fill |
| *Cocconeis* spp. | POM | 0.01 | 0.20 | 0.06 | Stable > (scour/fill) |
| | Total invertebrates | 0.06 | 0.80 | 0.06 | Stable > fill |
| Coccoid Cyanophyta | POM ♦ | 0.09 | 0.31 | 0.05 | Fill > scour |

**Table 4.** Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing the algal community in 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. Note that the covariate total epilithic bacteria was not calculated for the dependent variables GPP and P/R (for details see text).

| **Covariate and dependent variable** | **22 May** | **5 June** | **13 June** | **25 June** | **11 July** | **24 July** | **11 Sept** | **26 Sept** | **9 Oct** |
|---|---|---|---|---|---|---|---|---|---|
| **Water depth** | | | | | | | | | |
| Total algal density | * (-) | | | | | * (-) | | | * (-) |
| Periphyton vitality | | | | | | | | | * (-) |
| Gross primary production | no data | | | | * (-) | | | | |
| Primary production / respiration | no data | | | | * (+) | | | | |
| *Cymbella/Encyonema/ Amphora* spp. | | * (-) | | | | | | | * (-) |
| *Fragilaria.* spp. | | | | no data | ** (-) | | | | |
| *Meridion* spp. | | * (-) | | | | | | | |
| *Navicula* spp. | * (-) | | | | | | | | |
| *Nitzschia* spp. | * (-) | | | | | | | | |
| Coccoid Cyanophyta | | | | | | | | | ** (-) |
| Filamentous Cyanophyta | | | | * (+) | | | | | |
| Filamentous Chlorophyta | | * (+) | | | | | | | |
| Non-filamentous Chlorophyta | * (-) | | | | | * (-) | | * (+) | |
| **Near-bed current velocity** | | | | | | | | | |
| Total algal density | | | | | | * (-) | | | |
| Algal taxon richness | | | | * (+) | | | * (+) | | |
| Living algal biomass | | | | ** (+) | * (-) | | * (+) | | |
| Periphyton vitality | * (-) | | | | * (+) | | | * (+) | |
| Chl a / Phaeophytin | | | ** (+) | | | * (+) | | | |
| Gross primary production | no data | | * (+) | | | * (-) | | | |
| Primary production / respiration | no data | * (-) | | | | | * (-) | | * (+) |
| *Achnanthes* spp. | | | | | | | * (+) | | |
| *Cocconeis* spp. | | | | | | * (-) | | | |
| *Gomphonema* spp. | | | | * (+) | | * (-) | | | |
| *Meridion* spp. | | | | | | * (-) | | | |
| *Navicula* spp. | | | | * (+) | | | | | * (+) |
| *Nitzschia* spp. | | | | * (+) | | * (-) | | | |
| Coccoid Cyanophyta | | | * (+) | | * (+) | | | | |
| Filamentous Cyanophyta | | | | * (+) | * (+) | | * (+) | | |
| Filamentous Chlorophyta | | | | | * (+) | | | | |
| Non-filamentous Chlorophyta | | | | | | | * (-) | * (-) | |
| **Substratum size** | | | | | | | | | |
| Total algal density | | * (-) | * (+) | | | | | * (-) | |
| Algal taxon richness | * (+) | | * (+) | | * (+) | | | | * (+) |
| Living algal biomass | | | * (+) | * (+) | | | | | |
| Periphyton vitality | | * (-) | | | | * (+) | | | |
| Gross primary production | no data | | *** (+) | | | | | | |
| Primary production / respiration | no data | * (-) | | ** (+) | | | | * (-) | * (+) |

Table 4 (continued)

| **Covariate and dependent variable** | **22 May** | **5 June** | **13 June** | **25 June** | **11 July** | **24 July** | **11 Sept** | **26 Sept** | **9 Oct** |
|---|---|---|---|---|---|---|---|---|---|
| **Substratum size** (continued) | | | | | | | | | |
| *Achnanthes* spp. | * (+) | | * (+) | * (+) | | | | ** (-) | * (+) |
| *Cocconeis* spp. | | | | * (+) | | | | * (-) | |
| *Cymbella/Encyonema/ Amphora* spp. | | | * (+) | | | | | ** (-) | |
| *Fragilaria.* spp. | | | | no data | | | | ** (-) | |
| *Gomphonema* spp. | | * (-) | | | | | | * (-) | * (+) |
| *Meridion* spp. | | | * (+) | | | | | | |
| *Navicula* spp. | | | | | | | | * (-) | * (+) |
| Coccoid Cyanophyta | | ** (-) | * (+) | | | | | * (-) | |
| Filamentous Cyanophyta | | * (-) | ** (+) | | | | | ** (-) | ** (+) |
| Filamentous Chlorophyta | | * (-) | * (+) | | | | ** (-) | | |
| **Stone surface area** | | | | | | | | | |
| Total algal density | | | | | * (-) | | ** (-) | | ** (-) |
| Algal taxon richness | | | | | | | | * (+) | |
| Living algal biomass | | | | | | | * (-) | | * (-) |
| Periphyton vitality | | | * (+) | | | | ** (-) | | * (-) |
| Chl a / Phaeophytin | | | | | | | | ** (+) | |
| Gross primary production | no data | | * (+) | | | | | | * (+) |
| Primary production / respiration | no data | | | | | | * (-) | | |
| *Achnanthes* spp. | | | | | * (-) | | | * (+) | |
| *Cocconeis* spp. | * (+) | | | | | | | * (-) | |
| *Cymbella/Encyonema/ Amphora* spp. | | | * (+) | | | | * (+) | | |
| *Fragilaria.* spp. | | | | no data | | | | * (+) | |
| *Gomphonema* spp. | | | | ** (+) | | | | | |
| *Navicula* spp. | | | | | | | * (+) | | |
| *Nitzschia* spp. | | | | | | | | ** (+) | |
| Coccoid Cyanophyta | | | | | | * (-) | ** (-) | | ** (-) |
| Filamentous Cyanophyta | | | * (+) | | | | | * (+) | |
| Filamentous Chlorophyta | | * (+) | | | | * (-) | | * (+) | |
| Non-filamentous Chlorophyta | * (-) | | | | | * (-) | * (+) | | *** (-) |
| **POM** | | | | | | | | | |
| Total algal density | | | | | | | | | * (-) |
| Algal taxon richness | * (+) | * (-) | | | | | | * (+) | |
| Living algal biomass | | | | * (+) | | * (+) | | | |
| Gross primary production | no data | | | | | | | * (-) | |
| Primary production / respiration | no data | | | | | | | * (-) | |
| *Achnanthes* spp. | ** (+) | | | | | | | | |
| *Cocconeis* spp. | | | | | | | | | * (+) |
| *Cymbella/Encyonema/ Amphora* spp. | * (+) | | | | | | | | |
| *Fragilaria.* spp. | | | | no data | | * (+) | | | |
| *Gomphonema* spp. | | | | * (+) | | | | | |
| *Meridion* spp. | | * (+) | | | | * (+) | | | |
| *Navicula* spp. | | | | | * (-) | | | | |
| *Nitzschia* spp. | | | | | * (-) | ** (+) | | | |
| Coccoid Cyanophyta | | * (-) | | | | | | | * (-) |
| Filamentous Cyanophyta | | | | | | | | * (-) | |
| Non-filamentous Chlorophyta | | | | | | | | | * (-) |

Table 4 (continued)

| **Covariate and dependent variable** | **22 May** | **5 June** | **13 June** | **25 June** | **11 July** | **24 July** | **11 Sept** | **26 Sept** | **9 Oct** |
|---|---|---|---|---|---|---|---|---|---|
| **Total invertebrates (Surber)** | | | | | | | | | |
| Total algal density | | | | | | | * (-) | *** (-) | |
| Living algal biomass | | | | | | | * (+) | | |
| Periphyton vitality | | | | | * (+) | | * (-) | | |
| *Cocconeis* spp. | | | | | * (+) | | | * (+) | |
| *Cymbella/Encyonema/ Amphora* spp. | | | | | | | * (+) | | |
| *Fragilaria.* spp. | | | | no data | * (+) | | | | |
| *Gomphonema* spp. | | * (-) | | | | | | | |
| *Meridion* spp. | * (-) | | | | | | * (+) | | |
| *Navicula* spp. | * (-) | * (-) | | | | | | | * (+) |
| *Nitzschia* spp. | | * (-) | | | | | | | |
| Coccoid Cyanophyta | | | | | * (+/-) | | | ** (-) | |
| Filamentous Cyanophyta | | | | * (+) | | | | | |
| Non-filamentous Chlorophyta | * (-) | | | | | | * (-) | ** (-) | |
| **Total epilithic bacteria** | | | | | | | | | |
| Total algal density | | | | | | | * (+) | | * (+) |
| Algal taxon richness | | | | | | | | * (-) | |
| Living algal biomass | | | | | | | | | * (+) |
| *Achnanthes* spp. | * (+) | | | * (+) | | | | | |
| *Cocconeis* spp. | * (+) | | | | | | | | |
| *Cymbella/Encyonema/ Amphora* spp. | * (+) | | | | | | | | |
| *Gomphonema* spp. | * (+) | | | * (+) | | | | * (-) | |
| *Meridion* spp. | ** (+) | | | | * (-) | | | | |
| *Navicula* spp. | | | | | * (+) | | | * (-) | |
| *Nitzschia* spp. | | | | | | | * (-) | ** (-) | |
| Coccoid Cyanophyta | | * (+) | | * (+) | | | | | ** (-) |
| Non-filamentous Chlorophyta | | | * (-) | | | | | | * (+) |

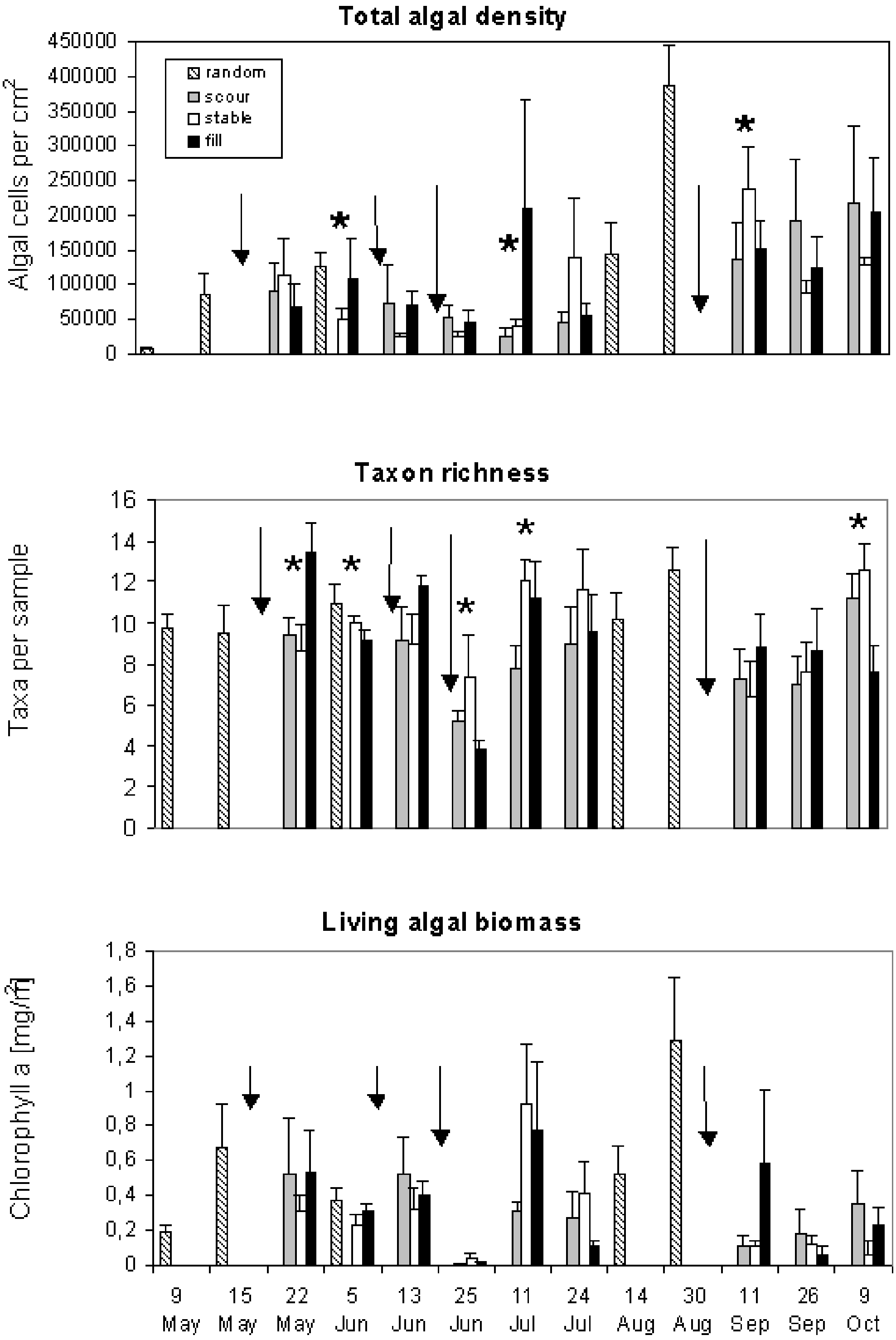

**Fig. 1**. Total epilithic algal density, taxon richness, and living algal biomass in random, scour, stable and fill patches in the **Schmiedlaine**. The arrows indicate the timing of the high-flow events (for details see text). Significant differences between patch types in the ANOVAs and ANCOVAs are shown by asterisks above the mean values. Error bars indicate standard errors. See Table 3 for *P*-values and statistical power of all comparisons between patch types. *P<0.10.

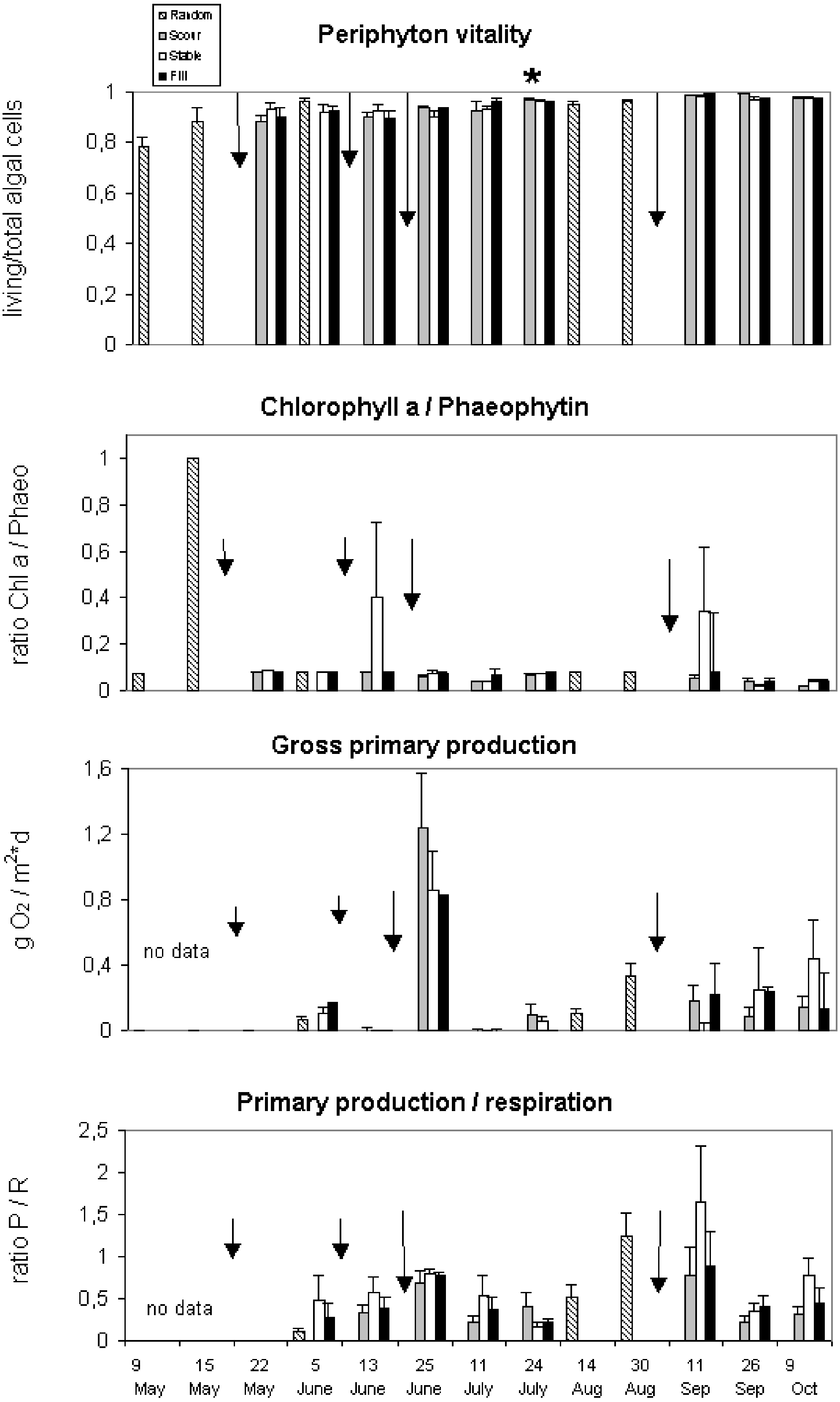

**Fig. 2**. Periphyton vitality, the ratio of chlorophyll a to phaeophytin, gross primary production and the ratio of primary production to respiration in random, scour, stable and fill patches in the **Schmiedlaine**. See Fig. 1 for further details.

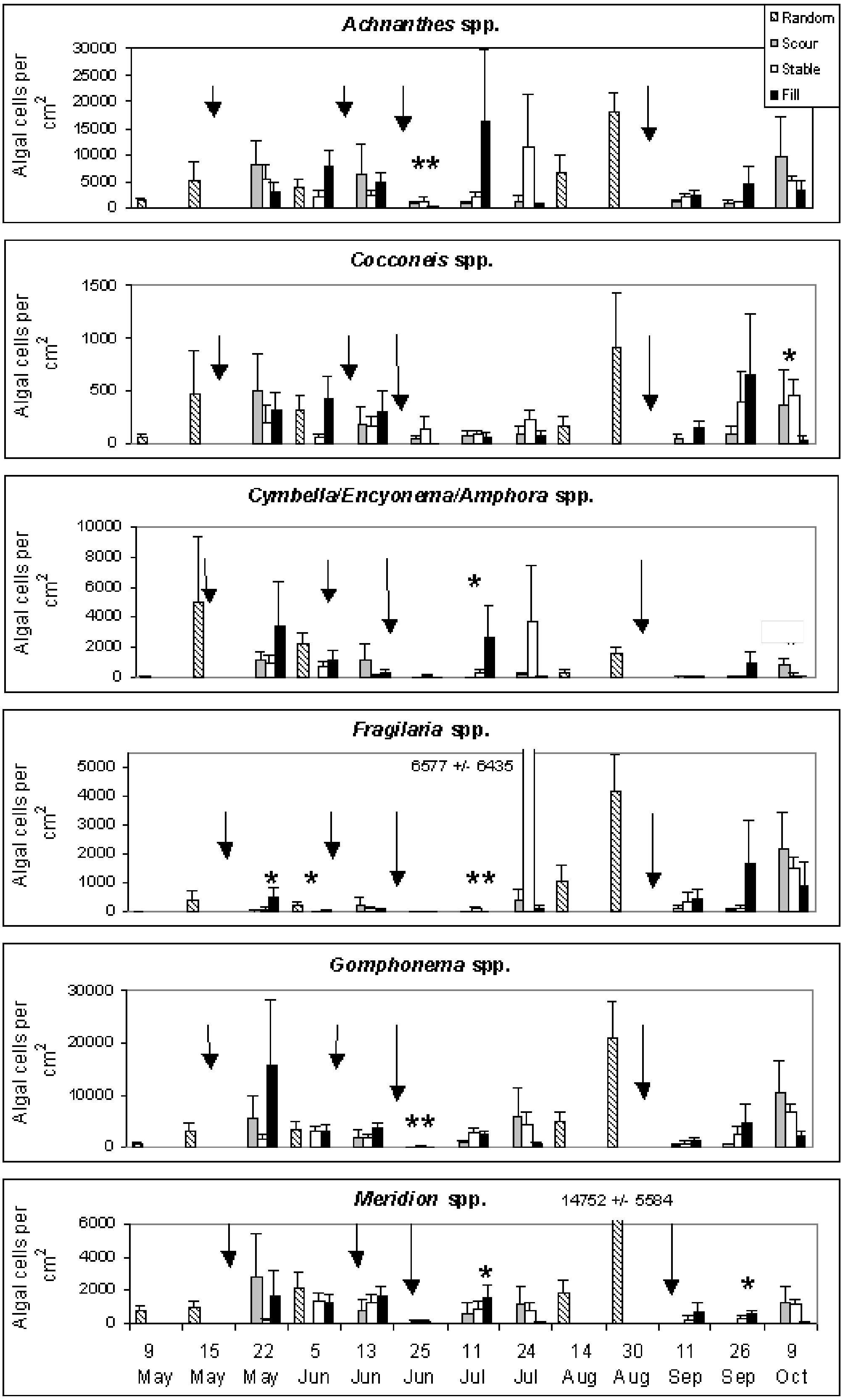

**Fig. 3.** Densities of *Achnanthes* spp., *Cocconeis* spp., *Cymbella/Encyonema/Amphora* spp., *Fragilaria* spp., *Gomphonema* spp. and *Meridion* spp. in random, scour, fill and stable patches in the **Schmiedlaine**. See Fig. 1 for further details.

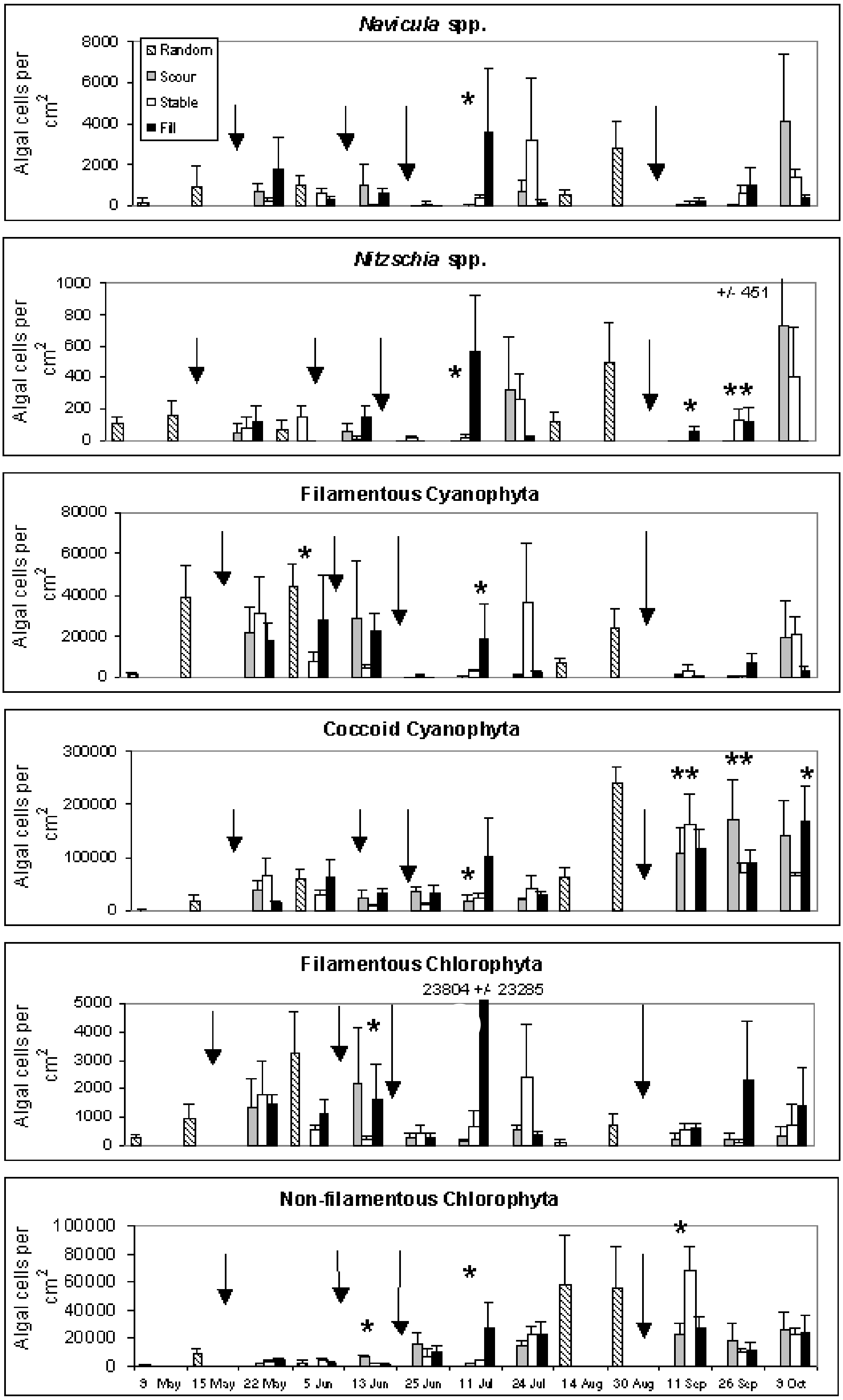

**Fig. 4.** Densities of *Navicula* spp., *Nitzschia* spp., filamentous and coccoid Cyanophyta, filamentous and non-filamentous Chlorophyta in random, scour, fill and stable patches in the **Schmiedlaine**. See Fig. 1 for further details.

**Kye Burn.** Total algal cell density (all patch types combined) was not quite significantly reduced by Event 2 in comparison to pre-disturbance values (p=0.07; Fig. 5). Algal density was similar across patch types on both patch-specific sampling dates after Event 1, as was vitality of periphyton (Fig. 5). Algal density was correlated with substratum size (in Surber samples) and stone surface area on 27 December (Table 6).

Taxon richness was reduced significantly by Event 1 (*P*=0.04) and Event 2 (*P*<0.0001). Richness was correlated with water depth, near-bed velocity and invertebrate density on one sampling date each (Table 6).

Algal biomass (measured as chl *a*) was reduced by Event 2 (*P*<0.0001) and was correlated with mean current velocity and substratum size on one date each (Table 6).

Periphyton vitality (living / total algal cells; Fig. 6) was generally high and increased even further shortly after Event 2 (*P*<0.0001). Vitality was similar across patch types on both sampling dates after Event 1 and correlated negatively with POM on 27 December (Table 6). The ratio of chl a to phaeophytin was unaffected by both events and was also similar across patch types on both dates after Event 1 (Table 5). This ratio was correlated once with substratum size in Surber samples and bacterial density and twice with the surface area of the sampled stones.

Gross primary production was reduced by Event 2 (*P*<0.0001), and the ratio of primary production to respiration (P/R) was unaffected by either event. Both parameters were similar across patch types on both dates after Event 1 (Table 5). Primary production was not correlated with any of the covariates, whereas P/R was correlated with both water depth and near-bed current velocity on 27 December (Table 6).

Densities of the common algal genera were affected little by Event 1 (no significant reductions) but strongly by Event 2 (Figs. 7 & 8). Event 2 caused significant density decreases in *Diatoma* (*P*=0.05), *Fragilaria* (*P*=0.02) and *Nitzschia* (*P*=0.0.04).

*Cocconeis* spp. was more common in scour than in fill patches on 11 December (Fig. 7; Table 5). *Cocconeis* density was correlated with water depth, substratum size in the Surber samples, POM, and epilithic bacteria on one sampling date each (Table 6). *Diatoma* was more abundant in scour than in fill patches on 27 December (Table 5). Densities of this taxon were correlated with water depth, near-bed velocity and epilithic bacteria on one sampling date each (Table 6).

Densities of all the other common algal taxa were similar across patch types on both sampling dates after Event 1 (Table 5). *Achnanthes* was correlated with all covariates at least once, except for substratum size, total invertebrates and epilithic bacteria (Table 6). Densities of *Cymbella/Encyonema/Amphora* were correlated with stone surface area and total invertebrates on one sampling date each. *Fragilaria* showed correlations with all covariates on at least one date, except for substratum size and epilithic bacteria. *Gomphonema* and *Navicula* were both correlated at least once with water depth and stone surface area, and *Gomphonema* was also correlated with epilithic bacteria on one sampling date. *Nitzschia* and filamentous Cyanophyta showed no correlations with any of the covariates. Densities of coccoid Cyanophyta were correlated with substratum size in Surber samples, stone surface area and total invertebrates on one or two dates each. Filamentous Chlorophyta were correlated with water depth and POM on one date each, whereas non-filamentous Chlorophyta were correlated with stone surface area and POM on one date each (Table 6).

**Table 5.** Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing the bacterial communities in scour, fill and stable patches in the **Kye Burn**. Prior to final analysis, data were log-transformed where necessary and potential factor x covariate interactions explored (see column 4). For each dependent variable, the results of the 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 covariate effects see Table 6). $\alpha$=0.10.

| Date and dependent variable | Covariate in ANCOVA | Covariate | Inter-action | Factor | Ranking |
|---|---|---|---|---|---|
| **11 Dec** | | | | | |
| *Cocconeis* spp. | Epilithic bacteria | 0.099 | 0.08 | 0.04 | Scour > fill |
| **27 Dec** | | | | | |
| *Diatoma* spp. | Epilithic bacteria | 0.06 | 0.94 | 0.01 | Scour > fill |

**Table 6.** Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing the algal community in scour, fill and stable patches in the **Kye Burn** (for factor effects see Table 5). Only significant results are shown; blanks indicate non-significant results. * P < 0.10; ** P <0.01; *** P <0.001; + positive correlation; - negative correlation. Note that the covariate total epilithic bacteria was not calculated for the dependent variables GPP and P/R (for details see text).

| Covariate and dependent variable | 11 Dec | 27 Dec |
|---|---|---|
| **Water depth** | | |
| Algal taxon richness | ** (-) | |
| Primary production / respiration | | * (+) |
| *Achnanthes* spp. | * (-) | |
| *Cocconeis* spp. | | ** (+) |
| *Diatoma* spp. | * (-) | |
| *Fragilaria.* spp. | * (-) | |
| *Gomphonema* spp. | | * (+) |
| *Navicula* spp. | | * (+) |
| Filamentous Chlorophyta | | * (-) |
| **Near-bed current velocity** | | |
| Algal taxon richness | * (-) | |
| Primary production / respiration | | * (+) |
| *Achnanthes* spp. | * (-) | |
| *Diatoma* spp. | * (-) | |
| *Fragilaria.* spp. | ** (-) | * (+) |
| **Substratum size** | | |
| Total algal density | | * (-) |
| Living algal biomass | * (+) | |
| Chl a / Phaeophytin | * (+) | |
| *Cocconeis* spp. | * (+) | |
| Coccoid Cyanophyta | * (+) | * (-) |
| **Stone surface area** | | |
| Total algal density | | ** (-) |
| Chl a / Phaeophytin | ** (+) | * (+) |
| *Achnanthes* spp. | * (+) | * (-) |
| *Cymbella/Encyonema/Amphora* spp. | ** (+) | |
| *Fragilaria.* spp. | | * (-) |
| *Gomphonema* spp. | | * (-) |
| *Navicula* spp. | * (+) | * (-) |
| Coccoid Cyanophyta | | ** (-) |
| Non-filamentous Chlorophyta | | * (-) |
| **POM** | | |
| Periphyton vitality | | * (-) |
| *Achnanthes* spp. | * (+) | |
| *Cocconeis* spp. | *** (+) | |
| *Fragilaria.* spp. | * (+) | |
| Filamentous Chlorophyta | | * (+) |
| Non-filamentous Chlorophyta | | * (-) |
| **Total invertebrates (Surber)** | | |
| Algal taxon richness | * (+) | |
| *Cymbella/Encyonema/Amphora* spp. | * (+) | |
| *Fragilaria.* spp. | * (-) | |
| Coccoid Cyanophyta | * (-) | |
| **Total epilithic bacteria** | | |
| Chl a/ Phaeophytin | | * (-) |
| *Cocconeis* spp. | * (+) | |
| *Diatoma* spp. | | * (+) |
| *Gomphonema* spp. | | * (+) |

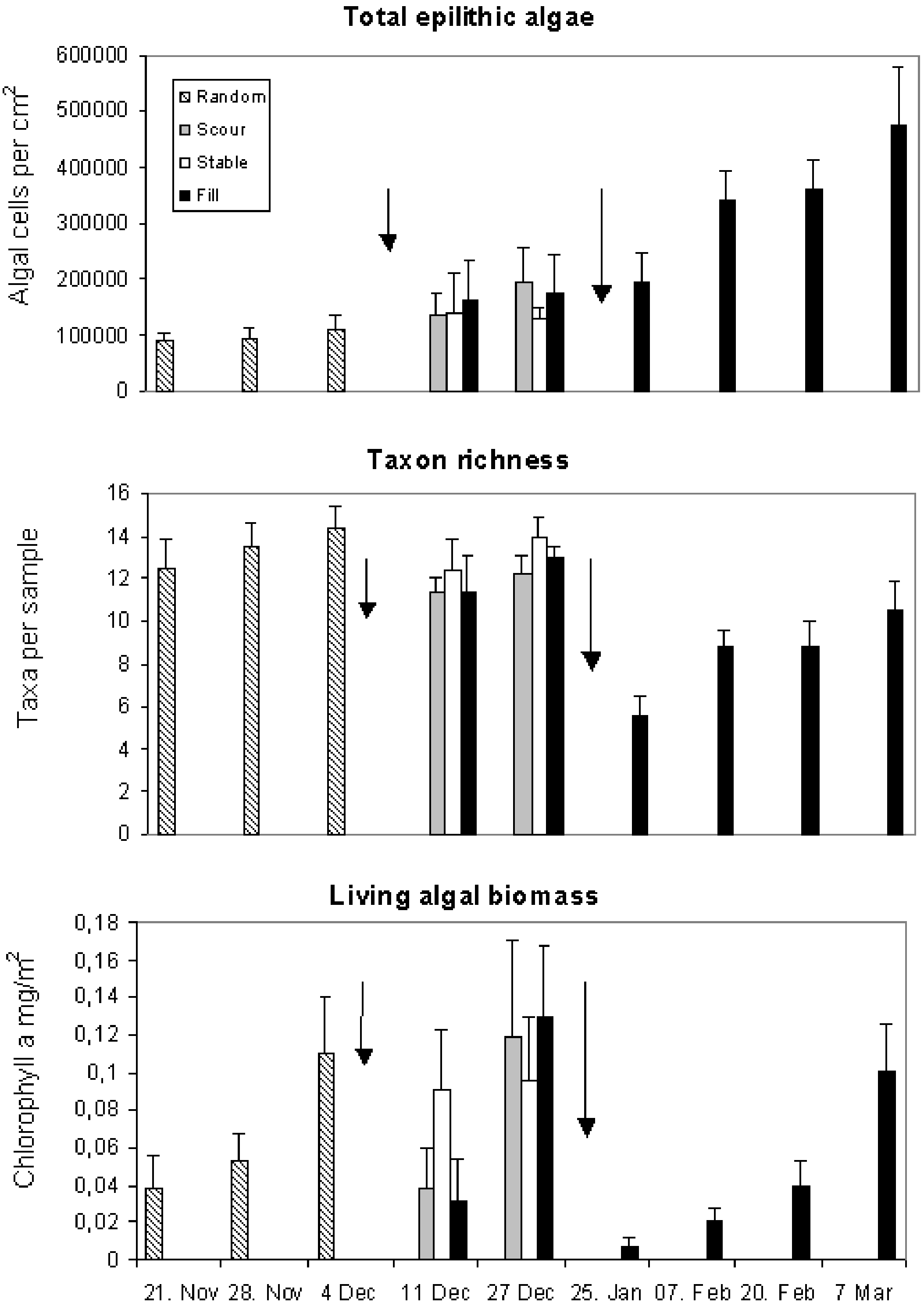

**Fig. 5**. Total epilithic algal density, taxon richness, and living algal biomass in random, scour, stable and fill patches in the **Kye Burn**. The arrows indicate the timing of the high flow events (for details see text). Significant differences between patch types in the ANOVAs and ANCOVAs are shown by asterisks above the mean values. Error bars indicate standard errors. See Table 5 for *P*-values and statistical power of all comparisons between patch types. *P<0.10.

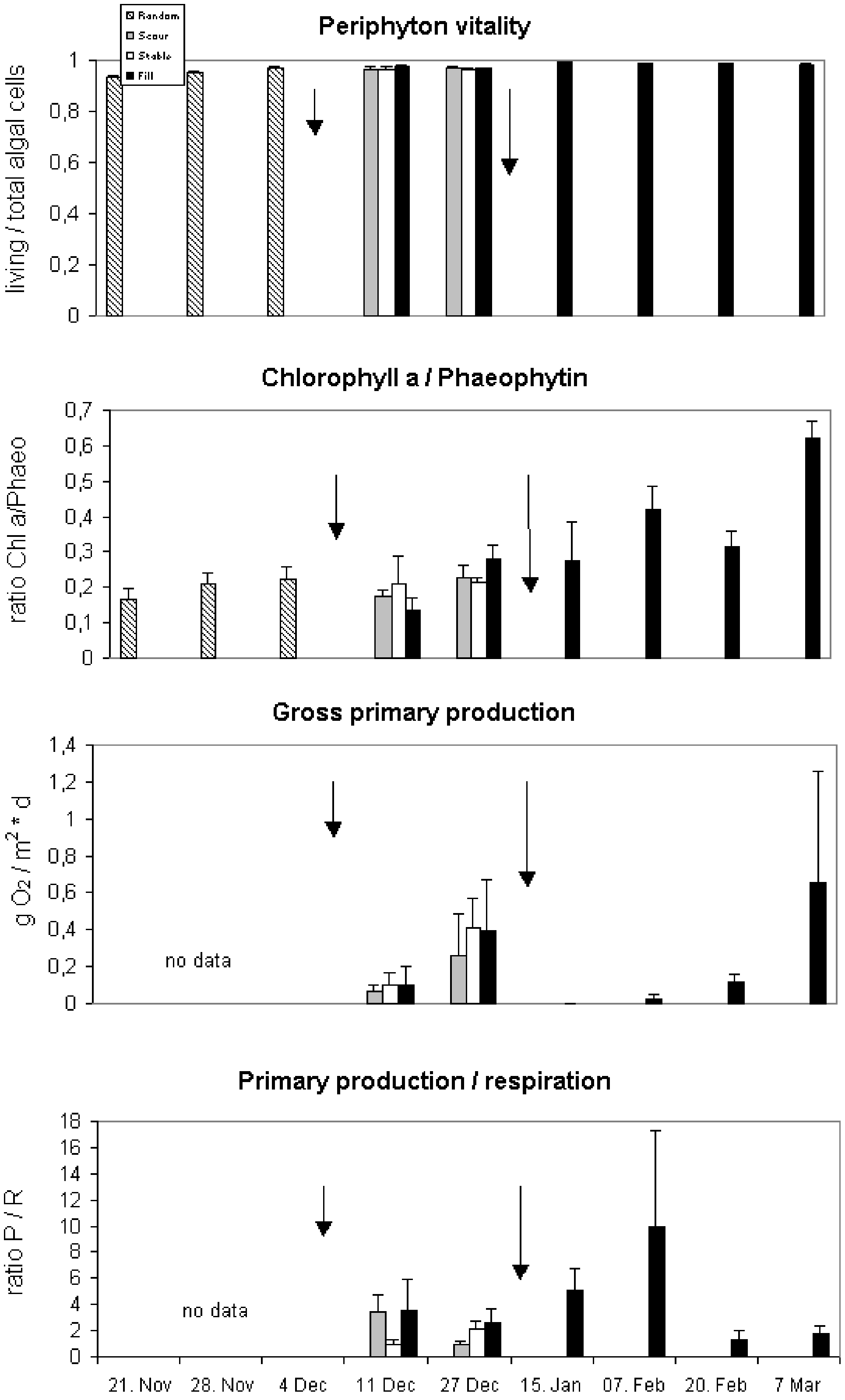

**Fig. 6**. Periphyton vitality, the ratio of chlorophyll a to phaeophytin, gross primary production and the ratio of primary production to respiration in random, scour, stable and fill patches in the **Kye Burn**. See Fig. 5 for further details.

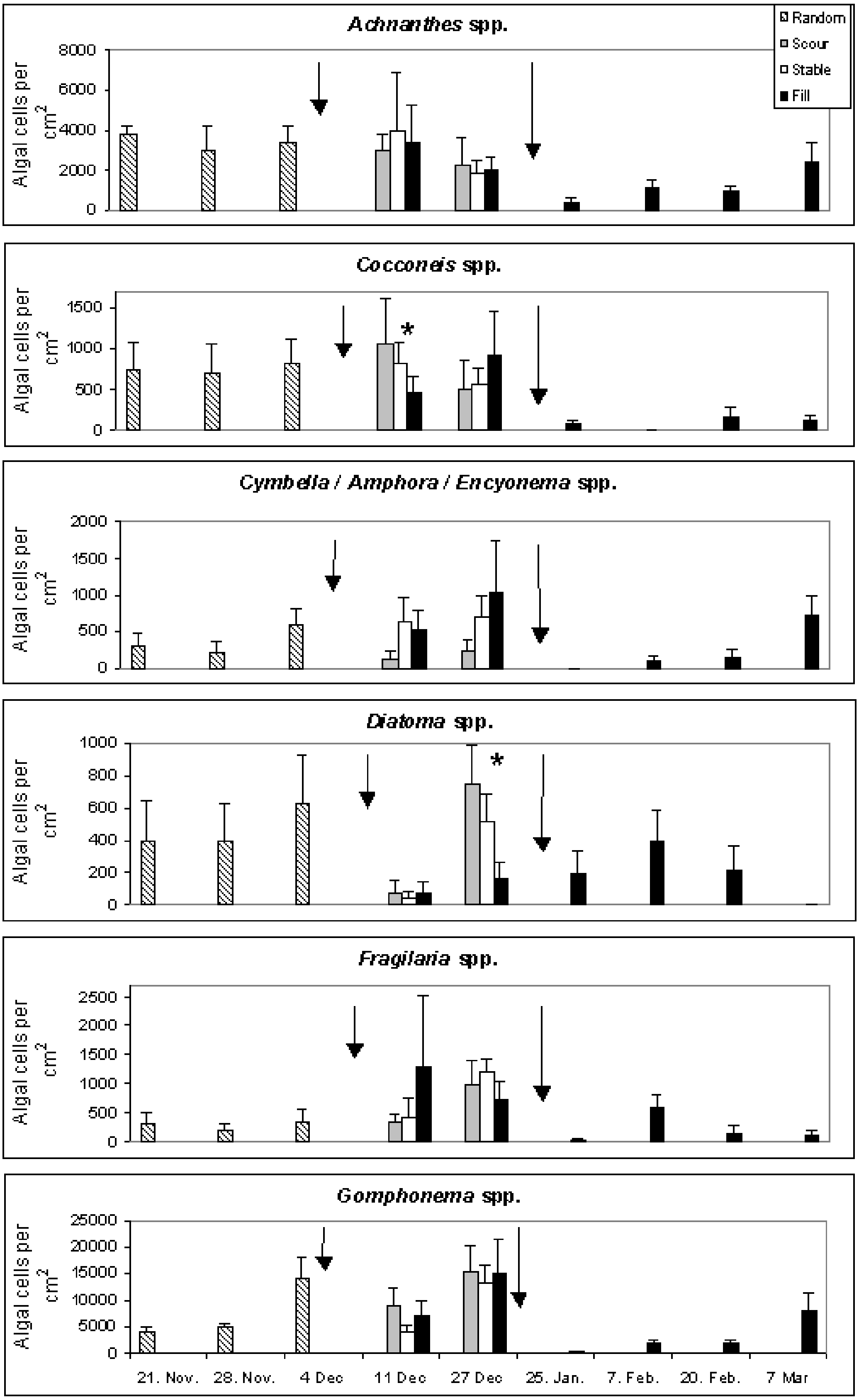

**Fig. 7.** Densities of *Achnanthes* spp., *Cocconeis* spp.,*Cymbella/Encyonema/Amphora* spp., *Diatoma* spp., *Fragilaria* spp. and *Gomphonema* spp. in random, scour, fill and stable patches in the **Kye Burn**. See Fig. 5 for further details.

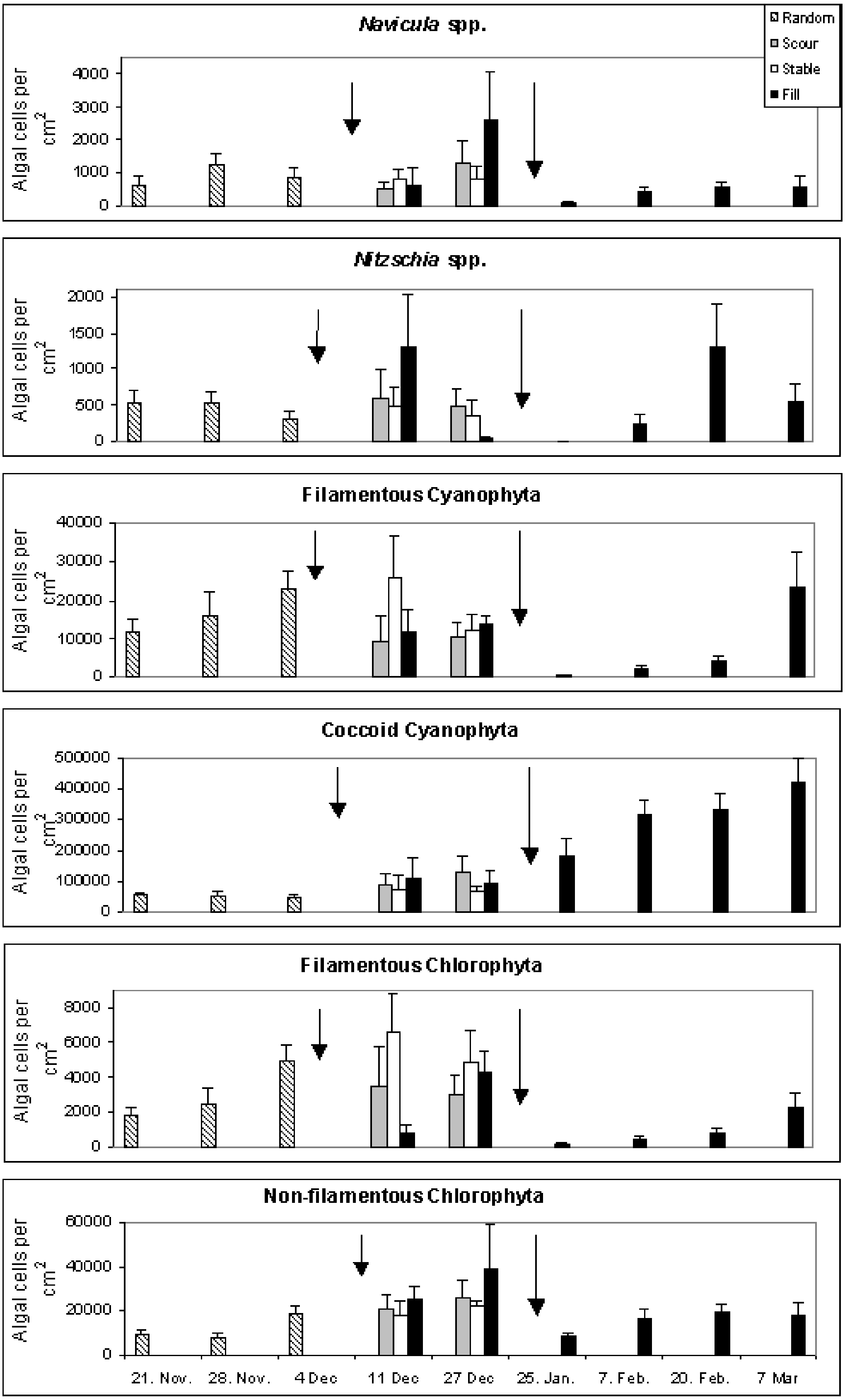

**Fig. 8.** Densities of *Navicula* spp., *Nitzschia* spp., filamentous and coccoid Cyanophyta, filamentous and non-filamentous Chlorophyta in random, scour, fill and stable patches in the **Kye Burn**. See Fig. 5 for further details.

## Interactions between disturbance history and habitat parameters

In all cases where a relationship of disturbance history with algal distribution in the ANOVA occurred simultaneously with a correlation of a habitat parameter with algal distribution in the ANCOVAs, the relationship with disturbance history remained valid (i.e. it was detected in at least 50% of all ANCOVAs with significant covariate effects; compare Tables 3 & 4 and see Methods). In addition, there were several cases when significant correlations with habitat parameters revealed relationships with disturbance history that had remained undetected in the ANOVAs (see Table 3). In the Kye Burn, the ANOVAs did not result in any significant differences between the three patch types, and the only two such differences were found in the ANCOVAs.

## Disturbance history effects on habitat parameters and indirect effects on stream biota

In the Schmiedlaine, disturbance history was related to the seven measured habitat parameters in five of 63 possible cases (8%) and in four of 14 possible cases (29%) 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 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). The surface area of the sampled stones was also larger in stable (929 ± 84 $cm^2$) than in scour patches (194 ± 34 $cm^2$) on 25 June (*P* = 0.04). Densities of epilithic bacteria were higher in fill patches ($1.3 \times 10^7 \pm 3.5 \times 10^6$ cells/cm²) than in scour patches ($4.0 \times 10^6 \pm 6.7 \times 10^5$ cells/cm²) on 13 June (*P* = 0.07).

One of these habitat parameters, in turn, was correlated with the distributions of total algal density, *Navicula*, *Nitzschia* (water depth on 22 May), non-filamentous Chlorophyta (water depth on 22 May and bacterial density on 13 June), gross primary production, P/R, *Fragilaria* (water depth on 11 July), living algal biomass, P/R, *Achnanthes*, *Cocconeis* (substratum size on 25 June), *Gomphonema* (stone area on 25 June) and periphyton vitality (substratum size on 24 July) in one or two cases each (see Table 4). Consequently, the habitat parameter effects on algae in these 14 cases (8% of 166 possible cases) can be seen as *indirect* effects of disturbance history on these stream biota. Note that total algal density, non-filamentous Chlorophyta, *Achnanthes*, *Fragilaria* and periphyton vitality were also related directly to disturbance history in these cases (see Table 3).

In the Kye Burn on 11 December, the water was deeper in fill than in stable patches (40 ± 2 versus 28 ± 4 cm; *P* = 0.09), substratum size was twice as large in stable than in scour patches (63 ± 13 versus 34 ± 7 mm; $P = 0.06$), and densities of epilithic bacteria were higher in fill patches ($1.0 \times 10^8 \pm 2.3 \times 10^7$ cells/cm²) than in stable patches ($2.5 \times 10^7 \pm 1.1 \times 10^7$ cells/cm²; $P = 0.04$). One or two of these parameters influenced the distributions of algal taxon richness, *Achnanthes*, *Diatoma*, *Fragilaria* (water depth), algal biomass, *Cocconeis*, coccoid Cyanophyta (substratum size) and Chl a/phaeophytin (substratum size and bacterial density) on this date (Table 6), resulting in eight indirect effects of disturbance history on stream algae. *Cocconeis* was also influenced directly by disturbance history (Table 5).

On 27 December, near-bed current velocity was three times faster in fill than in scour patches (11 ± 5 versus 33 ± 7 $\text{cm}\cdot\text{s}^{-1}$; $P = 0.04$). This parameter was related to the distributions of P/R and *Fragilaria* on this date (Table 6). Altogether, algae were thus influenced indirectly by disturbance history in ten cases (33% of 38 possible cases) in the Kye Burn.

## Discussion

### Relative importance of disturbance history and physical habitat

Disturbance history played an important role in determining algal distribution in the present study, augmenting conclusions from our previous research. This role was somewhat less dominant than in our study of river algae (where disturbance history had affected algal distribution more often than current velocity, substratum size and water depth combined; Matthaei *et al.*, 2003), possibly because fewer microhabitat parameters had been measured in the earlier research. In the flood-prone Schmiedlaine, substratum characteristics and current velocity were related to algal distribution at least as often as disturbance history. In the relatively more stable Kye Burn, we found few direct relationships of disturbance history with algal distribution, and substratum characteristics, water depth, current velocity and POM were the most influential habitat parameters. However, disturbance history also influenced algal distribution indirectly in both streams (see below), and this indirect influence was particularly strong in the Kye Burn.

The results for the known habitat parameters were largely in accordance with previous microhabitat studies for benthic algae (see e.g. Stevenson, 1996; Biggs, Stevenson & Lowe, 1998; Passy, 2001). Patterns in algal densities in the different bed stability types varied between individual floods, sampling dates and streams. However, densities were highest in stable patches and fill patches somewhat more often than in scour patches (see Tables 3 & 5).

### Direct versus indirect effects of disturbance history on stream algae

Disturbance history affected algal distribution 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 and disturbance history effects interacted strongly with each other. In our study of river algae (Matthaei *et al.*, 2003), by contrast, disturbance history effects had been largely independent of habitat parameter effects.

Matthaei and Townsend (2000) speculated that indirect effects of disturbance history on physical habitat parameters and food resources of benthic organisms are more likely to be responsible for long-term differences (several weeks after disturbance) in densities between patch history types. Our present results do not support this idea, at least not for benthic algae and the studied habitat parameters, because the majority of indirect effects of disturbance history in both streams were found relatively shortly (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 seven 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 seven covariates (see Methods). However, we included these covariates in our analysis to find out if “apparent” effects of disturbance history on algal distribution 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 results for stream invertebrates (Matthaei *et al.*, 2000; Matthaei & Townsend, 2000) and river algae (Matthaei *et al.*, 2003), we expected stable bed patches to serve as refugia for benthic algae during high-flow events. Our data partly support this expectation. In the Schmiedlaine, stable bed patches acted as an algal refugium during the two largest floods. Shortly after Event 3, algal taxon richness and density of *Gomphonema* were highest in stable patches. Similar patterns were observed for total algal density, coccoid Cyanaophyta and non-filamentous Chlorophyta shortly after Event 4.

In some cases in the Schmiedlaine, algal densities, P/R and taxon richness were 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 3 (P/R, *Fragilaria* and filamentous Cyanophyta on 11 July) and 3 weeks (*Nitzschia* on 26 September) and 5 weeks after Event 4 (taxon richness and *Cocconeis* on 9 October). These results suggest that benthic algae 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.

However, in the majority of cases where we found differences between patch types 3-5 weeks after disturbance (on 11 and 24 July, 26 September and 9 October), the benthic algae were most abundant in scour or fill patches. This result parallels that of Matthaei *et al.* (2003) for benthic algae in a somewhat larger German river. Again, the observed patterns are probably related to the relative favourability of conditions and resources in different patch types as these change with time since a disturbance.

We had initially expected changes in vitality of the algal mats with successional stage to be one of the reasons why benthic algae preferred scour or fill patches several weeks after disturbance. Peterson *et al.* (1990) showed that exposure to periodic disturbance (simulated waves on a lake shore) can delay senescence within algal communities and potentially increase resistance to subsequent disturbance. In their experiment, periphyton communities left undisturbed for 24 days contained far more dead algal cells than recently disturbed ones. Peterson (1996) combined these results with others to create a conceptual model for successional changes in algal mats following scour disturbance. In senescent algal mats, the basal cell layers die due to lack of light and water-column nutrients, which may lead to ‘autogenic sloughing’ (detachment of the entire mat caused by detachment of the dead basal cells). According to the model, these sloughing events are followed by a much slower recovery of the algal mats than after scour due to high-flow events, because vital basal cells are lacking after autogenic sloughing.

Adapting these predictions to the scour, fill and stable bed patches in our two streams, one would expect algal mats to be less vital in the relatively undisturbed stable patches than in the more severely disturbed scour or fill patches. Autogenic sloughing should then occur in stable patches, followed by a slow recovery, whereas recovery in the disturbed patches should be faster, eventually leading to higher algal densities than in stable patches. (The Peterson model does not distinguish between scour and fill patches, see above.) However, our data provide little support for these model predictions. Periphyton vitality (living / total algal cells) was lower in stable patches compared to scour patches on just a single sampling date (24 July; Fig. 2), and the ratio of chl a to phaeophytin never differed significantly between patch types, indicating that the algal mats in stable patches were generally as healthy as those in scour or fill patches. Consequently, algal growth and the timing of autogenic sloughing events ought to be similar between patch types. According to the model, one would also expect vitality of the algal mats in all three patch types to change with time since the last disturbance, from vital and fast-growing mats shortly after disturbance to senescent mats after longer stable periods, followed by low algal densities and slow recovery due to autogenic sloughing. By contrast, neither periphyton vitality nor the ratio of chl a to phaeophytin ever decreased with time since the last disturbance during our study.

### Differences between streams

We had expected local disturbance history to be relatively more important for algal distributions in the Schmiedlaine than in the Kye Burn because of the higher frequency of bed-moving floods in the former, and our results supported this expectation. Note that both streams are nutrient-poor, with slow algal growth and low algal biomass on surface stones (see Figures 1 & 5). Therefore, the observed differences in the frequency of disturbance history effects on algal distributions between streams are unlikely to be caused by differences in productivity.

### Recovery of stream algae after a purely depositional flood

We had expected algal 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 the 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.

In agreement with these expectations, living algal biomass, algal taxon richness and densities of most of the common algal taxa were all reduced strongly by the flood (see Figures 5, 7 & 8), Most of these parameters needed several weeks to recover to pre-flood levels, whereas recovery occurred much faster after the smaller Event 1. Nevertheless, total algal cell density was barely reduced by the large flood and exceeded pre-flood levels within a few weeks after disturbance, largely due to the highly flood-resistant and fast-growing coccoid Cyanophyta (Fig. 8). Interestingly, the post-flood algal community must have consisted of much smaller algal cells than the pre-flood community because algal biomass never exceeded pre-flood levels. Overall, these results imply that large and purely depositional floods may represent particularly harsh disturbance events for stream algae. Nevertheless, algal taxa that are especially well-adapted to floods may actually benefit even from such harsh disturbances.

## Acknowledgements

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

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## Summary

1. 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).
2. 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.
3. Patterns of invertebrate densities in the different bed stability types varied between floods, sampling dates and streams, but invertebrate densities were 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.
4. Averaged across both streams, only near-bed current velocity was correlated with invertebrate distributions in the stream bed more often than disturbance history. In the Kye Burn, disturbance history and water depth were the most influential habitat parameters.
5. 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.

# 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 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, Stevenson & Lowe, 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, Bely & Berg, 1992; Lancaster & Hildrew, 1993; Robertson, Lancaster & Hildrew, 1995; Palmer *et al.*, 1996; Winterbottom *et al.*, 1997). To address this deficiency further, Matthaei, Peacock & Townsend (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 ($\leq 1$ m$^2$) bed patches that had experienced scour (sediment removal), fill (sediment deposition) or remained stable ($\leq 1$ 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 are highly mobile (Mackay, 1992) and could have easily dispersed between the different patch types, which were separated by only a few meters, 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, Guggelberger & Huber (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, but in fill patches three months after another flood.

While clearly showing that disturbance history can affect benthic organisms, these first disturbance history 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, and
(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 densities 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 (particle width 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 cold, <13°C in summer in the Schmiedlaine and <16°C in the Kye Burn (G. Sailer, unpublished data). Both systems are nutrient-poor (Water Management Authority Weilheim, unpublished data; Niyogi, Simon & Townsend, 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 patterns were 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 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; leveling 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).

**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<br>*(=Before Event 2)* | Fill, Stable, Random | 5 each |
| | **Event 2 (10 - 11 June)** | | | | |
| | | 13 June | After Event 2<br>*(=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<br>*(=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 |

## 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, see Publications 1 and 2) 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, see Publications 1 and 2). Epilithic algal biomass was determined as chlorophyll a, and total density of epilithic bacteria was enumerated using epifluorescence microscopy. The surface area of each stone was determined by wrapping it in aluminum foil and weighing the foil (Townsend, Scarsbrook & Dolédec, 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 size classes inside the Surber sampler. These size classes were identified using a modified Wentworth scale (Harrelson, Rawlins & Potyondy, 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, Matthaei & Townsend, 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.

**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**<br>**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% | |

## 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, Arbuckle & Townsend, 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 $\alpha$ 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 $\alpha$ at 0.1 in all patch-specific analyses. Comparisons between sampling dates (in which all samples collected on each date were combined) were conducted with $\alpha$ 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 densities and taxon richness ($P \leq 0.02$). Densities of seven of the 10 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 densities ($P = 0.05$ and $P < 0.001$, respectively), whereas taxon richness decreased only after Event 2 ($P < 0.001$). While invertebrate densities recovered to pre-flood levels within 3 weeks of Event 1 ($P = 0.74$), they remained low 6 weeks after Event 2 ($P = 0.02$). Densities of *Deleatidium* spp. decreased after both events ($P \leq 0.001$), and densities of another 6 common taxa decreased after Event 2 (*Pseudotryssaturus* spp., Hydracarina, Chironomidae, Oligochaeta, *Hydora* spp. and Eriopterini; $P \leq 0.04$).

### Summary of effects of disturbance history and habitat parameter on invertebrates

In the Schmiedlaine, we analysed disturbance-history-specific patterns of total invertebrate densities, 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 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 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 densities 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* 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* 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* density was correlated with near-bed velocity, substratum size and epilithic bacteria, and *Simulium* 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* and Tanypodinae) and *Dicranota* spp. (Fig. 2) differed between bed stability types on two sampling dates each. *Liponeura* was more abundant in stable than in fill patches on 25 June and on 24 July (Table 3). *Thienemanniella/ Corynoneura* 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* 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* 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* 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* 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* density was related to substratum size, epitlithic bacteria and algal biomass on at least one date each (Table 4).

**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** | **Inter-action** | **Factor** | **Ranking** |
|---|---|---|---|---|---|
| **22 May** | **-** | | | | |
| **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 |
| *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.* spp. | Epilithic algal biomass | 0.07 | 0.26 | 0.07 | Scour > stable |

Table 3 (continued)

| **Date &<br>dependent variable** | **Covariate in ANCOVA** | **Covariate** | **Inter-action** | **Factor** | **Ranking** |
|---|---|---|---|---|---|
| **11 September** | | | | | |
| *Leuctra spp.* | - | - | - | 0.07 | Stable > scour |
| **26 September** | | | | | |
| *Thienem./ Corynon.* spp. | 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* | * (+) | | | | | | | | * (+) |
| *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 | |

Table 4 (continued)

| **Covariate & dependent variable** | **22 May** | **5 June** | **13 June** | **25 June** | **11 July** | **24 July** | **11 Sept** | **26 Sept** | **9 Oct** |
|---|---|---|---|---|---|---|---|---|---|
| **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 | *** (+) |

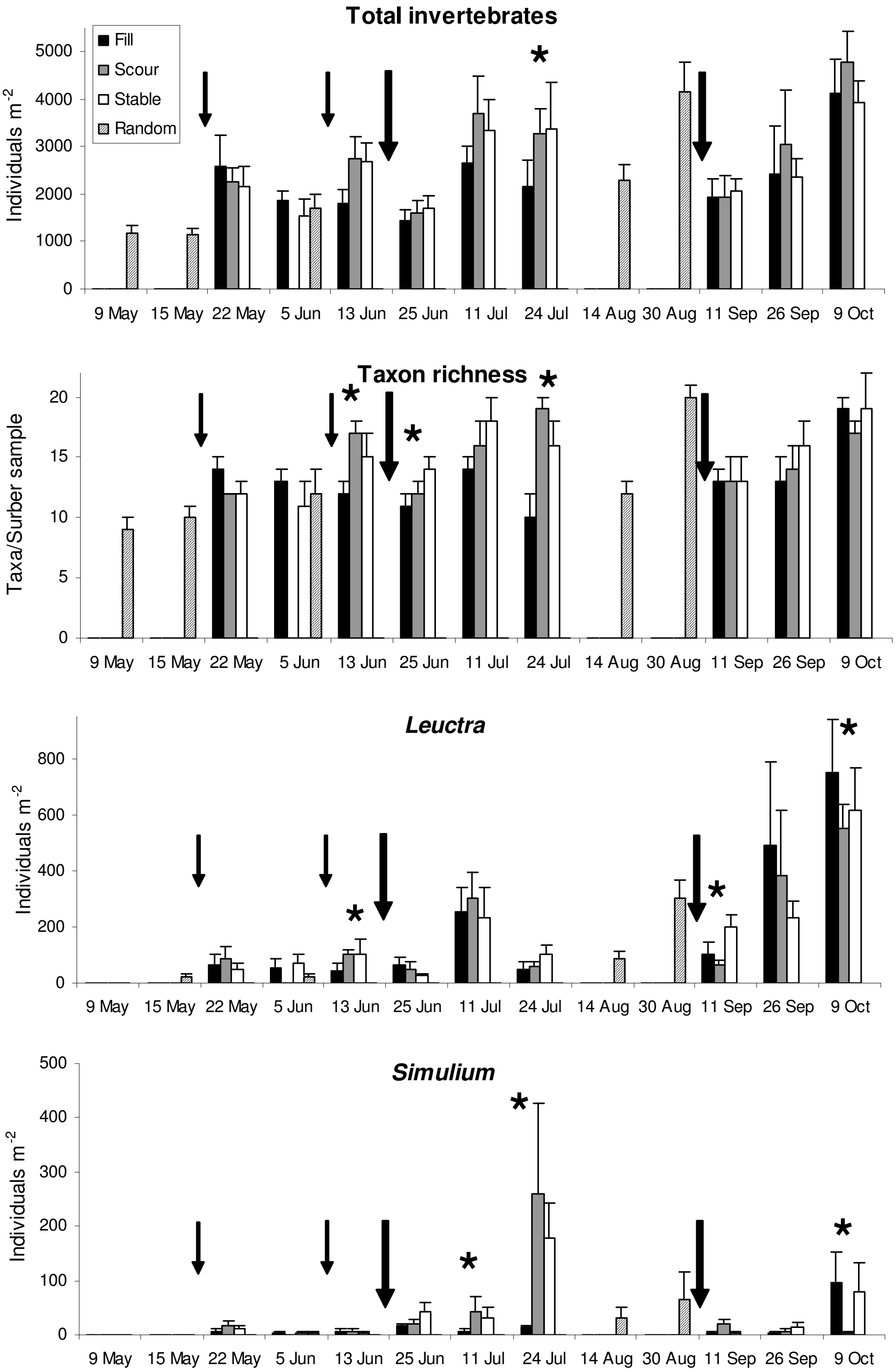

**Fig. 1.** Total invertebrate densities, taxon richness, and densities of *Leuctra* spp. and *Simulium* spp. in fill, scour, stable and random patches in the **Schmiedlaine**. The arrows indicate timing and magnitude (arrow length) of each flood (for details see text). Error bars indicate standard errors (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 (*$P < 0.10$; ** $P < 0.01$). See Table 3 for $P$-values of all significant differences between patch types.

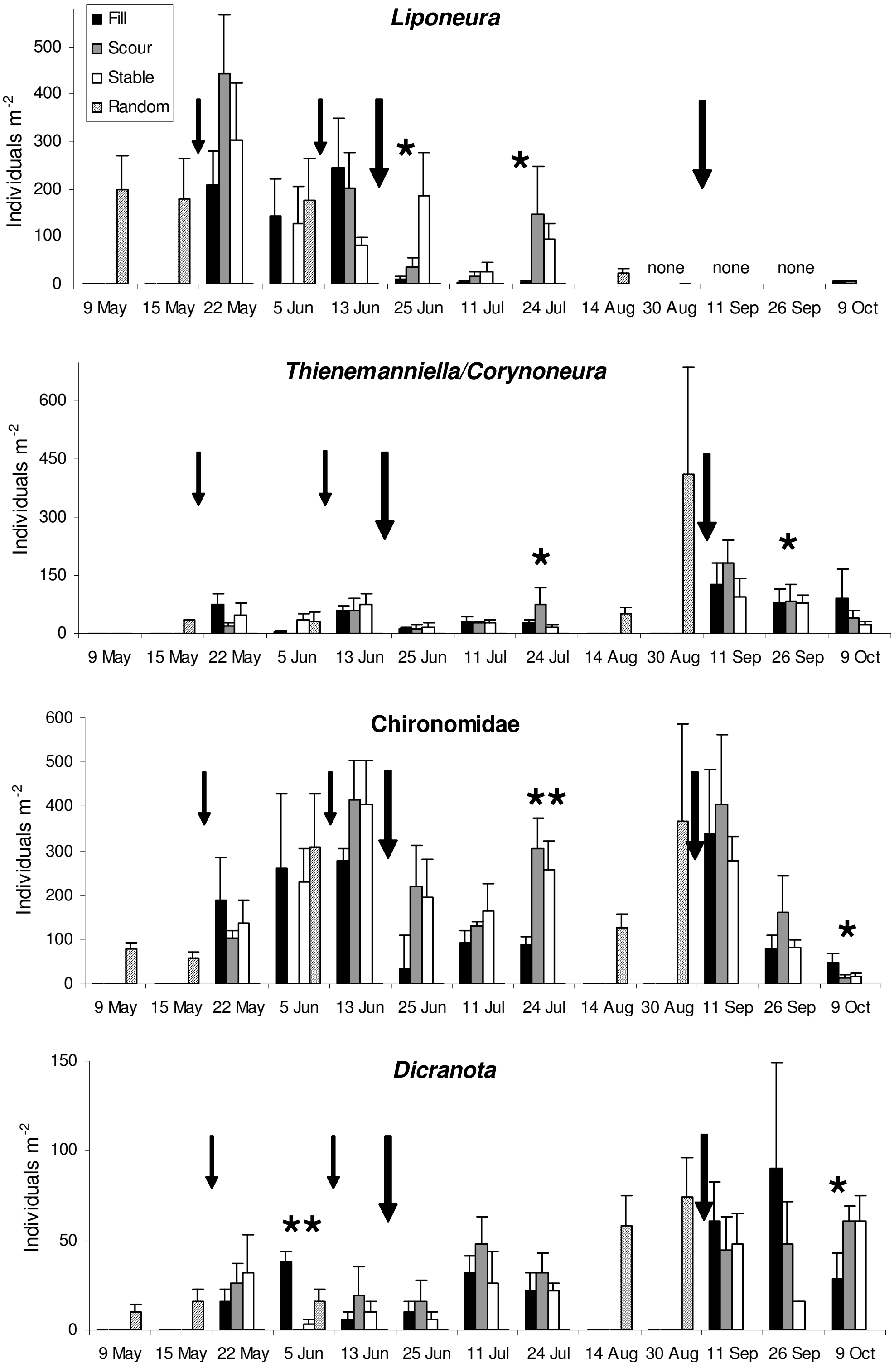

**Fig. 2.** Densities of *Liponeura* spp., *Thienemanniella/ Corynoneura* spp., Chironomidae and *Dicranota* spp. in fill, scour, stable and random patches in the **Schmiedlaine**. See Fig. 1 for further details.

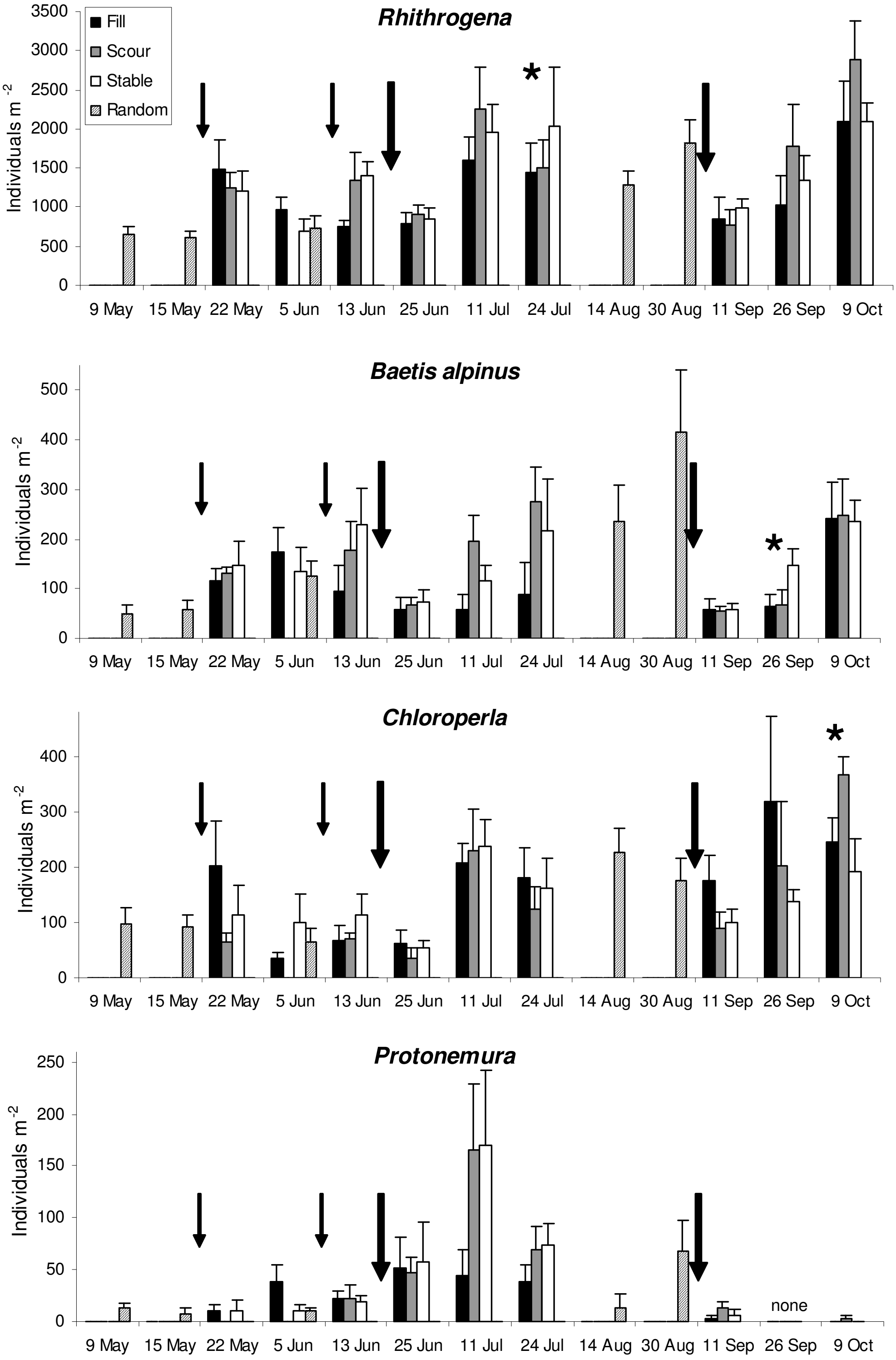

**Fig. 3.** Densities of *Rhithrogena* spp., *Baetis alpinus*, *Chloroperla* spp. and *Protonemura* spp. in fill, scour, stable and random patches in the **Schmiedlaine**. See Fig. 1 for further details.

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

**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 | Inter-action | 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. | ** (+) | |

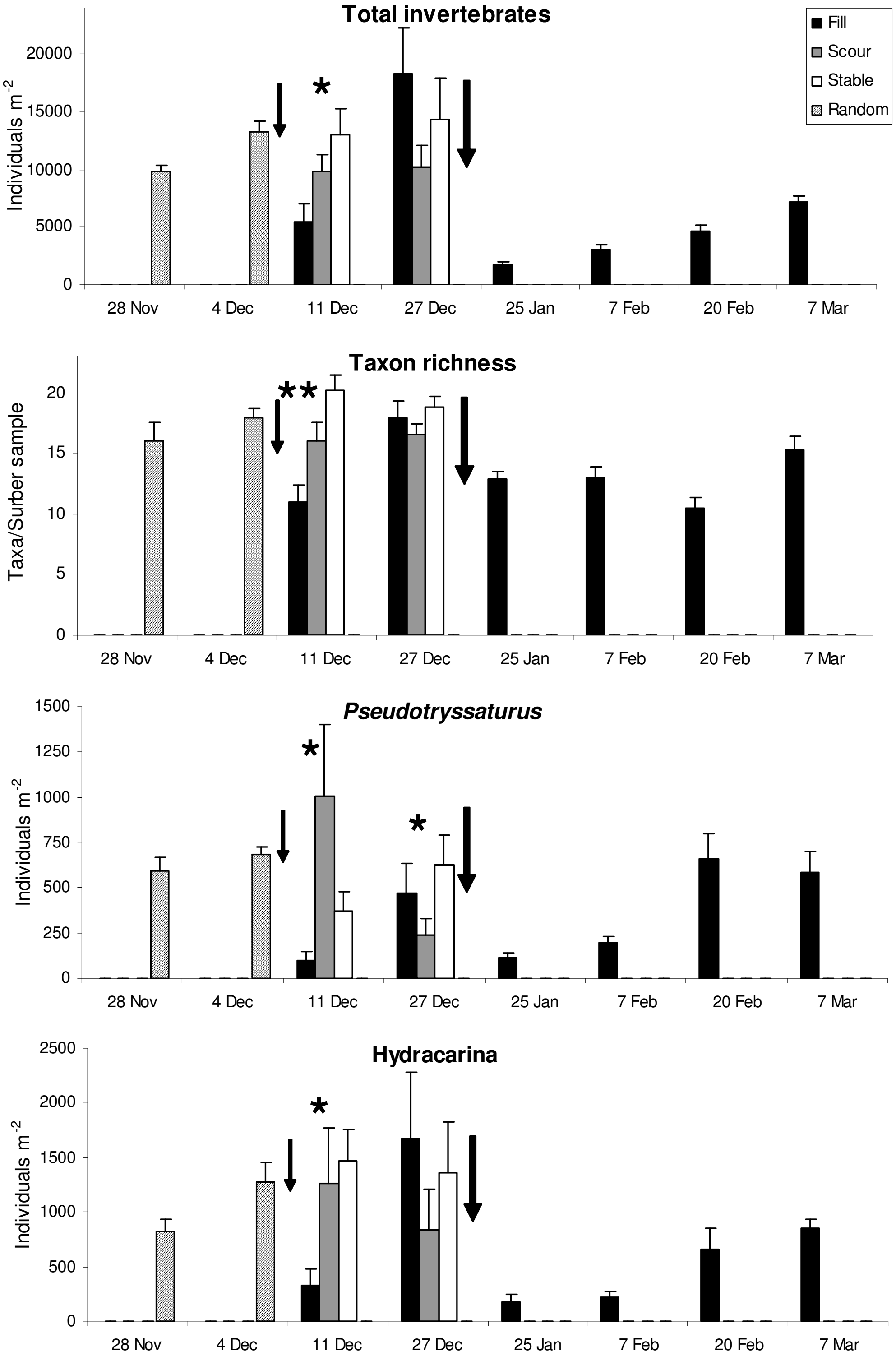

**Fig. 4.** Total invertebrate densities, taxon richness, and densities of *Pseudotryssaturus* spp. and Hydracarina in fill, scour, stable and random patches in the **Kye Burn**. The arrows indicate timing and magnitude (arrow length) of each flood (for details see text). Error bars indicate standard 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.

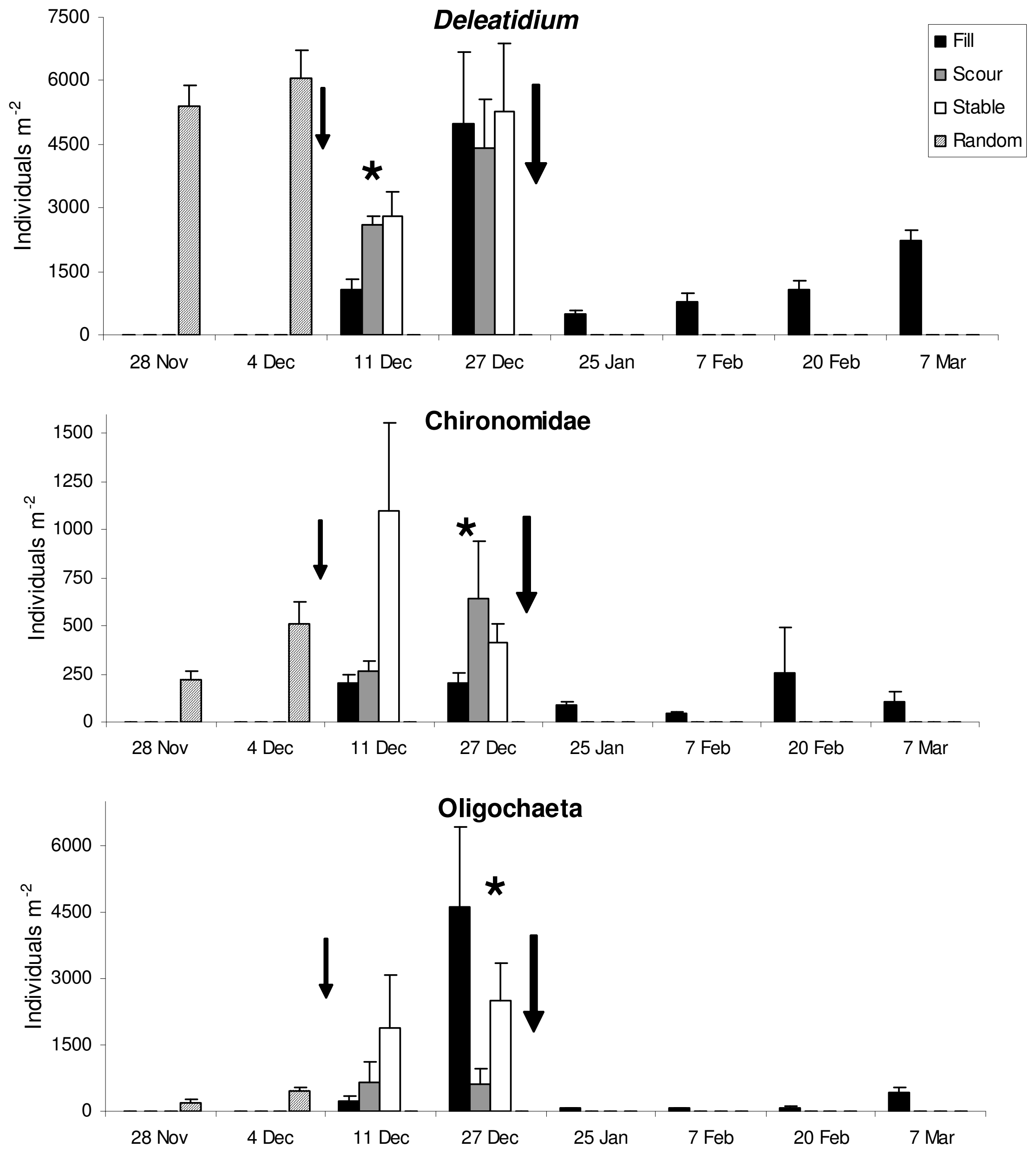

**Fig. 5.** Densities of *Deleatidium* spp., Chironomidae and Oligochaeta in fill, scour, stable and random patches in the **Kye Burn**. See Fig. 4 for further details.

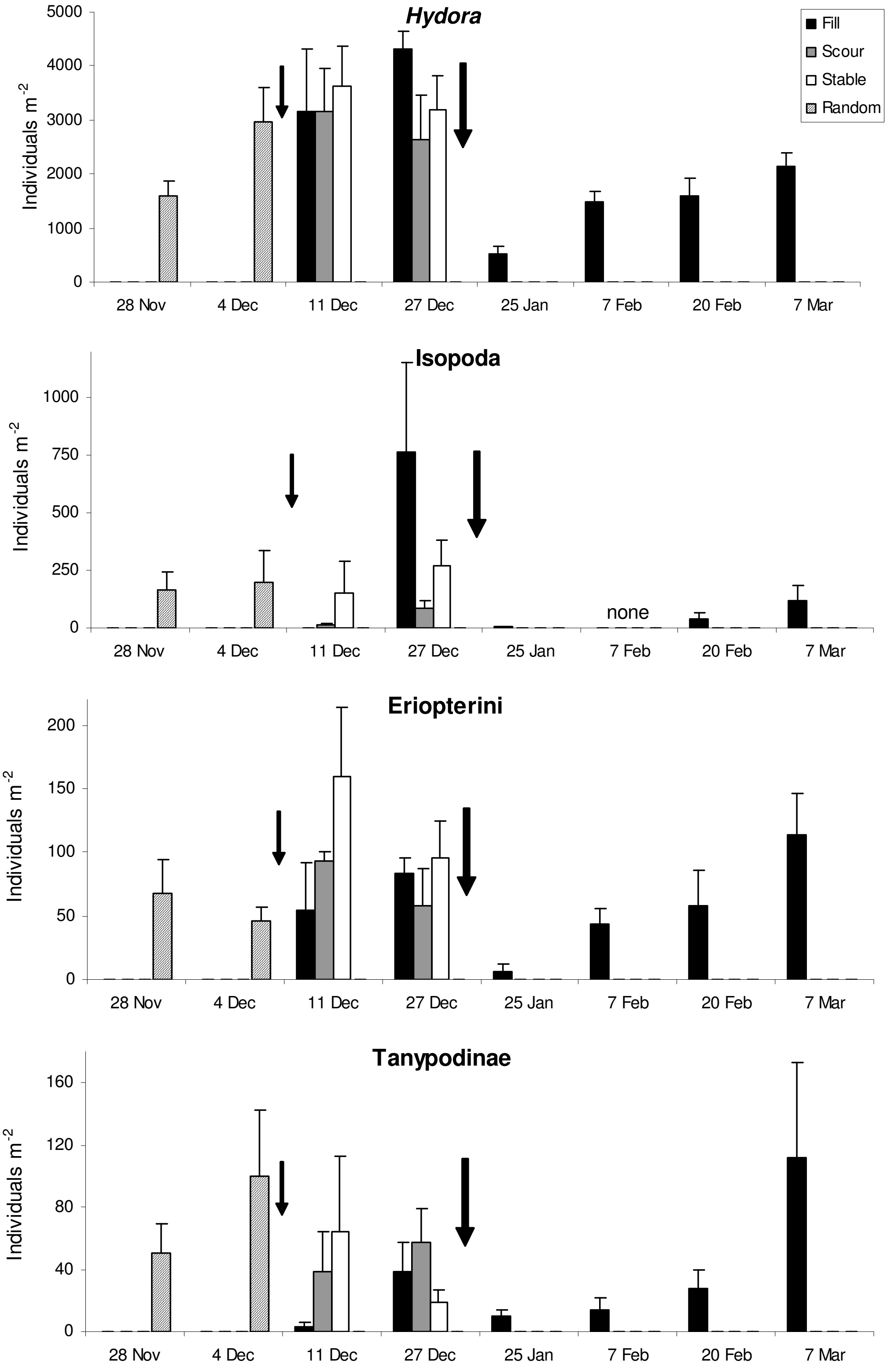

**Fig. 6.** Densities of *Hydora* spp , Isopoda, *Eriopterini* and Tanypodinae in fill, scour, stable and random patches in the **Kye Burn**. See Fig. 4 for further details.

### 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 patches 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 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 patches ($1.3 \times 10^7 \pm 3.5 \times 10^6$ cells/cm²) than in scour patches ($4.0 \times 10^6 \pm 6.7 \times 10^5$ cells/cm²) on 13 June ($P = 0.07$).

One or more of these three parameters, in turn, influenced the distributions of total invertebrates (substratum size on 11 July), taxon richness (substratum size, 25 June), *Leuctra* (epilithic bacteria, 13 June), *Liponeura* (substratum size, 25 June; bacteria, 13 June), *Dicranota* (water depth, 11 July), *Rhithrogena* (depth, 22 May), *Chloroperla* (depth, 11 July) and *Protonemura* (substratum size, 25 June). Consequently, the habitat parameter effects on invertebrates in these 9 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 $\mathrm{cm{\cdot}s^{-1}}$; $P = 0.04$) and the substratum was twice as large in stable than in scour patches on 11 December (63 ± 13 versus 34 ± 7 mm; $P = 0.06$). Densities of epilithic bacteria were higher in fill patches ($1.0 \times 10^8 \pm 2.3 \times 10^7$ cells/cm²) than in stable patches ($2.5 \times 10^7 \pm 1.1 \times 10^7$ cells/cm²) 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*, Hydracarina, *Deleatidium* and Tanypodinae (velocity, 27 December), Chironomidae (depth and substratum size, 11 December), Oligochaeta and *Hydora* (depth, 11 December), and Isopoda and *Eriopterini* (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 size and epilithic algal biomass, in accordance with previous microhabitat studies (Ulfstrand, 1967; Barmuta, 1989; Holomuzki & Messier, 1993; Hearnden & Pearson, 1991). Patterns in invertebrate densities in the different bed stability types varied between individual floods, sampling dates and streams. However, densities were 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 our study of benthic river algae (Matthaei *et al.*, 2003), by contrast, disturbance history effects had been largely independent of habitat parameter effects.

Matthaei and Townsend (2000) speculated that indirect effects of disturbance history on physical habitat parameters and food resources of benthic organisms are more likely to be responsible for long-term differences (several weeks after disturbance) in densities between patch history types. Our present results provide little support for this idea, at least not for invertebrates and the 5 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 5 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* and Hydracarina were highest in stable patches shortly after this spate. In the Schmiedlaine, similar patterns were observed for taxon richness and *Liponeura* after Event 3 and *Leuctra* 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 densities were 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* 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 densities, 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 densities by little more than 50%, while the large flood in the Kye Burn caused a reduction of almost 90% (compare Figs. 1 and 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, Reed & Minshall, 1992; Lytle & Poff, 2004). At the same time, the high frequency and intensity of disturbance in the Schmiedlaine may keep total invertebrate densities permanently at fairly low levels, whereas total densities can reach much higher values in the more benign Kye Burn (compare Figs. 1 and 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 densities and 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.

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# Local disturbance history and the microdistributions of stream algae and bacteria: an experimental approach

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## Abstract

We examined the relationships between local disturbance history, microhabitat parameters and the distributions of benthic algae, primary production and lotic bacteria during an experimental disturbance in a floodprone stream in southern Germany. A total of 200 patches of stream bed were manipulated by removing 10 cm of surface sediment (scour patches) or deposition of 10 cm of pre-disturbed sediment (fill), or were left unchanged (stable). Twice before and three times after the experimental disturbance, algal and bacterial samples were collected from surface stones in replicated scour, fill or stable patches. Primary production in each sampled position was measured under controlled laboratory conditions. For each sampled patch, we determined seven different abiotic and biotic habitat parameters (e.g. water depth, invertebrates in Surber samples). Algal and bacterial cell densities were determined per substratum area. Local disturbance history influenced algal microdistribution in the stream bed most often, followed by near-bed current velocity, invertebrate density and the surface area of the sampled stone. Bacterial microdistribution in the stream bed, by contrast, was related only to stone surface area. The results of this manipulative experiment complement those of previous disturbance history research and provide further evidence that local disturbance history is an important cause for the small-scale patchiness of stream organisms.

## Introduction

The patchy distribution of organisms in space and time is a prominent feature of natural ecosystems and the identification of factors that drive these “patch dynamics” is an important topic for ecologists in general (Pickett and White 1985) and stream ecologists in particular (Townsend 1989, Downes 1990, Poff and Ward 1990, Townsend and Hildrew 1994).

Many studies have shown that the microdistributions of both benthic invertebrates and algae in streams are correlated with abiotic factors, including shear stress, depth and substratum size, and with biotic factors including predation, competition and food (e.g. Peckarsky et al. 1990, Hearnden and Pearson 1991, Kohler 1992, Holomuzki and Messier 1993, Ruse 1994, Stevenson 1996, Biggs et al. 1998, Passy 2001). By contrast, the potential importance of hydrological disturbance in generating patchy distributions has received much less attention, probably because of the difficulty of mapping the local effects of spates and floods. To address this deficiency, Matthaei et al. (1999) used arrays of buried, metal-link scour chains to investigate the three-dimensional disturbance history of the bed in a New

Zealand stream and found that most high-flow events caused a complex mosaic of small ($\leq$ 1 m$^2$) bed patches that had experienced scour, sediment deposition (fill) or remained undisturbed (stable). This “local disturbance history” (Matthaei and Townsend 2000) had long-term effects on the microdistribution of macroinvertebrates, with higher densities in fill or scour patches two months after a disturbance (Matthaei and Townsend 2000).

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, but in fill patches three months after another flood. Although the response of benthic algae to physical disturbance during high-flow events has been investigated in numerous studies (see reviews or conceptual models by Fisher 1990, Steinman and McIntire 1990, Mulholland et al. 1991, Peterson 1996, Biggs et al. 1998), the effect of small-scale patchiness in bed movements on benthic algae had not been addressed prior to the study of Matthaei et al. (2003), especially the distinction between scoured and depositional bed patches.

In comparison to stream invertebrates and algae, ecologists know less about factors driving the patchiness of benthic bacteria, despite their abundance (Haack and McFeters 1982, Stock and Ward 1989), productivity (Marxsen 1996, 1999) and their important role in carbon dynamics (Meyer 1990, Ward and Johnson 1996, Hall and Meyer 1998). Because microbial ecology in running waters is a relatively young discipline (Ward and Johnson 1996), few researchers have studied the role of habitat parameters for bacterial microdistribution (Marxsen 1996, Fischer et al. 2002, 2003), and just a single study (Sailer et al. submitted, see Publication 1) has investigated effects of local disturbance history on bacteria in the Schmiedlaine, a Bavarian stream.

To date, all disturbance history research on algae and bacteria consists of correlative studies. While such studies allow the identification of existing patterns, they need to be complemented by manipulative experiments because only the latter can determine true causes and effects (Townsend 1989). Therefore, we experimentally created a mosaic of bed patches with different disturbance histories in the Schmiedlaine and investigated

(1) short- and long-term effects of disturbance history on the microdistributions of benthic algae, their primary production, and lotic bacteria,

(2) the relative contributions of disturbance history, physical habitat parameters and biotic parameters (food resources and invertebrate densities) to algal and bacterial distributions, and

(3) effects of disturbance history on the habitat parameters (which could cause indirect effects of disturbance history on algal distribution).

## Material and methods

### Study site

Our study was conducted from 5 June to 11 July 2002 in the Schmiedlaine in Germany (70 km south of the city of Munich; 47°40´N, 11°28´E). The Schmiedlaine is a prealpine stream with a steep catchment (area 9.4 km², altitude 750-1800 m a.s.l.; de Jong and Ergenzinger 1995) that lies in a high rainfall zone at the northern edge of the Alps (annual rainfall in the catchment is 1500-2150 mm; Felix et al. 1988, Becht and Wetzel 1989). The stream has a harsh discharge regime with frequent high-flow events (Ergenzinger and de Jong 1997, Matthaei and Huber 2002), a mean flow of about 0.54 $m^3 s^{-1}$ and a baseflow of about 0.12 $m^3 s^{-1}$ (Wagner 1987, de Jong and Ergenzinger 1995). The catchment lacks agricultural development and about 75% of its area is covered by forest.

The stream width at baseflow is about 5-10 m, flow regime and stream channel are natural, the water is cold (<13°C in summer in the Schmiedlaine; G. Sailer, unpublished data) and nutrient-poor (Bavarian Water Management Authority [Wasserwirtschaftsamt] Weilheim, unpublished data). The stream bed consists mainly of cobbles (particle width 64-256 mm) interspersed with small and medium boulders (256-1024 mm). The Schmiedlaine runs through a narrow, v-shaped valley with steep slopes about 200 m high. Sediment supply into the stream is high because of the presence of steep, unstable scree areas (Matthaei and Huber 2002), resulting in unstable stream beds that are easily moved at high flow. We selected a single study site of about 40 m length.

### Experimental disturbance

In 2001, two hundred scour chains (Matthaei et al. 1999) were installed at the study site in a systematic grid (Effenberger et al. in press, see Publication 3). Three to six chains were buried across each of 40 transects, with about 1 m between chains and transects. Most transects contained five chains. The exact location of each chain in the stream bed was determined by measuring distances to three pairs of permanently marked points on the banks that were situated at least 1.5 m above the water line (for more details of the method see Matthaei et al. 1999). In 2002, we randomly selected a subset of 146 of these chain locations as our experimental patches. The experimental disturbance was conducted on 18 and 19 June 2002. Daily rainfall data collected 5 km from the study site in April – June 2002 (J. Wurth, German Meteorological Service, unpublished data) and rainfall-discharge data from previous research (Matthaei and Huber 2002, Effenberger et al. in press, see Publication 3) indicated that no bed-moving floods had occurred for at least one month prior to the experimental disturbance. In 42 randomly chosen scour patches, we removed the top 10 cm of surface sediment from an area of about 50 × 50 cm with a shovel. In 39 similarly sized fill patches, we deposited 10 cm of pre-disturbed sediment. The deposited sediment was obtained from a stream section about 40 m downstream of the study site, where two people disturbed the sediment by kicking and shuffling vigorously for several minutes before shovelling it into buckets. This method has been shown to successfully simulate bed disturbance during a flood (Matthaei et al. 1996, 1997). To keep invertebrates from drifting into experimental patches located further downstream when scour and fill patches were created, we held two large kick nets (bottom width 60 cm, height 40 cm, mesh size 200 µm) on the stream bottom directly downstream of each manipulated patch. The scouring and filling depths of 10 cm correspond to a mid-sized disturbance in the Schmiedlaine (range of scour or fill 2-45 cm; Effenberger et al. in press/Publication 3). Moving from upstream to downstream, we created 18 scour and 19 fill patches in the upper 13 transects of the site on 18 June, plus 24 scour and 20 fill patches in the lower 27 transects on 19 June (see statistical analysis). The remaining 65 chain locations were left undisturbed (stable patches).

### Biological sampling

We collected two sets of random samples of epilithic algae and bacteria on 5 and 12 June, before the experimental disturbance. We also took samples directly after (on 20 June), six days after (26 June) and 21 days after disturbance (11 July). A minor flow peak ($Q_{max} \approx 4.5$ $m^3/s$) in the Schmiedlaine on 7 July removed some sediment from several of the experimental fill patches, which we avoided on 11 July. We terminated the experiment on this date because there were not enough fill patches left for another sampling occasion.

Our focus was on densities of epilithic algae and bacteria. A parallel study (Herrmann 2003) investigated densities of benthic invertebrates and standing stocks of particular organic matter (POM) using a Surber sampler (area 0.0625 m², mesh size 200 µm). These two parameters were used as additional covariates in our analysis (see below). The Surber samples also served as sampling units in the present study. On both pre-disturbance sampling dates, we collected eight samples at random across the site except that we carefully avoided the 146 scour chain locations that were used later in the experimental disturbance. On each post-disturbance sampling date, eight samples were collected randomly from scour positions, eight from patches that had experienced fill, and eight from stable patches.

In each bed patch, a Surber sample was taken in the immediate vicinity of the focal chain (with at least one side of the frame of the sampler touching the chain). A marked screwdriver fixed a sampling depth of 10 cm. Densities of epilithic algae and bacteria 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 back 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%) in the field and stored on ice in the dark.

Before the experimental disturbance, we collected a second surface stone from each of the eight random Surber samples as described above. This second stone was used to determine epilithic primary production and respiration in the laboratory (see below). These stones were transported in separate 5-litre buckets filled with stream water and transferred into individual production chambers directly after arrival in the laboratory. On each sampling date after disturbance, we collected stones for primary production measurements from the first five of the eight Surber samples in each of the three bed stability categories.

For each Surber sample, we determined water depth and near-bed current velocity (≈3 cm above the substratum). The velocity was measured with a propeller flow meter (Hoentzsch GmbH, Waiblingen, Germany; propeller diameter 2 cm). We also determined substratum composition by eye as the averaged b-diameter (particle width) of the first- to third-most common substratum sizes class inside the Surber sampler. These size classes were identified using a modified Wentworth scale (Harrelson et al. 1994), which uses the half-phi scale (e.g. 16-22 mm, 22-32 mm, 32-45 mm, 45-64 mm, 64-90 mm, 90-128 mm etc.). All particles smaller than 8 mm were combined in a single category. The four habitat parameters were used as additional covariates in our analysis.

### Sample processing

We collected 88 samples of algal and bacterial abundance and 61 samples for stream metabolism measurements. In the parallel study, Herrmann (2003) collected 88 invertebrate and POM samples. Each surface stone sample was divided into four equal parts in the laboratory. One quarter was used for quantitative counts of bacteria with the 4´, 6-diamidino-

2-phenylindol (DAPI) staining method (Porter and Feig 1980, Ward and Johnson 1996). We distinguished between coccoid and rod-shaped bacteria during counting.
The second quarter of each sample was used for quantitative counts of algae in a Neubauer counting chamber (model “improved”, volume 0.9µl; VWR International, Darmstadt, Germany) at a magnification of 400x under a Leitz microscope (model Laborlux K). Cox (1996) and Dillard (1999), keys to identify algae from live or formalin-preserved material, were used to make a list of the common genera. The genera *Amphora* spp., *Cymbella* spp. and *Encyonema* spp. were combined into a single taxon because the keys did not allow us to distinguish reliably between them. The taxon ’filamentous Chlorophyta’ often included the genus *Amphithrix* spp., and ’filamentous Cyanophyta’ often included *Phormidium* spp..

For each sample, 5-20 random subsamples of 0.1 µl each were counted, adding up to a total of at least 400 algal cells (Schwoerbel 1994). We found a total of 12 algal taxa and analysed taxon-specific density patterns for the nine taxa that occurred regularly in the samples. These taxa represented at least 99% of the total number of algal cells found in all samples.

The remaining two quarters of each surface stone sample were used to determine algal biomass as chlorophyll a and the ash free dry mass (AFDM) of the epilithic biofilm. The AFDM data were excluded from the statistical analysis because this parameter includes both epilithic algae and bacteria and we investigated these two variables separately in our experiment. The surface area of each stone was determined by wrapping stones in aluminum foil and weighing the foil (Townsend et al. 1997), and algal and bacterial counts were converted to densities per cm$^2$ of stone surface area. Further, stone surface area was used as a covariate in our analysis, because this parameter influenced densities of epilithic algae in a previous study (Matthaei et al. 2003).

### Stream metabolism measurements

Primary production and respiration of epilithic biofilms were measured in transparent respiration chambers made from acrylic glass (dimensions 40 cm x 18 cm x 13.5 cm, volume = 8 L). Each chamber was equipped with a pump to circulate the water (Universal 1060, capacity 38 l/min, Eheim GmbH, Deizisau, Germany) and an oxygen probe with a thermistor. This probe was fitted to an oxygen meter (Oxi 340, WTW, Weilheim, Germany) with the capacity to log oxygen concentration and temperature data. Fifteen chambers (five for each bed stability category) were deployed in a climate chamber at a temperature of 15 °C.

One day after each sampling date, each chamber was loaded with one stone and filled with stream water from the study site. For each chamber run in the Schmiedlaine, we applied the following light-dark regime (in µE $m^{-2}$ $sec^{-1}$): 0 (darkness), 49.2, 71.1, 107.1, 228.3, and once again 0. In the Kye Burn, the corresponding figures were 0, 51.3, 73.3, 102.2, 157.9 and 0 µE $m^{-2}$ $sec^{-1}$. Each dark and light period lasted 100 minutes. Temperature (T) and dissolved oxygen ($O_2$) were recorded twice per minute. Average net oxygen production rates (β) during each light or dark period were obtained by linear regressions of $O_2$-concentration against time. Because chamber temperatures increased during the incubations (on average from 11 to 25°C), β was normalized on 20°C using the equation $\beta(20°C) = \beta(T)/1.072^{(T-20°C)}$ for oxygen saturation of water at an air pressure of 712.1 mm Hg. In this equation, β is the net oxygen production rate (mg $O_2L^{-1}h^{-1}$) and T the average chamber temperature during a light or dark period (Uehlinger *et al.*, 2000).

Calculations of the metabolic parameters respiration and gross primary production rates (gpp) were based on β(20°C). Dark respiration ($r_D$) was calculated by averaging β(20°C) of the two dark periods. Respiration rates during the light periods ($r_L$) were assumed to equal $r_D$., GPP was computed as mean of all light intensities ($R_L$) and the corresponding β(20°C), the ratio of P/R as GPP/$R_L$. Rates of gross primary production and dark respiration were normalized on stone surface area. Algal biomass and stone volume were determined at the conclusion of each metabolism run.

### Data analysis

To determine the overall initial effect of the experimental disturbance on the algal and bacterial community, we compared the last pre-disturbance sampling date with the first post-disturbance date, using one-way analysis of variance (ANOVA). For this analysis, all three disturbance history categories on the first post-disturbance date were combined. Comparisons between disturbance history categories were conducted using one-way ANOVAs and one-way analysis of covariance (ANCOVA), with “patch type” as factor and the six studied habitat parameters as covariates. Exploratory correlation matrices (all samples combined) had shown that none of the six covariates were strongly correlated with each other ($r_p < 0.33$ in all cases). Because our experimental disturbance had been conducted over a period of two days (see above), we also included “disturbance date” as a blocking factor in the analyses.

Dependent variables for epilithic algae were total density, taxon richness, living biomass (measured as chlorophyll a), the ratio of chlorophyll a to phaeophytin (Peterson et al. 1990), periphyton vitality (living algal cells / total algal cells), gross primary production (GPP), the ratio of primary production to respiration, and the densities of each common algal taxon. Dependent variables for epilithic bacteria were total density and densities of coccoid and rod-shaped bacteria. Direct effects of disturbance history on the 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 and Townsend 2000) and algae (Matthaei et al. 2003), we expected the effects of disturbance history to change with time since the last previous high-flow event. Consequently, we analysed all three history-specific sampling dates separately. We also calculated separate ANCOVAs for each covariate to avoid collinearity problems (Quinn and Keough 2002). If a significant factor x covariate interaction was found, we verified the reliability of the estimated marginal means for each patch type. This test was performed by comparing the actual adjusted means for each patch type (determined using the individual regression lines of the dependent variable against the covariate) with the estimated marginal means calculated by the ANCOVA (see Matthaei and Huber 2002). Only covariates with significant effects on the dependent variable are discussed. In cases where no covariate had a significant effect, all covariates were dropped from the analysis and a simple one-way ANOVA was calculated. An effect of disturbance history was only considered as valid if it was detected in at least 50% of all ANCOVAs with significant covariate effects (or in the ANOVA, if none of the covariates had a significant effect on the dependent variable).

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 $\alpha$ for multiple testing (Perneger 1998, Quinn and Keough 2002, see also Discussion). 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 and Quinn 1989). With the ANOVAs, we used Tukey-HSD tests, except in cases of persisting heteroscedasticity, where we performed Games-Howell tests (Quinn and 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 1 & 2 below). Here we selected the ranking that had been determined in the majority of these tests. All analyses were calculated in SPSS® version 11.0 (SPSS Inc., Chicago).

# Results

## Summary of disturbance history and habitat parameter effects

We analysed patch-specific patterns of algal and bacterial densities for the three post-disturbance sampling dates. For benthic algae, we analysed a total of 47 cases for the factor disturbance history with six covariates (three sampling dates x 16 variables minus one case on 20 June where non-filamentous Chlorophyta were absent). The corresponding total for the bacteria was 9 cases (three sampling dates x three variables).

Local disturbance history was related to algal microdistribution in the stream bed most often (in 23% of all analysed cases), followed by near-bed current velocity and total invertebrates (13% each), the surface area of the sampled stone (11%), substratum size in the Surber samples (9%), and water depth (6%). POM was never correlated significantly with algal distribution. Bacterial microdistribution in the stream bed was related only to stone surface area (in 56% of all analysed cases).

## Specific relationships of benthic flora with disturbance history and habitat parameters

Total algal density (all patch types combined) was not reduced by the experimental disturbance (*P*=0.61; Fig. 1). Algal density was higher in stable than in disturbed patches on 26 June, six days after disturbance (Table 1), and was correlated positively with near-bed current velocity and total invertebrate density in Surber samples on 11 July (Table 2).

Algal taxon richness and living algal biomass (measured as chlorophyll a) were also not reduced by the disturbance ($P \geq 0.56$; Fig. 1). Taxon richness was higher in stable and scour patches than in fill patches on 26 June, and algal biomass was higher in stable than in fill patches on the same date (Table 1). Taxon richness was correlated positively with stone surface area, and algal biomass likewise with current velocity, on 11 July (Table 2).

The ratio of chl a to phaeophytin was consistently low (Fig. 1) and remained unchanged by the disturbance (*P*=0.09). This ratio was higher in stable relative to scour patches on 20 June and relative to scour and fill patches on 11 July (Table 1). It was correlated positively with total invertebrate density on 11 July. Periphyton vitality (living / total algal cells), by contrast, was consistently high and was also not affected by the experimental disturbance (*P*=0.15; Fig. 2). Vitality never differed between patch types (Table 1) and was correlated positively with water depth and current velocity on 11 July (Table 2).

Gross primary production (GPP) and the ratio of primary production to respiration (P/R) were both reduced by the disturbance ($P \leq 0.01$; Fig. 2). GPP was always similar between patch types, whereas P/R was higher in stable than in scour and fill patches on 26 June

(Table 1). GPP was correlated negatively with substratum size on 26 June, whereas P/R was correlated positively with stone surface area on the same date (Table 2).

Densities of none of the common algal taxa were reduced by the experimental disturbance (P≥0.27 in all cases; Figs. 3 & 4). *Cocconeis* spp. was more common in scour than in fill patches on 20 June, whereas the opposite pattern was found for filamentous Chlorophyta on the same date (Fig. 3, Table 1). *Cocconeis* was correlated positively with substratum size on 20 June (Table 2). Filamentous Chlorophyta were correlated negatively with both water depth and stone surface area on 20 June and positively with current velocity on 11 July.

Densities of *Achnanthes* spp., *Gomphonema* spp. and filamentous Cyanophyta all differed between bed stability types on 26 June, six days after the experimental disturbance, with densities generally being highest in stable bed patches (Fig. 3). *Achnanthes* was more abundant in stable and scour patches than in fill patches and was correlated negatively with invertebrate density on 26 June (Table 2). Densities in stable patches were higher than in fill patches for *Gomphonema* and higher than in both disturbed patch types for filamentous Cyanophyta (Table 1). *Gomphonema* was correlated with current velocity and invertebrate density on 26 June, and filamentous Cyanophyta with water depth on 20 June and with current velocity on 11 July.

Non-filamentous Chlorophyta also appeared to be more common in stable than in scour patches on 26 June (Fig. 3), but this difference between patch types was found in only one out of three ANCOVAs with significant covariate effects and was therefore considered invalid (see Tables 1 & 2 and Methods). Densities of non-filamentous Chlorophyta were correlated positively with substratum size and stone surface area and negatively with invertebrate density on 26 June (Table 2).

The remaining three common taxa (*Cymbella/Encyonema/Amphora* spp., Meridion spp. and coccal Cyanophyta) showed no differences between patch types on all post-disturbance sampling dates (Fig. 4, Table 1). Densities of the first taxon were correlated positively with substratum size and stone surface area on 26 June, whereas the other two taxa showed no correlations with any of the studied microhabitat parameters (Table 2).

Densities of total epilithic bacteria, coccoid bacteria and rod-shaped bacteria were not affected by the experimental disturbance (*P*≥0.08; Fig. 4). All three bacterial parameters showed no differences between the three patch types (Table 1) and were correlated negatively with stone surface area on one or two sampling dates each (Table 2).

## Interactions between disturbance history and habitat parameters

In all cases where an effect of disturbance history on algal or bacterial distributions in the ANOVA occurred simultaneously with a correlation of a habitat parameter with algal or bacterial distributions in the ANCOVAs, the disturbance history effect remained valid; i.e. it was detected in at least 50% of all ANCOVAs with significant covariate effects (compare Tables 1 & 2 and see Methods). In addition, there were two cases (*Cocconeis* and filamentous Chlorophyta on 20 June) when significant correlations with habitat parameters revealed disturbance history effects which had remained undetected in the ANOVAs.

## Disturbance history effects on habitat parameters and indirect effects on stream biota

Disturbance history influenced the six measured habitat parameters in seven of 18 possible cases (39%). On 20 June, water depth was higher in scour patches (mean 24 ± 2 [SE] cm) than in stable (17 ± 2 cm) or fill patches (15 ± 2 cm; $P$=0.01), substratum size in Surber samples was larger in fill (64 ± 10 mm) than in scour patches (36 ± 7 mm; $P$=0.04), the surface area of the sampled stones was larger in fill (518 ± 7 $cm^2$) than in scour patches (248 ± 7 $cm^2$; $P$=0.01), and POM was more abundant in scour (11.2 ± 2.4 $g/m^2$) than in fill positions (1.6 ± 2.4 $g/m^2$; $P$=0.03).

One or more of these four habitat parameters, in turn, were correlated with the distributions of filamentous Chlorophyta (water depth), filamentous Cyanophyta (water depth and stone surface area), *Cocconeis* (substratum size) and all three bacterial parameters (stone surface area) on this date (see Table 2). Consequently, these six correlations of habitat parameters with algal and bacterial densities can be seen as *indirect* effects of disturbance history on these stream biota. Note that filamentous Chlorophyta and *Cocconeis* were also influenced directly by disturbance history on this date (see Table 1).

On 26 June, water depth was higher in scour (21 ± 2 cm) than in fill patches (11 ± 1 cm; $P$=0.001), stable patches (69 ± 9 mm) and fill patches (53 ± 4 mm) contained larger substrata than scour patches (28 ± 4 mm; $P$=0.001), and the surface area of sampled stones was larger in stable (481 ± 6 $cm^2$) than in scour patches (239 ± 6 $cm^2$; $P$=0.05). One or both substratum parameters were related to the distributions of gross primary production (substratum size), *Cymbella*/*Encyonema*/*Amphora* and non-filamentous Chlorophyta (substratum size and stone area) and primary production to respiration (stone area) on this date (Table 2), resulting in another four indirect effects of disturbance history on stream algae. Altogether, algae were thus influenced indirectly by disturbance history in seven cases (15% of 47 possible cases), and bacteria in three cases (33%). The ratio of primary production to respiration was also influenced directly by disturbance history (Table 1).

**Table 1.** Summary (*P*-values) of factor effects in the one-way ANOVAs and ANCOVAs comparing the algal and bacterial communities in scour, fill and stable patches in the **Schmiedlaine**. Prior to final analysis, data were log-transformed where necessary and potential factor x covariate interactions explored (see column 4). For each dependent variable, the results of the 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 (a complete list of all covariate effects is given in Table 2). For more details see text. $\alpha$=0.05.

| **Date and dependent variable** | **Covariate in ANCOVA** | **Covariate** | **Inter-action** | **Factor** | **Block** | **Ranking** |
|---|---|---|---|---|---|---|
| **20 June** | | | | | | |
| Chlorophyll a / phaeophytin | - | - | - | 0.04 | 0.09 | Stable > scour |
| *Cocconeis* spp. | Substratum size | 0.02 | 0.17 | 0.05 | 0.01 | Scour > fill |
| Filamentous Chlorophyta | Surface area | 0.03 | 0.49 | 0.04 | 0.20 | Fill > scour |
| **26 June** | | | | | | |
| Total algal density | - | - | - | 0.004 | 0.75 | Stable > scour/fill |
| Algal taxon richness | - | - | - | 0.002 | 0.01 | Stable/scour > fill |
| Living algal biomass | - | - | - | <0.0001 | 0.15 | Stable > fill |
| Primary production / respiration | - | - | - | 0.002 | 0.14 | Stable > scour |
| | Surface area | 0.05 | 0.43 | 0.001 | 0.52 | Stable > fill/scour |
| *Achnanthes* spp. | - | - | - | 0.01 | 0.04 | Scour > fill |
| | Total invertebrates | 0.05 | 0.52 | 0.003 | 0.04 | Scour/stable > fill |
| *Gomphonema* spp. | - | - | - | 0.01 | 0.01 | Stable > fill |
| | Current velocity | 0.03 | 0.46 | 0.02 | 0.004 | Stable > fill |
| | Total invertebrates | 0.01 | 0.39 | 0.003 | 0.01 | Stable > fill |
| Filamentous Cyanophyta | - | - | - | 0.02 | 0.04 | Stable > fill/scour |
| Non-filamentous Chlorophyta | Total invertebrates | 0.03 | 0.32 | 0.02 | 0.25 | Stable > scour |
| **11 July** | | | | | | |
| Chlorophyll a / phaeophytin | - | - | - | 0.02 | 0.44 | Stable > fill/scour |

**Table 2.** Summary (*P*-values) of covariate effects in the one-way ANCOVAs comparing the algal and bacterial community in scour, fill and stable patches in the **Schmiedlaine** (for factor effects see Table 1). Only significant results are shown; blanks indicate non-significant results. * P < 0.10; ** P < 0.01; *** P < 0.001; + positive correlation; - negative correlation.

| Covariate and dependent variable | 20 June | 26 June | 11 July |
|---|---|---|---|
| **Water depth** | | | |
| Periphyton vitality | | | * (+) |
| Filamentous Cyanophyta | * (-) | | |
| Filamentous Chlorophyta | * (-) | | |
| **Near-bed current velocity** | | | |
| Total algal density | | | * (+) |
| Living algal biomass | | | * (+) |
| Periphyton vitality | | | * (+) |
| *Gomphonema* spp. | | * (-) | |
| Filamentous Cyanophyta | | | * (+) |
| Filamentous Chlorophyta | | | ** (+) |
| **Substratum size** | | | |
| Gross primary production | | ** (-) | |
| *Cocconeis* spp. | * (-) | | |
| *Cymbella/Encyonema/Amphora* spp. | | * (+) | |
| Non-filamentous Chlorophyta | none | * (+) | |
| **Stone surface area** | | | |
| Algal taxon richness | | | * (+) |
| Primary production/respiration | | * (+) | |
| *Cymbella/Encyonema/Amphora* spp. | | * (+) | |
| Filamentous Chlorophyta | * (-) | | |
| Non-filamentous Chlorophyta | none | ** (+) | |
| Total epilithic bacteria | * (-) | | * (-) |
| Coccoid epilithic bacteria | * (-) | | * (-) |
| Rod-shaped epilithic bacteria | | | * (-) |
| **POM** | | | |
| **Total invertebrates (Surber)** | | | |
| Total algal density | | | * (+) |
| Chlorophyll a/phaeophytin | * (+) | | * (+) |
| *Achnanthes* spp. | | * (-) | |
| *Gomphonema* spp. | | ** (-) | |
| Non-filamentous Chlorophyta | none | * (-) | |
| **Total epilithic bacteria** | | | |
| Chlorophyll a/phaeophytin | | ** (-) | |
| Filamentous Cyanophyta | | * (-) | |
| **Total epilithic algae** | | | |

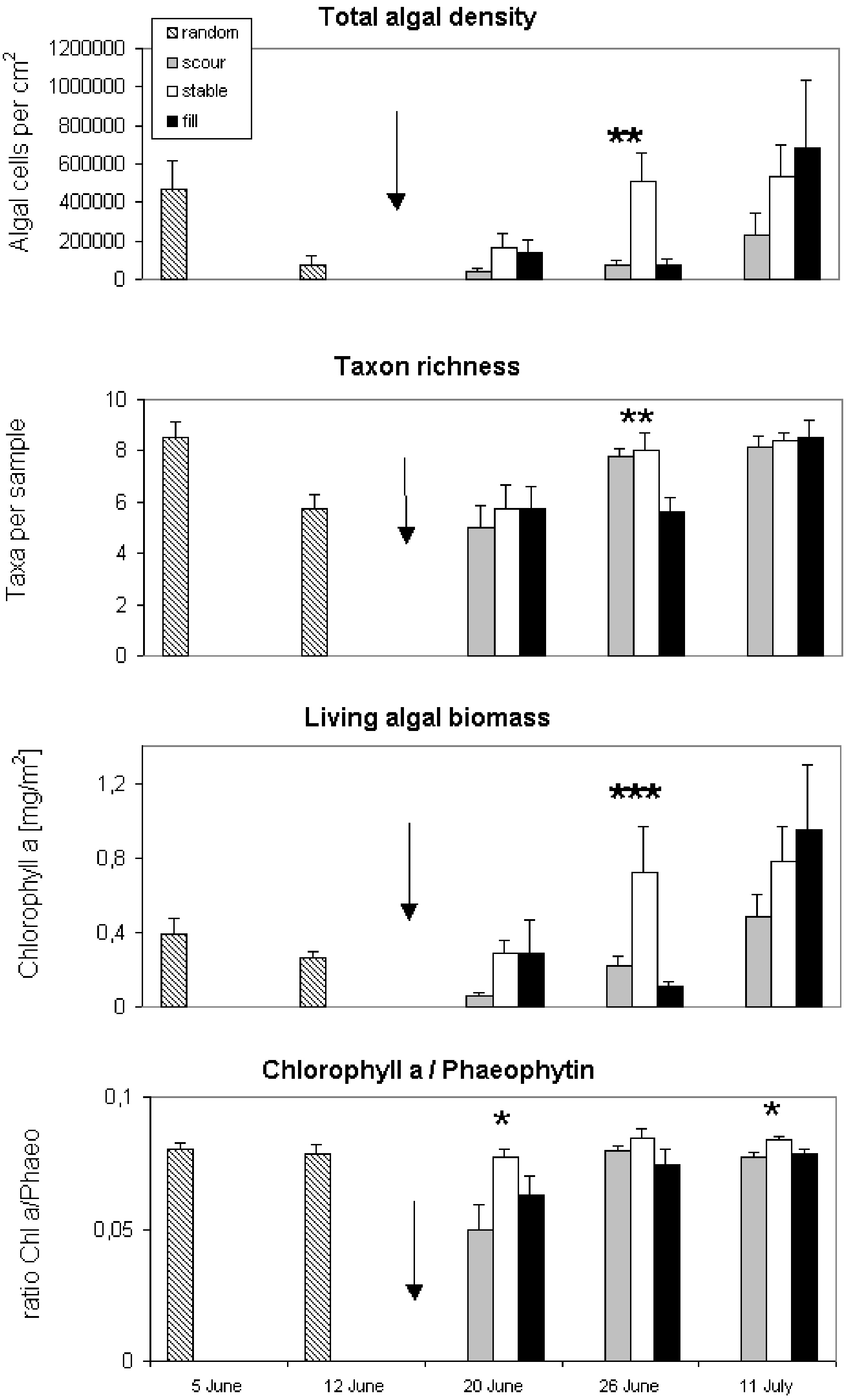

**Fig. 1**. Total epilithic algal density, taxon richness, living algal biomass and the ratio of chlorophyll a to phaeophytin in random, scour, stable and fill patches. The arrow indicates the timing of the experimental disturbance (for details see text). Significant differences between patch types in the ANOVAs and ANCOVAs are shown by asterisks above the mean values. Error bars indicate standard errors. See Table 1 for *P*-values and statistical power of all comparisons between patch types. $*P<0.05$; $**P<0.01$; $***P<0.001$.

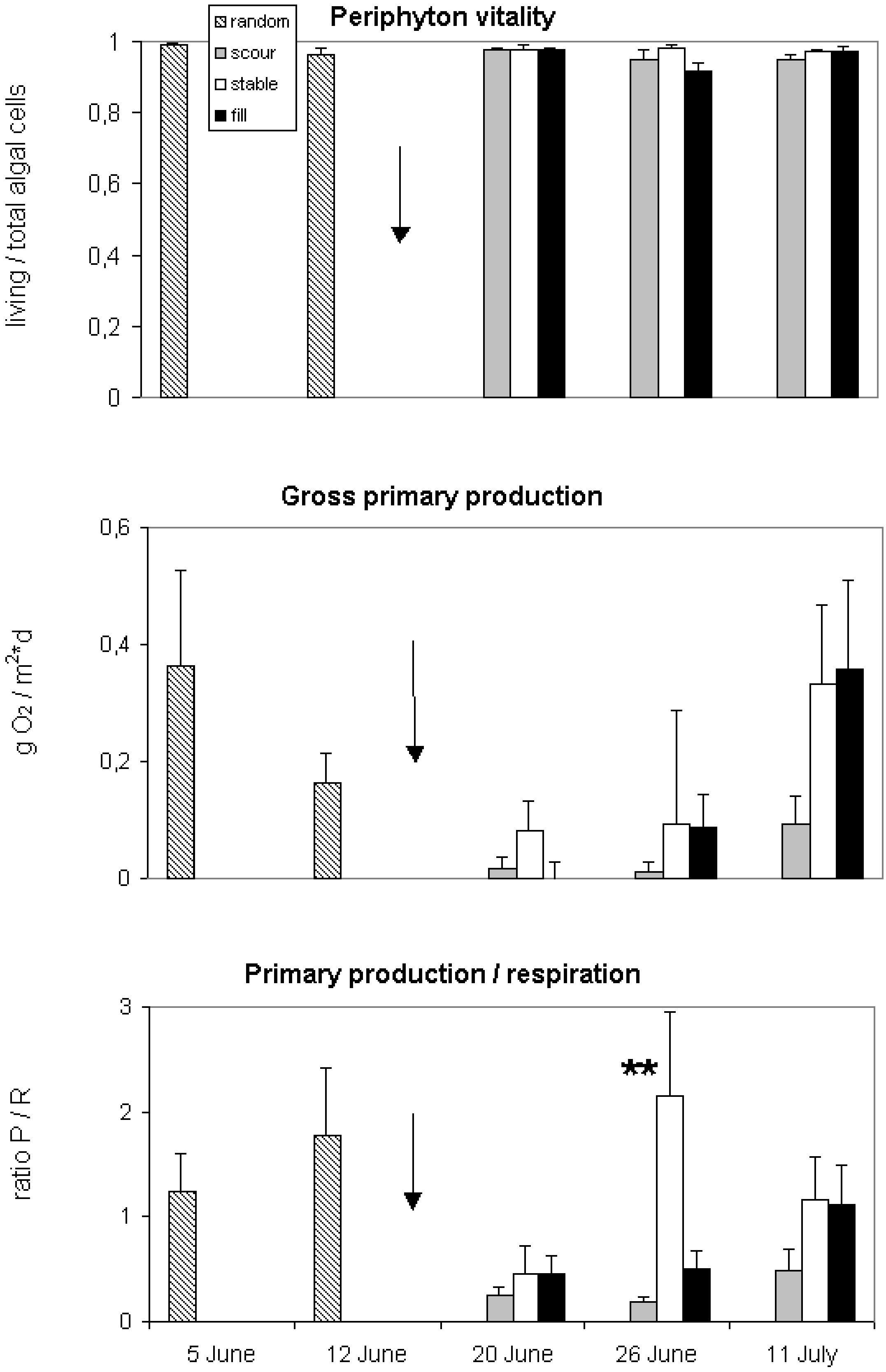

**Fig. 2**. Periphyton vitality, gross primary production and the ratio of primary production to respiration in random, scour, stable and fill patches. See Fig. 1 for further details.

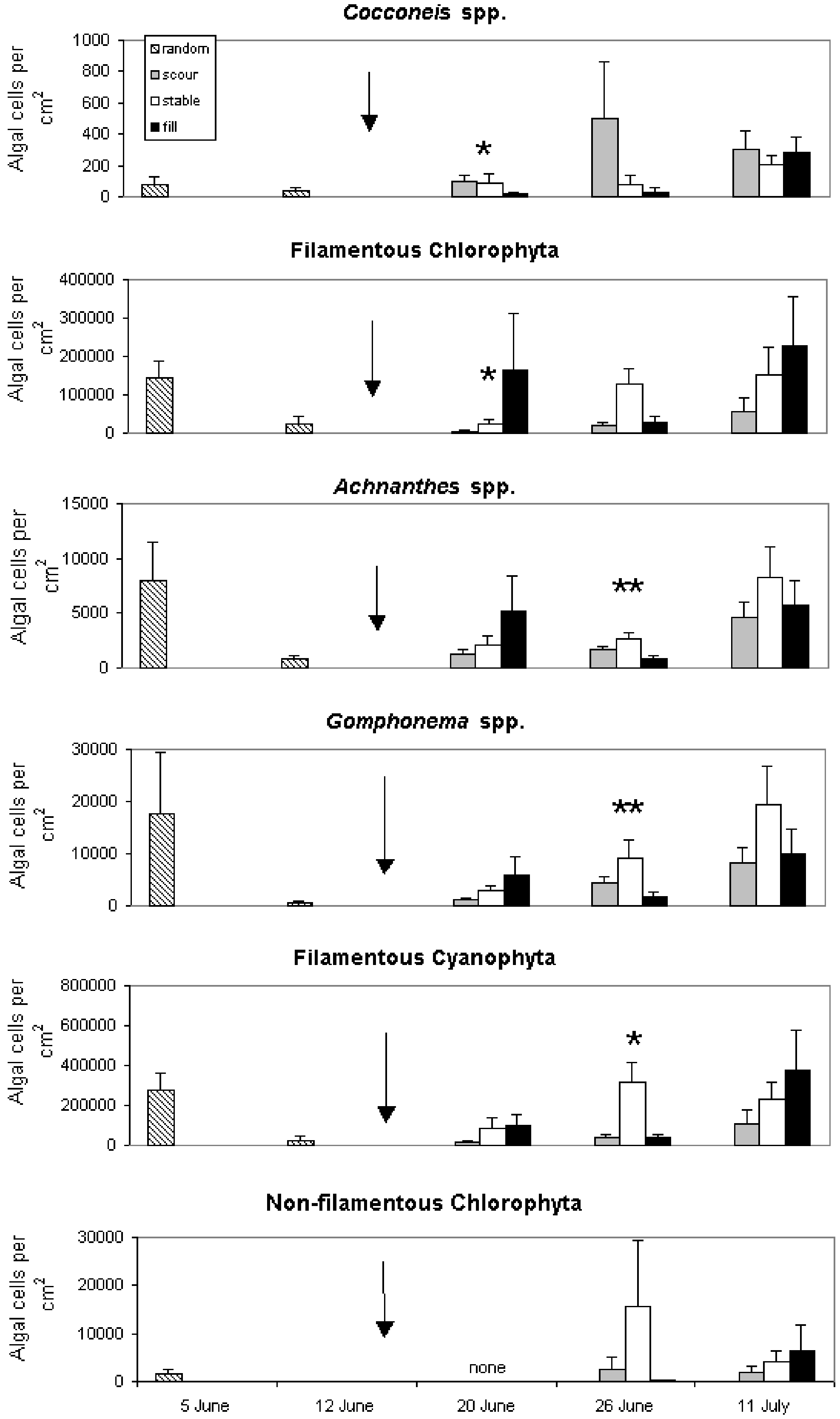

**Fig. 3.** Densities of *Cocconeis* spp., filamentous Chlorophyta, *Achnanthes* spp., *Gomphonema* spp., filamentous Cyanophyta and non-filamentous Chlorophyta in random, scour, fill and stable patches. See Fig. 1 for further details.

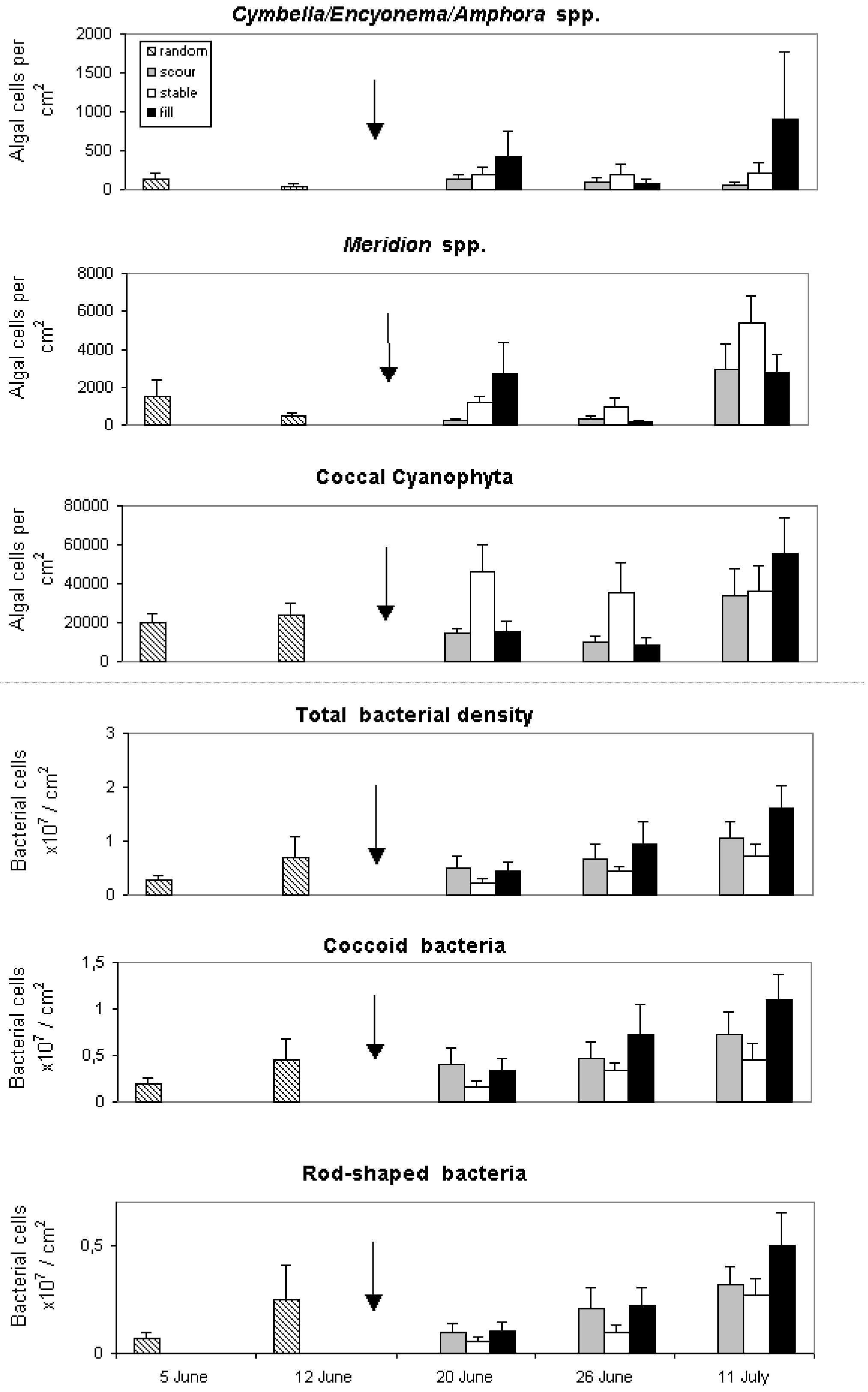

**Fig. 4.** Densities of *Cymbella/Encyonema/Amphora* spp., *Meridion* spp., coccal Cyanophyta, total epilithic bacterial density, coccoid and rod-shaped bacteria in random, scour, fill and stable patches. See Fig. 1 for further details.

## Discussion

### Relative importance of disturbance history and physical habitat

Local disturbance history affected algal microdistribution in the bed most often in our experiment in the flood-prone stream Schmiedlaine, followed by near-bed current velocity, total invertebrate density and the surface area of the sampled stone. This result corresponds well with results from previous, correlative research on river algae (Matthaei et al. 2003), in which disturbance history had affected algal distribution more often than current velocity, substratum size and water depth combined. In a correlative study in the Schmiedlaine (Sailer et al. submitted, see Publication 2), substratum characteristics and current velocity were related to algal distribution at least as often as disturbance history. The results for the better-studied habitat parameters were largely in accordance with previous microhabitat studies for benthic algae (see e.g. Stevenson 1996, Biggs et al.1998, Passy 2001). Disturbance history also had several indirect effects on algal distribution (see below).

In contrast to the benthic algae, bacterial microdistribution was related solely to stone surface area in our experiment, and disturbance history had only indirect effects on the bacteria (see below). In our correlative research in the same stream (Sailer et al. submitted, see Publication 1), stone surface area was also correlated with bacterial distribution most often, implying that this parameter plays an important role for the microdistribution of benthic stream bacteria. However, disturbance history, POM, substratum characteristics, near-bed current velocity and several other habitat parameters were also related to bacterial distribution in the correlative research. One reason for this difference from the present disturbance experiment may be that we were unable to simulate all aspects of a bed-moving flood realistically in the experiment. Related studies documenting effects of local disturbance history or habitat parameters on benthic stream bacteria are scarce. In the only study known to us (Fischer et al. 2003), the movement speed of different layers of sand affected bacterial activity in a moving sand dune in a German lowland river, with activity being higher in the faster-moving upper layer than in the slower-moving deeper layer.

### Direct versus indirect effects of disturbance history

Disturbance history affected algal distribution both directly (in 23% of all cases) and indirectly, via history effects on habitat parameters (15%). Distribution of benthic bacteria was influenced only indirectly by disturbance history (in 33% of all cases). In addition, significant correlations of aquatic biota with habitat parameters revealed previously undetected disturbance history effects in two cases. Consequently, habitat parameters and disturbance history interacted strongly with each other when influencing algal and bacterial distributions. In our study on river algae (Matthaei et al. 2003), by contrast, disturbance history effects had been largely independent of habitat parameter effects. This difference may be partly caused by the fact that we had investigated only three habitat parameters in our earlier study.

Matthaei and Townsend (2000) speculated that indirect effects of disturbance history on physical habitat parameters and food resources of benthic organisms are more likely to be responsible for long-term differences (several weeks after disturbance) in densities between patch history types. Our present results do not support this idea, at least not for benthic algae and bacteria, the studied habitat parameters and the 21 days of our experiment, because all indirect effects of disturbance history were found relatively shortly (1 day or 7 days) after the experimental disturbance.

One might argue that our chosen analysis caused inflated effect frequencies for disturbance history relative to those for habitat parameters, because six 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 covariate (see Methods). However, we included these covariates in our analysis to find out if “apparent” effects of disturbance history on algal or bacterial 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 and Keough 2002).

### Density patterns in bed patches with different disturbance histories

Algal densities were highest in stable patches in the majority of cases when densities differed significantly between patch types. Interestingly, most of these differences occurred seven days after, rather than directly after, the experimental disturbance (Table 1). Further, the higher densities in stable patches seven days after disturbance was caused by faster algal growth in stable patches relative to disturbed patches (compare patterns for algal density and biomass on

20 June and 26 June in Fig. 1). Consequently, the density differences seven days after disturbance were not simply a result of the experimental disturbance which resulted in somewhat (but not significantly) lower algal densities in scour patches relative to fill or stable patches (Fig. 1). Instead, the stable patches seem to have provided better growth conditions for benthic algae than the recently disturbed patches, presumably due to some advantage in terms of physical habitat, food availability or lack of enemies. This result parallels some of the findings of our correlative study in the Schmiedlaine (Sailer et al. submitted, see Publicatoin 2), in which certain algal taxa (*Fragilaria*, filamentous Cyanophyta, *Nitzschia* and *Cocconeis*) had higher densities in stable than in scour and fill patches up to five weeks after a natural flood.

In addition to the high algal densities in stable patches seven days after disturbance, we found that the ratio of chl a to phaeophytin (an index of periphyton mat health, Peterson et al. 1990) was higher in stable than in disturbed patches shortly after and 21 days after the experimental disturbance (Fig. 1). Periphyton vitality (the ratio of living algal cells to total algal cells) was similar between patch types throughout the experiment (Fig. 2). Both parameters changed little with time. These results contrast with predictions of a conceptual model for successional changes in algal mats following scour disturbance (Peterson 1996). According to this model, the basal cell layers in senescent algal mats are prone to dying due to lack of light and water-column nutrients, which eventually leads to ‘autogenic sloughing’ (detachment of the entire mat caused by detachment of the dead basal cells). These sloughing events are followed by a much slower recovery of the algal mats than after scour due to floods, because vital basal cells are lacking after autogenic sloughing.

Adapting these predictions to the scour, fill and stable bed patches in our experiment, algal mats ought to be less vital in stable patches than in the more severely disturbed scour or fill patches. (The Peterson model does not distinguish between scour and fill patches.) Peterson et al. (1990) found in a manipulative experiment on a lake shore that periphyton communities left undisturbed for 24 days had much lower ratios of chl a to phaeophytin than recently disturbed ones, and the stables patches in the Schmiedlaine had been undisturbed for at least one month when we conducted our experimental disturbance (see Methods). Senescence, reduced growth, and possibly autogenic sloughing should occur in stable patches, followed by a slow recovery. By contrast, algal growth in the recovering disturbed patches should be faster, eventually leading to higher algal densities than in stable patches. Further, vitality of the algal mats in all three patch types should change with time since the last disturbance, from vital and fast-growing mats shortly after disturbance to senescent mats after longer stable periods, followed by low algal densities and slow recovery due to autogenic sloughing.

Our data provide little support for any of the above predictions. We acknowledge that the duration of our experiment (21 days) may have been too short for major changes to occur since the experimental disturbance because algal growth is relatively slow in the cold and nutrient-poor Schmiedlaine (see Methods). Nevertheless, we found a similar lack of support for the predictions of the Peterson model in our correlative study in the Schmiedlaine (Sailer et al. submitted, see Publication 2), and this research included two 5-week periods after natural floods. Consequently, the combined results of our correlative and experimental research call into question the applicability of this model to algal communities in cold, nutrient-poor streams.

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# Additional work

## Introduction

During biological sampling at the Schmiedlaine, geologically different stones were collected. To ascertain that there was no difference between the algal biofilms growing on these rocks, a laboratory experiment was initiated to test if stones of different geological origin actually harboured different algal communities.

At the Schmiedlaine, the most frequently sampled stone types were limestone (58 % of all sampled stones), ferrit (17 %), sandstone (8 %) and slate (2 %). Therefore, these four stone types were used to investigate their colonization by benthic stream algae under controlled laboratory conditions. Because ceramic tiles have been used as artificial substrates in many stream studies (e.g. Biggs et al. 1999; Peterson & Stevenson 1989), we also included tiles in our experiment (unglazed, white ceramic tiles, dimensions 4.7 x 4.7 x 0.4 cm).

## Material and Methods

The experiment was conducted in four circulating artificial stream channels (see Fig. 1, length 99 cm, width 29 cm, high 37 cm) in a climatised room. The water temperature was 14°C and light conditions were 62.6 µE/sec*m$^2$.

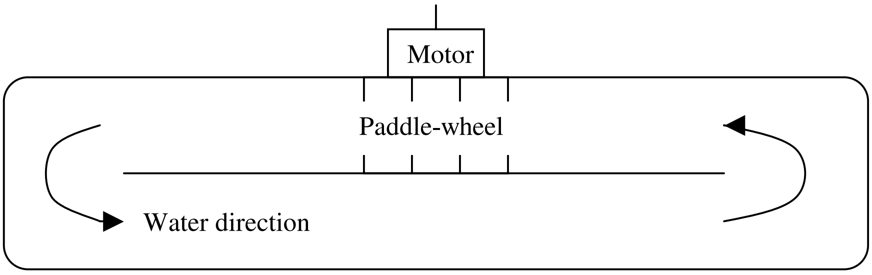

**Fig. 1** View of a stream channel from above.

To every stream channel, we added five stones of each of the four rock types, plus five tiles. The mean surface areas of the stones were: limestone 133.4 cm$^2$, sandstone 151 cm$^2$, slate 110.1 cm$^2$, and ferrit 152.3 cm$^2$. The tiles had a surface area of 95.4 cm$^2$. Each channel was filled with 24 l of stream water collected from the Schmiedlaine, resulting in a water depth of about 10 cm. Current velocity in the channels ranged between 0.16 and 0.37 m/s, depending on the location in the circular channel (the fastest areas were just downstream of the paddle-wheel, the slowest areas just upstream of the wheel). Every experimental substrate was autoclaved (for 15 min at 121°C) and scrubbed clean prior to the experiment. Before the start of the experiment, we randomly collected six surface stones from the Schmiedlaine, brushed them clean with a toothbrush and collected the resulting algal slurry in a glass vial. To inoculate the water of the stream channels, we added 40 ml of this algal slurry to each channel.

The experiment was started on 6 May 2003, and algal samples were collected on 13 May, 20 May, 3 June, 17 June and 1 July 2003. On each occation, one specimen of each stone type in each of the four stream channels were sampled, resulting in four replicates of each stone type and a total of 20 samples on each sampling date. All samples taken on the first date (13 May) contained very few algal cells.

The algal cells in each sample were counted with the same methods as in Publications (2) and (4). A total of eleven algal taxa were found and taxon-specific density patterns were analysed for the nine taxa that occurred regularly in the samples. Algal biomass (as chlorophyll a) per surface area of the stone was also measured for each substrate type, using standard techniques (Brock & Brock 1967).

To test for effects of stone type on the algal communities, we performed one-way ANOVAs with stone type as treatment factor. Dependent variables were total density of epilithic algae, algal taxon richness, living algal biomass (as chlorophyll a), ratio of Chl a to phaeophytin (Peterson, Hoagland & Stevenson 1990) and the densities of each common algal taxon.

## Results

With three exceptions, the 65 separate ANOVAs (four summary parameters plus nine common taxa multiplied by five sampling occations) revealed no statistically significant effects of geological stone type on algal response variables (Fig. 2) The exceptions were densities of *Achnanthes* spp. and/or *Meridion* spp. on two of the sampling dates. On 20 May, *Achnanthes* was more abundant on sandstone than on tiles (*P*=0.033). On 3 June, the same taxon was more common on sandstone than on tiles (*P*=0.001), limestone (*P*=0.002) and slate (*P*=0.001). Finally, density of *Meridion* was higher on sandstone than on limestone on 20 May (*P*=0.021).

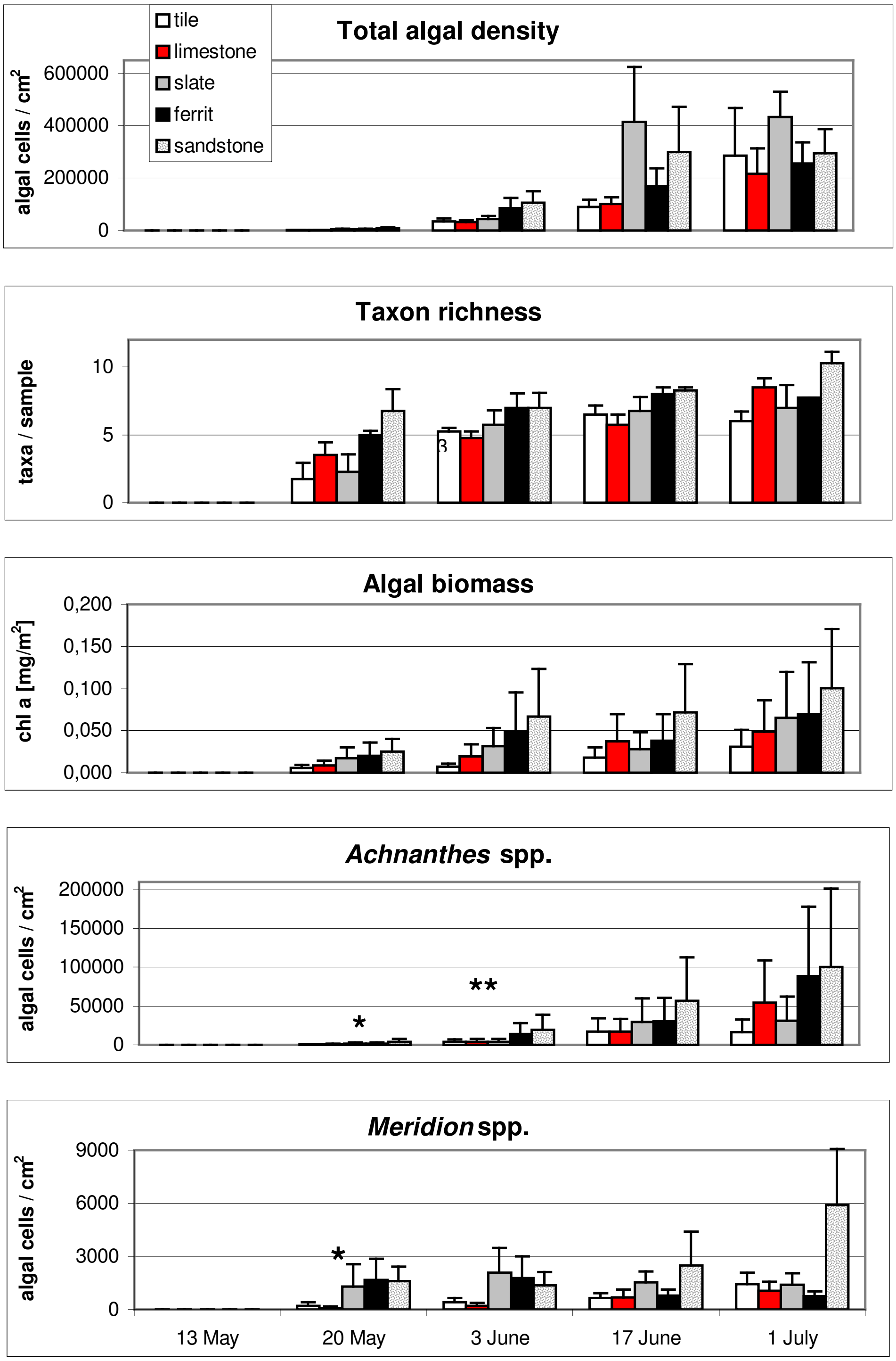

**Fig. 2**. Total epilithic algal density, taxon richness, algal biomass as chl a, *Achnanthes* spp. and *Meridion* spp. on tiles, limestone, slate, ferrit and sandstone. Significant differences between substratum types in the ANOVAs are shown by asterisks above the mean values. Error bars indicate standard errors. *P<0.05.

## Summary

In this laboratory experiment, the algal communities in the Schmiedlaine were quite similar across the most common substratum types that occur naturally in this stream. The few existing differences indicated a weak preference of certain algal taxa for sandstone substrata. Because sandstones made up only 8 % of the sampled stones in the Schmiedlaine, these weak preferences are unlikely to have influenced the results from our field studies relating the microdistribution of the algae to disturbance history.

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# Synopsis

Figures 1 - 3 in this chapter summarise the most important results of the present dissertation. Only direct relationships between microdistributions of stream biota and local disturbance history or microhabitat parameters (determined using ANOVAs or ANCOVAs, see Chapters 2 - 5) are shown. In addition to these direct relationships with the biota, disturbance history was often related indirectly to densities of bacteria, algae and invertebrates, especially in the Kye Burn and after the experimental disturbance in the Schmiedlaine (see Table 1).

**Table 1.** Overview of indirect relationships of disturbance history with microdistributions of aquatic biota after the natural disturbances in 2001/02 and the experimental disturbance in 2002. All invertebrate data were taken from Herrmann (2003).

| | **Schmiedlaine 2001** | | | **Kye Burn 2001/02** | | | **Schmiedlaine 2002** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Bacteria** | **Algae** | **Inverts.** | **Bacteria** | **Algae** | **Inverts.** | **Bacteria** | **Algae** | **Inverts.** |
| **Frequency** [as % of all analysed cases] | 13 | 8 | 8 | 21 | 33 | 59 | 33 | 15 | 22 |

These indirect relationships were caused by direct relationships of disturbance history (determined using ANOVAs) with certain habitat parameters which, in turn, were correlated with the distributions of the biota in these cases (determined using ANCOVAs). The frequent occurrence of such indirect relationships of disturbance history with the distributions of aquatic biota implies that habitat parameters and disturbance history interacted strongly with each other when influencing the microdistributions of the benthic organisms. In earlier research on benthic river algae (Matthaei et al. 2003), by contrast, disturbance history effects had been largely independent of habitat parameter effects.

Further, significant relationships of biota with certain habitat parameters revealed previously undetected relationships of these biota with disturbance history in several cases for all organism groups, whereas the opposite effect was much less common (see Publications 1 - 4). These results imply that few ’apparent’ relationships of disturbance history with the distributions of the aquatic biota were actually explained by relationships of the biota with the habitat parameters measured in the present research. This could mean that the three bed stability categories differed in one or several parameters that we did not measure, and that these parameters influenced the distributions of the aquatic biota. Such parameters could be unknown abiotic habitat variables, or possibly also the consequences of biotic interactions such as predation or competition.

The laboratory experiment examining algal colonisation on different geological rock types in the Schmiedlaine showed that algal communities were remarkably similar across the four common rock types (see ’Additional work’). Consequently, it is very unlikely that geological rock type could have had a confounding effect on algal microdistribution in the Schmiedlaine in the present research.

We investigated three different bed stability types after each disturbance: stable, scour and fill positions. We distinguished between scour and fill patches instead of sampling only stable and ’disturbed’ patches because the two patch types are likely to differ in certain ways that may affect their post-disturbance recovery dynamics. For instance, it is more likely that parts of the original biofilm survive on surface stones deposited in fill patches, whereas there should be a total lack of biofilm on the newly exposed bed surface in scour patches. The biofilm in ’stable’ bed patches (without bed movement on a scale detectable with the scour chains) may still be affected by a ’sandblasting effect’ of suspended fine sediment during high-flow events, therefore these patches may not be entirely undisturbed (see also a critique of the scour chain method in the next chapter). However, this sandblasting is likely to have less severe consequences for epilithic biofilms than the rolling and tumbling of entire stones associated with sediment scour or fill in a given bed patch.

### Disturbance history and physical habitat parameters

In the correlative research in the Schmiedlaine, the habitat parameter that was most frequently related to the microdistribution of the benthic bacteria was the surface area of the sampled stones, followed by local disturbance history, POM, substratum size in the Surber samples, near-bed current velocity and water depth (see Fig. 1, except for POM, see Publication 3). In the Kye Burn, bacterial distribution was most frequently related to local disturbance history, followed by water depth, substratum size in Surber samples, near-bed velocity and POM (see Fig. 2; except POM, see Publication 3).

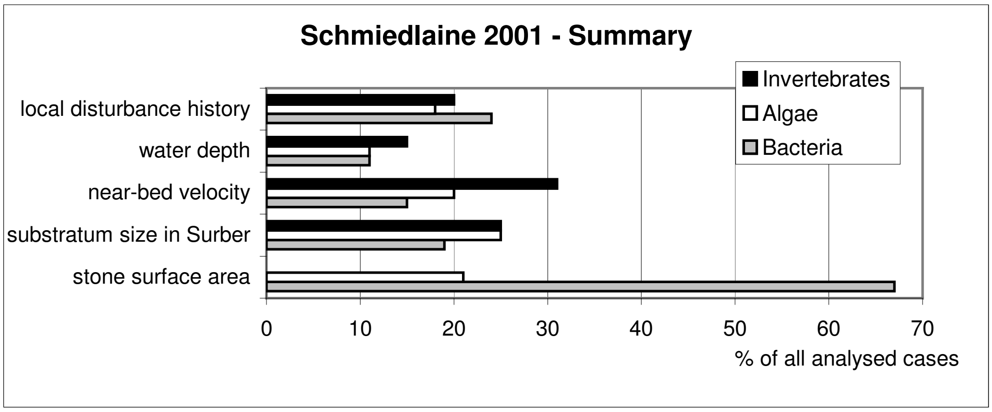

**Fig. 1.** Frequency of statistically significant relationships among habitat parameters and organismal abundances as percentage of all analysed cases in the correlative research in the **Schmiedlaine 2001**. Note that invertebrates distributions were not related to stone surface area because the sampling unit for these organisms was a Surber sample, and not an individual surface stone.

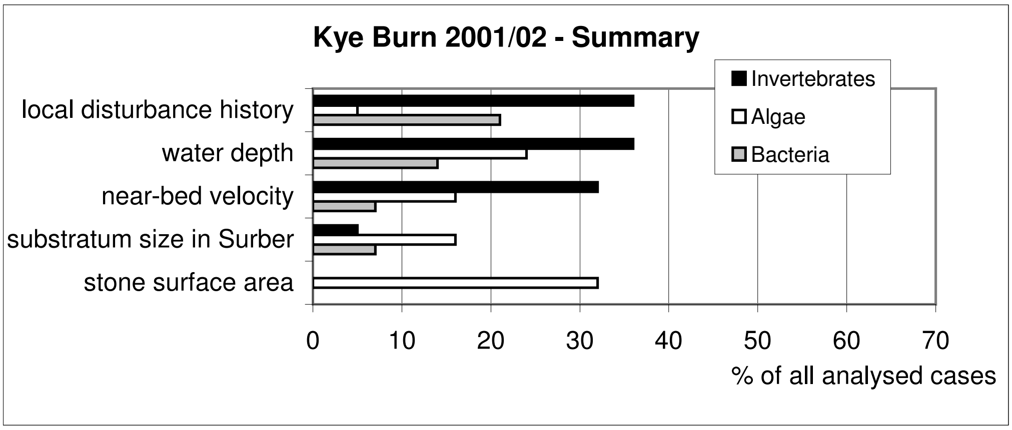

**Fig. 2.** Frequency of statistically significant relationships among habitat parameters and organismal abundances as percentage of all analysed cases in the correlative research in the **Kye Burn 2001/02**. Note that invertebrates distributions were not related to stone surface area because the sampling unit for these organisms was a Surber sample, and not an individual surface stone.

Algal microdistributions were slightly more often related to substratum size in Surber samples, the surface area of the sampled stone and near-bed current velocity than to disturbance history in the Schmiedlaine (Fig. 1), but history still played a significant role. In the Kye Burn, all seven measured habitat parameters were related to algal distributions more often than disturbance history, and the role of history for algal distribution was relatively minor (Fig. 2 and Publication 2). Algal primary production showed no significant relationships with local disturbance history, only with some of the studied microhabitat parameters (see Publication 2).

Invertebrate distributions in the Schmiedlaine were affected most often by near-bed current velocity, followed by substratum characteristics, local disturbance history and water depth (Fig. 1). In the Kye Burn, disturbance history and water depth had the highest number of significant relationships with invertebrate distributions, followed by current velocity and algal biomass (Fig. 2 and Publication 3).

Overall, the combined data from the correlative research suggest that local disturbance history played an important role for the microdistributions of benthic bacteria, algae and invertebrates in the Schmiedlaine. In the Kye Burn, disturbance history appeared to be important for invertebrates and bacteria, but relatively unimportant for the algae. One possible reason for this difference between streams could be that the sediment structure of the stream bed surface in the Kye Burn is more homogeneus than in the Schmiedlaine. The greater habitat heterogeneity in the Schmiedlaine may be linked somehow to the greater importance of local disturbance history, which can differ at the level of individual stones depending on their size and embeddedness (see Matthaei et al. 1999a and Matthaei et al. 2000), for algal distributions in this stream. Note, however, that the present research was unreplicated at the stream level. Consequently, any attempts to explain differences in biotic patterns between the two streams have to remain largely speculation. The present study was not designed to investigate differences in disturbance history effects between stream types.

In the Schmiedlaine, the distributions of benthic algae and invertebrates were also related to densities of benthic bacteria (see Publications 2 and 3). For the algae, these correlations were mainly positive (see Table 4 in Publication 2), indicating that the presence of epilithic bacteria may facilitate establishment and/or growth of certain algal taxa. In return, the benthic bacteria also showed a few (mainly positive) correlations with epilithic algal biomass (see Table 4 in Publication 1), which may imply that the facilitation effect may act both ways.

For the invertebrates, we found a similar number of positive and negative correlations with the benthic bacteria (see Table 4 in Publication 3). This result may imply that certain invertebrate taxa (mainly grazers or filter feeders, e.g. the net-winged midge *Liponeura* and the black fly *Simulium*) profit from epilithic bacteria (and/or the benthic algae facilitated by the presence of the bacteria), while other invertebrate taxa (e.g. the predatory stonefly *Chloroperla*) tend to avoid substrata that are rich in benthic bacteria. In the Kye Burn, the benthic algae were also related to bacterial densities (once again showing mainly positive correlations), but not the benthic invertebrates. This difference to the Schmiedlane data may be due to certain differences in the invertebrate communities between the two streams which are situated in different hemispheres of the world.

In both streams, invertebrate densities were correlated (mainly positively) with algal densities (see Table 4 in Publication 3). This result is in agreement with findings in the literature that grazing invertebrates tend to seek out substrata rich in benthic algae and spend more time feeding in these high-quality patches (e.g. Hart 1981; Kohler 1984). In keeping with this interpretation, densities of benthic algae were also correlated significantly with invertebrate densities in a number of cases in both streams (see Tables 4 & 6 in Publication 2), and the majority of these correlations were negative. This negative correlation may be a consequence of reduced algal cell densities due to intense grazing in patches were grazers were common.

In contrast to the evidence of two-way interactions between benthic bacteria and algae and between benthic algae and invertebrates, benthic bacteria were never related to the densities of benthic invertebrates (in both streams during the correlative study and also during the manipulative experiment – see Table 4 in Publication 1 and Table 4 in Publication 4). This result suggests that benthic invertebrate may have few direct effects on benthic bacteria. This finding may also imply that the occasional positive correlations of invertebrate densities with bacterial densities (see above) are more likely to be a consequence of a positive effect of the bacteria on algal growth than an indication for the ability of certain invertebrate taxa to feed on benthic bacteria.

### Natural versus experimental disturbance

Following the experimental disturbance in the Schmiedlaine, bacterial microdistribution was related directly only to the surface area of the sampled stones (Fig. 3). The other habitat parameters were unrelated, and local disturbance history had only indirect effects on bacteria (see Publication 4). These results partly support the findings of the correlative research on stream bacteria after natural disturbance. In the correlative study in the Schmiedlaine, stone surface area was also the parameter that was related most frequently to bacterial distributions. However, other habitat parameters and disturbance history were also related significantly to bacterial microdistribution in several cases (see Fig. 3).

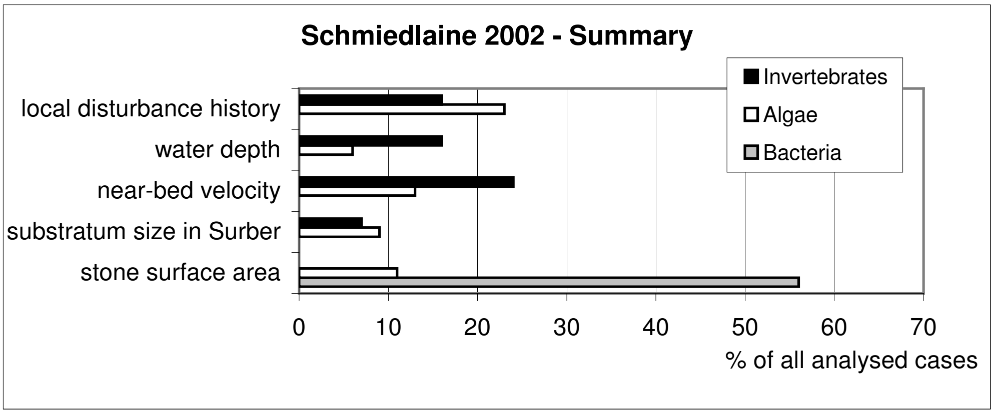

**Fig. 3.** Frequency of statistically significant relationships among habitat parameters and organismal abundances as percentage of all analysed cases of the experimental disturbance in the **Schmiedlaine 2002**. Note that invertebrates distributions were not related to stone surface area because the sampling unit for these organisms was a Surber sample, and not an individual surface stone. All invertebrate data were taken from Herrmann (2003).

In the manipulative experiment, effects of local disturbance history on algal microdistribution were observed more frequently than relationships with the remaining habitat parameters, i.e. near-bed current velocity, total invertebrate density and the surface area of the sampled stone (see Fig. 3 and Publication 4). These results for stream algae correspond well with those from previous research on river algae (Matthaei et al. 2003). The differences from the correlative study at the Schmiedlaine in 2001 are also relatively minor. Consequently, the results of the experimental disturbance lend more weight to the results of the earlier, correlative studies of disturbance history effects on benthic algae. Collectively, these studies suggest that local disturbance history is a newly identified habitat parameter that can influence the microdistribution of algae in running waters and should therefore not be ignored in future research.

Invertebrate distribution during the experiment was influenced most often by near-bed velocity, followed by POM, local disturbance history and water depth. While disturbance history did play an important role for invertebrate distribution in both the correlative (see Fig. 1) and the experimental research, current velocity was the parameter that affected invertebrate distribution most consistently. This result agrees with the findings of many microhabitat studies on benthic invertebrates in the literature (e.g. Ulfstrand 1967; 1968; Osborne & Herricks 1987; Horne et al. 1992; Peckarsky et al. 1990).

In summary, the experimental disturbance largely yielded results for benthic bacteria, algae and invertebrates and supported that were consistent with earlier, correlative research on these organism groups. Differences between the correlative and experimental study, especially for the bacteria, may be related to the fact that a bed-moving flood includes several aspects than our experiment could not simulate realistically (e.g. the ‘sandblasting effect’ of suspended fine sediment, see above, or the rise and fall of stream discharge prior and after the event). In addition, new and more sophisticated methods to quantify bed movements at small spatial scales may need to be developed before the effects of local disturbance history on benthic stream bacteria can be fully understood (see ‘Future Research’).

### Density patterns in different patch types after the disturbances

The density patterns in scour, fill and stable patches found for epilithic bacteria in the Schmiedlaine differed between high-flow events in the correlative study in 2001. However, significant relationships between disturbance history types and bacterial microdistribution were found mainly directly after the events (13 of 16 cases in total; see also Fig. 3, Publication 1). In the majority of these cases, bacterial densities were highest in fill patches.

In the Kye Burn, we also found the majority of significant relationships between disturbance history and bacterial densities directly after the first spate, again with highest densities in fill patches (see Fig. 5 in Publication 1). Overall (both streams combined), these results suggest that local disturbance history may have predominantly short-term effects on epilithic stream bacteria. This result may be linked to the short generation times of the bacteria which allow rapid growth in favourable bed patches that may ‘even out’ initial density differences after disturbance.

For benthic algae, density pattern also differed between high-flow events in the Schmiedlaine in 2001 (see Fig. 3 in Publication 2). Directly after the first and third high-flow events, the highest algal densities occurred in fill positions. Directly after the second event, algal densities were highest in scour patches. After the fourth event, algal densities were highest in stable patches. The majority of these differences between patch types occurred three or five weeks after disturbance.

For the algae in the Kye Burn, disturbance history was related to algal density on both patch-specific sampling dates, with more algae in scour than in fill patches in both cases (see Fig. 5 in Publication 2). Overall, most of the significant effects of local disturbance history on the algae were found several weeks after disturbance, implying that disturbance history may have more longer-term effects on the microdistribution of stream algae than it has on stream bacteria, and also more longer-term than short-term effects. The latter result parallels the findings of Matthaei et al. (2003) for river algae, where long-term effects of disturbance history were also more common than short-term effects. Algal primary production was always similar across the three bed stability types in both streams.

Invertebrate densities in the Schmiedlaine in 2001 showed no consistent patterns (see Fig. 3 in Publication 3). After the first high-flow event, invertebrate densities were higher in fill than in stable patches, whereas after the second event scour patches contained more invertebrates than fill patches. After the third and fourth events, stable positions had higher densities than fill positions. Five weeks after the fourth event, by contrast, densities in disturbed patches were mostly higher than in stable patches.

In the Kye Burn directly after the first high-flow event, more invertebrates were found in stable than in fill patches (see Fig. 3 in Publication 3). Three weeks after this event, all three patch types were preferred by the invertebrates. Overall, it appears that local disturbance history can have both short- and long-term effect on the small-scale distributions of stream invertebrates. This result agrees with earlier findings regarding disturbance history effects on benthic invertebrates in the Kye Burn (Matthaei et al. 2000; Matthaei & Townsend 2000).

When bacteria, algae and invertebrates are considered together, a few common distribution patterns emerge. Directly after the third high-flow event in the Schmiedlaine, all three organism groups were more abundant in stable than in fill patches (see Table 3 in Publications 1, 2, 3), indicating a refugium effect of stable bed patches (see also Matthaei et al. 2000; Matthaei et al. 2003). This major flood, which was the largest investigated event in the Schmiedlaine and exceeded bankfull flow (return period 2-3 years, see Table 2 in Publication 3), apparently influenced all three benthic biota in the same way. The second and fourth events resulted in the same pattern for algae and invertebrates, with higher densities in scour than in fill patches. Both events were mid-sized spates with a duration between one and four days and return periods of 0.5-1 years (i.e. below bankfull flow).

In the Kye Burn directly after the first high-flow event, which also had a peak flow below bankfull, both algal and invertebrate densities were also lowest in fill patches (see Table 3 in Publications 2, 3). By contrast, benthic bacteria were most abundant in fill patches in the majority of cases with significant differences between patch types (see Table 3 in Publication 1). In the Kye Burn, this preference of bacteria for fill patches was even more apparent (see Table 5 in Publication 1). The combined data may imply that high-flow events disturb fill positions more strongly than scour and (of course) stable patches, despite the fact the original surface sediment are removed from scour patches (see above), and that disturbance of fill patches reduces densities of benthic algae and invertebrates in the short term. In contrast, benthic bacteria, with their shorter generation times, may be best suited among the three organism groups to (re-)colonise these highly unstable patches.

### Positive versus negative correlations with habitat parameters

In the Schmiedlaine in 2001, water depth was correlated mostly negatively with the density of benthic algae, but mostly positively with bacteria and invertebrates. Near-bed current velocity was correlated mainly positively with all three groups. Substratum size in the Surber samples was correlated predominantly negatively with bacterial density but positively with algal and invertebrate densities in the majority of cases. A similar picture was found for the surface area of the sampled stones: for bacteria a negative correlation in all cases, for algae a positive correlation in most cases.

**Table 2.** Overview of all correlations between aquatic biota and the investigated habitat parameters after the natural disturbances in 2001/02 and the experimental disturbance in 2002. 'None ' means that no significant effects of this parameter were found in the ANCOVAs, and 'not rel.' means that the parameter stone surface area was not relevant for the invertebrates because they were collected with a Surber sampler. All invertebrate data were taken from Effenberger et al. (2005) and Herrmann (2003).

| | **Schmiedlaine 2001** | | | **Kye Burn 2001/02** | | | **Schmiedlaine 2002** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Bacteria** | **Algae** | **Inverts.** | **Bacteria** | **Algae** | **Inverts.** | **Bacteria** | **Algae** | **Inverts.** |
| **Water depth** | 4+<br>2- | 4+<br>14- | 12+<br>4- | 2+ | 4+<br>5- | 8- | none | 2+<br>1- | 6+<br>1- |
| **Current velocity** | 7+<br>1- | 21+<br>12- | 31+<br>1- | 1- | 2+<br>4- | 6+<br>1- | none | 5+<br>1- | 8+<br>3- |
| **Substratum size** | 1+<br>9- | 24+<br>18- | 20+<br>6- | 1+ | 4+<br>2- | 1+ | none | 2+<br>2- | 3- |
| **Stone surface area** | 18- | 21+<br>14- | not rel. | none | 5+<br>7- | not rel. | 5- | 1+<br>4- | not rel. |

In the Kye Burn in 2001/2002, the bacteria were correlated positively with water depth in all cases (there were only two), whereas the algae showed predominantly negative correlations, and the invertebrates only negative correlations, with this parameter (Table 1). Near-bed current velocity was correlated negatively with the bacteria (only a single case) and the algae (in most cases), but mainly positively with the invertebrates. Substratum size (Surber samples) was correlated positively with bacteria and invertebrates (only a single case each), and mostly positively with algae. Stone surface area was correlated mainly negatively with algal density. Bacteria, by contrast, did show no any significant correlation with this parameter.

During the manipulative experiment in the Schmiedlaine in 2002, bacteria were correlated only with stone surface area, and this negatively in all cases (Table 1). Algae were correlated mostly positively with water depth and near-bed current velocity, positively and negatively in equal proportions with substratum size in Surber samples, and mostly negatively with stone surface area. The invertebrates were correlated mostly positively with water depth and current velocity, but exclusively negatively with substratum size.

In summary (all three data sets combined), water depth showed no consistent pattern, but more negative correlations were found for algae than for bacteria and invertebrates (Table 2). Near-bed current velocity showed altogether far more positive correlations than negative ones with the aquatic biota, regardless of organism group. Substratum size in the Surber samples was correlated mainly positively with algae and invertebrates, but mainly negatively with bacteria. Finally, the surface area of the sampled stone showed only negative correlations with bacteria, whereas no consistent pattern was found for the algae. These results suggest that different organism groups can be affected in different ways by the same habitat parameters. The predominantly positively correlations of near-bed current velocity and substratum size with the densities of benthic invertebrates and algae in the present research agree with findings in the literature (Ulfstrand 1967; 1968; Osborne & Herricks 1987; Peckarsky et al. 1990; Horne et al. 1992; Stevenson 1996; Biggs et al. 1998) indicating that many stream invertebrates and algae prefer (up to a point) relatively fast current velocities and large surface particles. By contrast, our findings for benthic bacteria (for which hardly any microhabitat preference studies exist) imply that epilithic stream bacteria seem to benefit from relatively slow current velocities and small grain size of the substrate, possibly because such conditions allow deposition of fine particulate organic matter, which can be a valuable food resource for benthic stream bacteria (Findlay et al. 1986; Kamauchi 2005).

The present research represents another important step towards a better understanding of the small-scale distributions of benthic stream biota in space and time. Our results show that not only previously known habitat parameters may play an important role in influencing these distributions, but that local disturbance history can affect the organisms to a similar degree.

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## Future research

While the scour chain method was well suited for determining bed stability patterns in relation to densities of epilithic bacteria on individual surface stones, it was less suitable for determining bed stability patterns in relation to densities of bacteria in fine surface sediments. It is likely that a sampled bed patch of 25 x 25 cm (the area within the Surber Sampler) represented a mixture of much smaller fine sediment patches (about 2 x 2 cm, or even smaller) of differing disturbance histories, especially in ′stable′ bed patches where in fact some of the smaller fine sediment patches may have experienced scour or fill. Using a more sophisticated and smaller-scale method to measure bed stability (e.g. the metal pins used by Miyake & Nakano 2002) may allow determining more subtle effects of disturbance history on sediment bacteria than the ones found in my thesis.

Furthermore, when sampling bacteria in fine sediment, we could not collect a sediment core of several cm length and subdivide this core into different depth layers, because the substratum was too heterogeneous and included many larger particles in the sediment layers below the top 0.5-1 cm of fine sediment. Such a subdivision can be done only in streams with sandy substrata (e.g. Marxsen & Fiebig 1993; Marxsen et al. 1997). It would be desirable to develop a sampling method that allows distinguishing between different depth layers of fine sediment in coarse-substratum streams like the Schmiedlaine and the Kye Burn.

The original DAPI staining method (Porter & Feig 1980; Ward & Johnson 1996) proved to be poorly suited for counting benthic stream bacteria, especially for sediment bacteria, because the benthic samples often contained considerable amounts of fine sediment or detritus particles, which made it hard to see and count bacteria. Consequently, the method needed to be modified using a trial- and error approach, different dilution factors and different centrifugation treatments prior to counting. In addition, a chemical was needed to ensure that bacteria did not remain stuck to the insides of the sample vials due to sedimentation and adhesive forces (see Schallenberg et al. 1989). Therefore, future researchers wanting to investigate benthic bacteria in gravel-bed streams using the DAPI method need to be aware that a considerable amount of time may be required to adjust the standard method to allow reliable counting of the samples collected from their study stream.

Measuring primary production of benthic algae using the chambers in the laboratory is labour-intensive, especially when the time needed to built the experimental setup is taken into account, and requires expensive equipment.

In order to get the best possible picture of the microdistribution patterns of the benthic algal community, the different algal taxa should be identified to the lowest possible taxonomic level. For the diatoms, this level is the species level. In the present research, biological samples suitable for identification of algal species have been collected and preserved from all study periods in both streams. It is intended that these samples will be processed in the nearer future.

Abiotic disturbance is just one of many factors influencing biological communities in running waters. Biotic interactions such as competition (e.g. McAuliffe 1984; Feminella & Resh 1991; Kohler & Wiley 1997; Kuhara et al. 1999), grazing (e.g. Power 1992; Feminella & Resh 1991; Kohler & Wiley 1997) or predation (e.g. Englund & Evander 1999; Nakamo et al. 1999; Diehl et al. 2000) can also be important in determining the structure and function of stream and river communities. Nevertheless, almost all evidence for biotic interactions in running waters was collected in streams with permanently stable flow conditions, during long periods of stable flow in periodically disturbed streams, or in stable experimental channels. One of the few exceptions from this rule is the study of Pringle & Hamazaki (1997) in a flood-prone rainforest stream where grazing fishes were shown to influence the response of benthic algae to flood disturbance.

In their conceptual papers, Townsend (1989) and Poff & Ward (1989) argued that, while biotic interactions were likely to be important in stable streams, their importance ought to decrease with increasing frequency of hydrologic disturbance. Further, Townsend (1989) expected the majority of running water ecosystems to be ’frequently disturbed’ or ’very frequently disturbed’, therefore biotic interactions should be unimportant in these systems. In agreement with the first part of this hypothesis, Poff & Ward (1989) classified only 27 % out of 78 streams and rivers in the U.S.A. as having a ’stable’ or ’periodically stable’ flow regime. On the other hand, Chesson & Huntly (1997) argued in a theoretical study that biotic interactions can play an important role in frequently disturbed ecosystems after all, because even a relatively minor stress caused by competition or predation could be enough to ’push over the edge’ a species already weakened by abiotic disturbance. Similarly, Biggs et al. (1998) developed a conceptual model of a habitat matrix for benthic stream algae that included a hypothetical influence of mayfly predators (grazers) on periphyton communities at high disturbance frequencies.

In contrast to the abundance of conceptual and theoretical papers, there is a marked lack of empirical and especially experimental studies in this area, presumably because of the practical difficulties involved in conducting research in frequently disturbed streams or rivers. Therefore, determining the interplay between abiotic disturbance and competition, grazing and predation in these frequently disturbed systems is one of the most current and challenging research objectives for future ecological research in running waters. Such studies may also lead to a better understanding of the exact mechanisms by which local disturbance history influences the small-scale distributions of aquatic organisms.

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## Curriculum vitae

| | |
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Part-time teaching assistant in several practical courses at the Technical University of Munich (Grundpraktikum der Limnologie, Fließgewässerpraktikum, Großpraktikum der Limnologie) and at the Ludwig-Maximilians-University Munich (Methoden der Fließgewässerforschung).

Research assistant during three years at the Technical University of Munich, Limnological Station, in Iffeldorf, Germany.

Co-supervisor of Diplom students Claudia Happe, Torsten Stadthagen and Peter Herrmann during their Diploma theses (November 2001 – February 2003 and March 2002 – March 2003, respectively) at the Ludwig-Maximilians-University Munich.

Member of the ‘Verband deutscher Biologen’ (VdBiol) since 2001.

Member of ‘International Association of Theoretical and Applied Limnology’ (SIL) since 2001.

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Annual meeting of the ‘Deutsche Gesellschaft für Limnologie’ (DGL) and of the German section of ‘Societas Internationalis Limnologiae’ (SIL) in Braunschweig: ‘Die Bedeutung der kleinräumigen Sohlstabilität für benthische Algen, Primärproduktion und benthische Bakterien im Fließgewässer’, oral presentation and published conference proceedings, Germany, 2002.
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# Contributions of each co-author to the publications

## Gabriele Sailer$^{\text{Publications 1, 2, 3, 4}}$

*Publications 1&2:* I participated in all parts of the field work in both Germany and New Zealand, collected and processed all bacterial and algal samples, conducted all measures of algal primary production, and determined all stone surface areas. I also did all statistical analyses, evaluated all results, and wrote several drafts of the two manuscripts..

*Publication 3:* I participated in all parts of the field work and helped with processing of the POM samples. I also provided the algal biomass data for the analysis, and contributed to the discussion of the experimental design, the statistical analyses, and to several drafts of the written manuscript..

(All field work for the publications 1, 2 and 3 was carried out simultaneously).

*Publication 4:* I participated in all parts of the field work, collected and processed all bacterial samples, and supervised and helped Diplom student Torsten Stadthagen (see below) with the measures of algal primary production and the processing of the algal community samples. I also did all statistical analyses on the combined data set (bacteria and algae), evaluated the combined data, and wrote several drafts of the manuscript

## Claudia Happe[1]

C. Happe conducted the bacterial production part of the research in the Kye Burn in New Zealand. She also helped with the field work in this stream. This work was part of her Diplom thesis (title „Die Bedeutung der kleinräumigen Sohlstabilität und lokaler Mikrohabitats-parameter für benthische Bakterien im Fließgewässer”).

## Jürgen Marxsen[1]

J. Marxsen gave helpful advice for the practical work with the stream bacteria, and provided useful comments on an earlier draft of publication 1.

## Urs Uehlinger[2]

U. Uehlinger provided helpful advice on how to build the experimental chambers for the primary production measurements and how to to analyse and write up the primary production data in publication 2.

**Michael Effenberger**[1, 2, 3]

M. Effenberger participated in all parts of the field work in the Schmiedlaine in 2001 during his Diplom thesis research (thesis title „Die Bedeutung der kleinräumigen Sohlstabilität und lokaler Habitatsparameter für die Besiedelung wirbelloser Tiere in einem bayerischen Wildbach“). He processed all the invertebrate samples collected in the Schmiedlaine in 2001 and most of invertebrate samples collected in the Kye Burn in 2001/02. He also determined POM standing stocks for the Schmiedlaine data in 2001. He did all statistical analyses on the invertebrate data collected in the correlative research, evaluated all results, and wrote several drafts of the corresponding invertebrate manuscript (publication 3).

**Torsten Stadthagen**[4]

T. Stadthagen conducted his Diplom thesis in the Aquatic Ecology group at the LMU Munich (thesis title “Die Bedeutung der kleinräumigen Sohlstabilität für benthische Algen während einer experimentellen Hochwasser-Simulation in einem bayerischen Wildbach“). He participated in all parts of the field work of the manipulative experiment, collected and processed all algal samples and carried out the primary production measurements.

**Peter B. Herrmann**[4]

P. Herrmann also conducted his Diplom thesis in the Aquatic Ecology group at the LMU Munich (thesis title „Der Einfluß der kleinräumigen Sohlstabilität auf die benthischen Invertebraten eines bayerischen Wildbaches am Beispiel eines manipulativen Experiments”). He participated in all parts of the field work of the manipulative experiment, collected and processed all invertebrate and particular organic matter samples (POM). He also determined ash free dry mass values (AFDM) for the algal samples, and analysed and interpreted the invertebrate data from the manipulative experiment.

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**Christoph D. Matthaei**[1, 2, 3, 4]

C. D. Matthaei was the main supervisor of the entire research project. He gave valuable advice throughout the practical work, participated in all parts of the field work and provided substantial help with the statistical analyses and the writing of the publications.

[1] **Publication 1**: Effects of local disturbance history and microhabitat parameters on benthic bacteria in streams.

[2] **Publication 2**: Local disturbance history and habitat parameters affect benthic stream algae and their primary production.

[3] **Publication 3**: The roles of local disturbance history and habitat parameters for the microdistribution of stream invertebrates.

[4] **Publication 4**: Local disturbance history and the microdistributions of stream algae and bacteria: an experimental approach.

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