

# Disturbance frequency influences patch dynamics in stream benthic algal communities

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**Abstract** Disturbance is integral to the organisation of riverine ecosystems. Fluctuating low flows caused by supra-seasonal drought and water management periodically dewater habitat patches, potentially creating heterogeneity in the taxonomic composition and successional dynamics of benthic communities. The frequency of disturbance induced by low flows is contingent upon the topography of the river bed and thus varies among patches. We investigated whether the frequency of patch dewatering influenced the structure and temporal dynamics of benthic algal communities attached to the upper surfaces of stones in stream mesocosms (4 m<sup>2</sup>). In a 693-day disturbance experiment, we applied short dewatering disturbances (6 days) at high (33-day cycles) and low frequencies (99-day cycles) and compared algal assemblages with undisturbed controls at 21 endpoints. In the absence of disturbance, epilithic space was dominated by the green encrusting alga *Gongrosira incrustans*. However, drying disturbances consistently reduced the dominance of the green alga, and crust abundance decreased with increasing disturbance frequency, thereby opening space for a diversity of mat-forming

diatoms. The response of mat diatoms to disturbance varied markedly during the experiment, from strong reductions in the abundance of loosely attached mats in mid-late 2000 to the exploitation of open space by closely adhering mats in 2001. Contrary responses were attributed to changes in the species composition of mat diatoms, which influenced the physiognomy and hence stress-resistance and resilience of the assemblage. Our results indicate that patchy dewatering of habitat patches during periods of low flow influences the successional dynamics of algae, thereby creating distinctive mosaics on the stream bed.

**Keywords** Algae · Community structure · Drought · Heterogeneity · Perturbation

## Introduction

Ecological communities are shaped by the interplay of physical disturbance and biological processes (Sousa 1979; Collins 2000). In the absence of disturbance, diversity often declines as early colonists are displaced by long-lived or competitively dominant species, which then monopolise resources (Sousa 1979; McGrady Steed and Morin 1996). Several theoretical models predict how disturbance influences the structure and development of ecological communities. Some models propose that disturbance promotes the local coexistence of species by disrupting competitive exclusion (Hutchinson 1961; Connell 1978; Huston 1979). However, the diversity-promoting role of disturbance has been challenged by the reverse prediction, that disturbance enhances population variability, increasing local extinction rates (Pimm 1991; Bengtsson et al. 1997; Wootton 1998).

In many ecological systems, disturbance, defined by Pickett and White (1985) as “any relatively discrete event

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in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment”, varies spatially among habitat patches (Caswell 1978; Tilman 1982; Townsend 1989). Patchy disturbances can create successional mosaics, with the frequency of disturbance dictating local community structure (Sousa 1979; Chesson and Huntly 1997). Examples of disturbances that create patchiness include storms over northern temperate forests (Turner et al. 1998), tropical forests and coral reefs (Connell 1978), fire on grassland (Collins 2000) and wave action in marine intertidal zones (Sousa 1979; Menge and Sutherland 1987). In stream ecosystems, the focus of our research, water level fluctuations typically have patchy effects on physically complex benthic habitat (Resh et al. 1988; Townsend 1989; Hildrew and Giller 1992), and benthic assemblages are regarded as being in a state of continuous recovery from the last flood or drought (Reice 1985). High flows are known to generate spatial patchiness in biodiversity – for example, through heterogeneous scouring and filling of substratum patches (Matthaei and Townsend 2000; Matthaei et al. 2003). By comparison, the ecological effects of drought and drying disturbance are poorly understood (Lake 2000, 2003; Boulton 2003) although they are expected to play an increasingly important role in the organisation of aquatic ecosystems in the face of flow modification and global change (Lytle and Poff 2004; Gibson et al. 2005; Dewson et al. 2007).

Supra-seasonal drought and water management practices, including irrigation, abstraction and impoundment, can lower stream base flows for extended periods, thereby reducing wetted area and periodically dewatering the stream bed (Extence et al. 1999; Stromberg et al. 2005). The spatial and temporal scale of dewatering and substratum drying is governed by the flow regime and varies from regular short disturbances of small habitat patches to infrequent but prolonged reach-scale events (Stanley et al. 1997). Within river reaches, the frequency of habitat emersion is patch-specific, being dependent on the topography of the water body channel (Ruetz et al. 2005; Trexler et al. 2005). For example, substratum patches at stream bed margins or on riffle crests may experience frequent dewatering whereas those in deeper water remain undisturbed. Recurrent patchy dewatering disturbances have the potential to influence community structure in river reaches and may be particularly significant for sessile assemblages, including benthic algae (see Peterson 1996; Robson and Matthews 2004), but they require further investigation.

Numerous studies have examined the influence of physical disturbance on benthic algae (see reviews by Fisher 1990; Steinman and McIntire 1990; Peterson 1996), with particular foci on the resistance and resilience of algae to high flow events (Power and Stewart 1987; Peterson et al.

1994; 2001; Biggs and Thomsen 1995; Biggs et al. 1998; Death and Zimmermann 2005), whereas there remains a paucity of research on the response of algae to drought (but see, for example, Peterson 1996; Peterson and Boulton 1999; Robson 2000; Ledger and Hildrew 2001), especially at small spatial scales (Stanley et al. 2004). The main objective of this study was to examine the effects of recurrent, drought-induced, disturbances on benthic algal communities. We adopted an experimental approach, using stream mesocosms adjacent to a chalk stream as mimics of benthic habitat patches, in order to manipulate the frequency of substratum emersion. In chalk streams, speciose mixtures of benthic diatoms, cyanobacteria and green algae coat the upper surfaces of stones and may be structured by patchy flow fluctuations. Benthic algae are particularly amenable to experimentation because they are predominantly attached, short-lived and respond rapidly to environmental change (Steinman and McIntire 1990; Huntly 1991), facilitating observations of their intergenerational dynamics (e.g. Peterson et al. 2001). Being small and sessile, algae can also be manipulated easily within the confines of stream mesocosms. We manipulated the frequency of drying disturbance by controlling the flow of water into mesocosms and assessed the impact of two disturbance treatments by comparing disturbed communities with undisturbed controls at multiple endpoints. We predicted that algal diversity would decline with increasing disturbance frequency and that the taxonomic composition and temporal dynamics of algal communities would change in response to recurrent disturbance events.

## Materials and methods

### Experimental facility

The research was conducted over a 2-year period between February 2000 and 2002 in stream mesocosms located at the Freshwater Biological Association River Laboratory, East Stoke, Dorset, UK (50°40'48''N, 2°11'06''W). Four blocks, each consisting of three mesocosms, were sited adjacent to a chalk stream (the Mill Stream) from which they received water and suspended particles, including algae and detritus (Harris et al. 2007). The blocks were spaced 2.5 m apart and arranged at an angle (approx. 140°) to the source stream. Each block consisted of three aluminium linear channels (width 0.33 m, length 12 m, × depth 0.30 m) that received stream water diverted from the Mill Stream through a branching 110-mm-diameter pipe (approx. 6 m in length). The upper end of each mesocosm was closed, except for an inflow duct (110 mm in diameter, with valve), which regulated discharge. Water and suspended particles from the outlet of the mesocosms drained

into the Mill Stream further down its course. The mesocosms were positioned 5 cm below the inflow ducts and 10 cm above the outlet stream to prevent cross-contamination among mesocosms. Channels were filled with a 20-cm layer of substrate dominated by gravel (volumetric proportions of particle sizes: 85% 11–25 mm, 5% 2–11 mm, 5% 0.35–2 mm, 5% <0.35 mm), mimicking patches of substratum on the bed of the source stream (Armitage 1995; Ledger et al. 2006). Mean water velocity and depth over the gravel was 0.20 m s<sup>-1</sup> (range 0.10–0.44 m s<sup>-1</sup>) and 81 mm (range 35–143 mm), respectively. Water residence times were short (mean 66 s, range 28–162 s).

### Experimental design and application

Unfiltered water from the source stream was diverted into all mesocosms, initiating natural algal-community development. After 2 months (February–March 2000), a 693-day disturbance experiment was initiated in the mesocosms. The experiment consisted of two disturbance treatments – high (HF) and low frequency (LF) – and an undisturbed control. Each disturbance was a short (6-day) period of substratum dewatering, designed to mimic the exposure of substratum patches (4 m<sup>2</sup>) during low flows. The extent and duration of the disturbance applications falls within the range of natural events in perennial chalk streams, where substratum drying occurs at spatial scales ranging from patches to sections and at time scales ranging from days to months (Harris 2006). Disturbances were applied by slowly closing the valves at the inflow of each mesocosm. Water drained from the channel over approximately 24 h, exposing the substratum surface to the air. The upper surfaces of stones in the channels dried naturally, but interstitial spaces beneath the surface remained damp or wet, and several small pools also remained in depressions of the gravel bed. Disturbances were applied either approximately monthly (33-day cycles, HF disturbance) or quarterly (99-day cycles, LF disturbance) (Table 1). In controls, by comparison, flows were continuous for 693 days. The total dry period was 16.7% (HF disturbance), 5.6% (LF disturbance) and 0% (control). Treatments were applied between April 2000 and February 2002. Each treatment was replicated four times in a randomised complete blocks design.

### Sampling and processing

Benthic algae on the upper surfaces of six stones (mean surface area 5.6 cm<sup>2</sup>) were sampled monthly from each mesocosm on 21 occasions, all immediately before the disturbances were applied. Algae were removed using a scalpel and toothbrush and concentrated in 25 ml of water. An aliquot (2 ml) of thoroughly mixed sample was transferred

**Table 1** Disturbance treatments applied in stream mesocosms

	Patch disturbance		
	High frequency	Low frequency	Control
Mean dry days/cycle	6	6	0
Mean wet days/cycle	27	93	693
Disturbance events ( <i>n</i> )	20	7	1
Total duration (days)	693	693	693
Percentage of time disturbed	16.7	5.6	0

to a 2-ml vial and drawn repeatedly through a syringe to disperse cell aggregates. Algae were identified to the lowest practicable taxonomic level (species or genus), and cells containing chloroplasts were counted (approximately 400 cells) using a Neubauer haemocytometer and binocular microscope (×400 magnification). The sampled surface was traced on acetate, and its area, calculated from the mass of the tracings, was used to calculate algae density on the upper surface of each stone (Ledger and Hildrew 1998, 2000). Data from each of the six sampled stones were pooled to provide a single estimate of algal species composition for each replicate mesocosm on each sampling occasion. Two contrasting algal patch types (calcareous crusts and filamentous mats) were identified macroscopically during the experiment. Algae were sampled from each patch type (as above) at 3-month intervals during the experiment and the taxonomic composition of patch types compared subsequently in a detrended correspondence analysis of algal densities (cm<sup>-2</sup>).

### Statistical analysis

Repeated measures analysis of variance (ANOVA) tested the effect of the disturbance treatment (between-subject factor), time (within-subject factor) and their interaction on (1) taxon richness and (2) algal densities. Data were log-transformed and, where necessary, departures from sphericity were corrected using the Huynh–Feldt adjustment. One-way ANOVA and Tukey HSD tests were used subsequently to examine differences between treatment means at endpoints. Non-sequential Bonferroni corrections were applied to groups of tests to preserve an alpha of 0.05 (Sokal and Rohlf 1995).

Dynamics within the algal assemblage were also examined using partial constrained ordination (redundancy analysis) carried out with CANOCO 4.5 (ter Braak and Šmilauer 2002). A series of ordinations were conducted to test terms analogous to univariate repeated measures ANOVA. Thus, four ordinations with various combinations of explanatory variables and covariables tested the effect of treatment, time and their interaction on algal

assemblage composition (Leps and Smilauer 2003; see Table 2). Treatment, block, mesocosm and season were coded as binary dummy variables (0 or 1). Sampling times (endpoints) were coded both as binary dummy variables and as quantitative variables (experimental time, days). Species data were  $\log x + 1$  transformed algal densities (cells  $\text{cm}^{-2}$ ). Taxa occurring in <10% of samples were excluded from the redundancy analyses (RDA). Temporal variation of algal assemblages was examined in two ordinations (analyses 1 and 2, Table 2). In analysis one, time was coded as 21 dummy explanatory variables, and mesocosm identifiers were used as covariables, to partial out variance among channels. In this ordination, variance attributable to time indicated shifts in assemblage composition among seasons and sampling endpoints as well as progressive change occurring through the experiment. In a second ordination, time coded as elapsed experimental time (days), with season and mesocosm identifiers as dummy covariables, was used to investigate the degree of directional change in assemblage structure during the experiment (analysis 2, Table 2). In analysis three, disturbance effects on algae were determined using the three treatments as dummy explanatory variables (0 or 1) and the four blocks and 21 times (0 or 1) as covariables (Table 2). A fourth ordination examined the interaction between disturbance treatment and experimental time, with each treatment  $\times$  experimental time as explanatory variables (analysis 4, Table 2). In this analysis, mesocosm identifiers and experimental time were used as covariables, removing the “main effects” of each treatment (Control, HF, LF) in each mesocosm, to reveal trends specific to particular treatments through time (Lepš and Šmilauer 2003). Redundancy analysis was used because dummy environmental variables were categorical (0 or 1), and gradient lengths on axes 1 and 2 of a preliminary detrended correspondence analysis were short (<1 SD). Monte Carlo permutation tests (999 permutations, with appropriate permutation schemes) were used to test the statistical significance of each model.

## Results

### Species ensembles

Thirty-two taxa of benthic algae were found in the mesocosms during the experiment [Appendix 1 in the [Electronic Supplementary Material \(ESM\)](#)]. In a preliminary detrended correspondence analysis, species (i.e. algal taxa) scores were strongly associated with one of two clusters of sample (i.e. algal mats or crust) scores, indicating that the macroscopically distinct patch types were of contrasting algal species composition. A speciose group of unicellular and chain-forming diatoms, mainly *Melosira varians*, *Planothidium lanceolatum*, *Navicula menisculus*, *Navicula lanceolata*, *Nitzschia perminuta* and *Staurosira elliptica*, formed filamentous mats on mineral substrata (Appendix 2 in the [ESM](#)). A second group of encrusting algae and cyanobacteria, dominated numerically by *Gongrosira incrustans* (Chlorophyceae), with *Phormidium* (cyanobacteria) and epiphytic diatoms (*Amphora pediculus*, *Gomphonema olivaceum* and *Rhoicosphenia abbreviata*), formed hard calcite-impregnated crusts on the upper surfaces of stones (Appendices 1 and 2 in the [ESM](#)).

### Temporal variability

The structure of benthic algal communities differed strongly among sampling times and seasons (RDA 1, Table 2) and underwent statistically significant ( $P < 0.05$ ) directional change during the experiment (RDA 2, Table 2). In undisturbed mesocosms, maximum abundance ( $5.6 \times 10^6$  cells  $\text{cm}^{-2}$ ) of the dominant mat-forming diatoms occurred in the summer of 2000 (Figs. 1, 2) and declined rapidly thereafter as encrusting algae progressively increased in numerical dominance (maximum  $5.7 \times 10^7$  cells  $\text{cm}^{-2}$ , mean 84% of total numbers; Figs. 1, 3). In controls, some but not all mat taxa increased again in the spring and summer of 2001, although total numbers were lower than in 2000 (Fig. 2). An initial shift from diatom mats to crustose forms also occurred to some degree in both

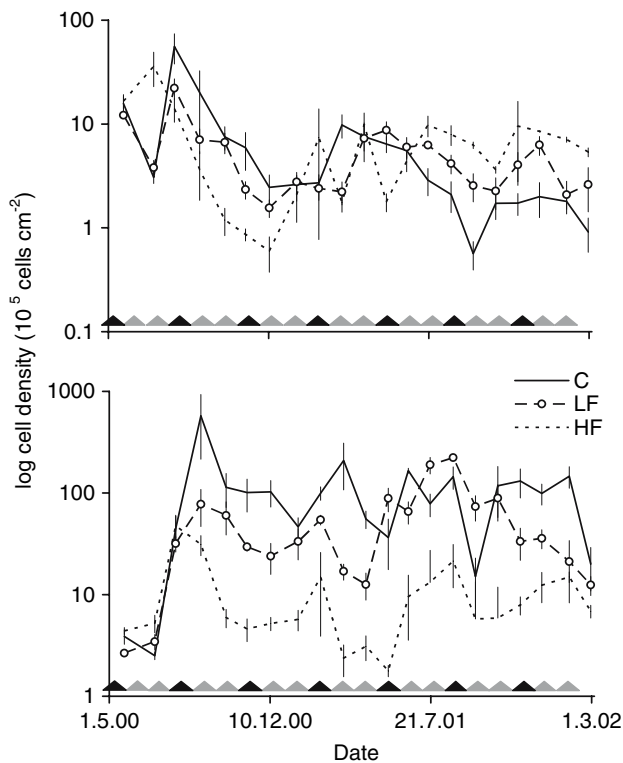
**Table 2** Results of partial redundancy analyses (1–4) examining algal community structure in stream mesocosms

Redundancy analysis	Explanatory variables <sup>a</sup>	Covariables <sup>b</sup>	Percentage variation	<i>r</i>	<i>F</i>	<i>P</i>
1	TimeD	Mesocosm	29.2	0.676	90.85	0.001
2	TimeQ	Mesocosm, Season	6.2	0.603	15.53	0.001
3	Treatment	Block, Time	20.7	0.551	58.93	0.001
4	Treatment $\times$ TimeQ	Mesocosm, TimeQ	3.4	0.305	3.12	0.001

Percentage variation, percentage of species variability explained by the first ordination axis; *r*, species-environment correlation of the first axis; *F*, *P*, *F* ratio and corresponding probability value of each Monte Carlo permutation test

<sup>a</sup> TimeD and TimeQ indicate the use of dummy and quantitative time variables, respectively

<sup>b</sup> Mesocosm denotes use of dummy identifying variables for stream channels



**Fig. 1** Mean ( $\pm 1$  SE) total densities of mat-forming diatoms (*upper panel*) and crustose algae (*lower panel*) in mesocosms disturbed at high frequency (HF) and low frequency (LF) and in the controls (C) over a 21-month period. Note different scaling on the y-axes. Black triangles indicate onset of 6-day disturbances in HF and LF treatments, grey triangles indicate disturbances in HF treatments only

disturbed treatments, but disturbances influenced the dynamics and abundances of these core groups and of their component species during the experiment (Figs. 1–3).

#### Disturbance effects on taxon richness

Repeated-measures ANOVA revealed that taxon richness varied among treatments and sampling occasions. The main effects of treatment ( $P < 0.0001$ ) and time ( $P < 0.0001$ ) were statistically significant as was their interaction ( $P < 0.0001$ ). Taxon richness was initially high in all treatments and subsequently declined (Fig. 4). ANOVA with multiple comparisons also demonstrated that taxon richness in LF disturbance treatments was not significantly different from the controls (Tukey HSD,  $P < 0.05$ ), whereas richness under HF disturbance was significantly different from the controls on 11 occasions, being lower in mid-late 2000 and higher in mid-late 2001 ( $P < 0.05$ ; Fig. 4).

#### Disturbance effects on community structure

Disturbance had a significant effect on algal community structure (RDA 3, Table 2) and on the abundances of

component species (repeated measures ANOVA, Table 3). The RDA with the time effects partialled out indicated that both disturbed treatments contained fewer crustose *Phormidium* and *A. pediculus* than control patches. The abundances of other encrusting algae, namely *G. incrustans*, *R. abbreviata* and *G. olivaceum*, declined with increasing disturbance frequency and were most strongly reduced in HF patches (Figs. 3, 5). *Placoneis clementis* was the most abundant species and *S. leptostauron* the scarcest in low-disturbance patches, whereas *N. capitata* and *S. elliptica* increased with disturbance frequency. However, repeated-measures ANOVA indicated that treatment effects on several common taxa depended on the time of sampling (Table 3). For *G. incrustans*, *A. pediculus* and *Phormidium* spp., abundances decreased as disturbance frequency increased at most endpoints (Tukey HSD,  $P < 0.05$ ; Fig. 3). Thus, the dominance of encrusting algae was mitigated by recurrent substratum drying and, overall, the degree of reduction increased with increasing disturbance frequency (Fig. 6).

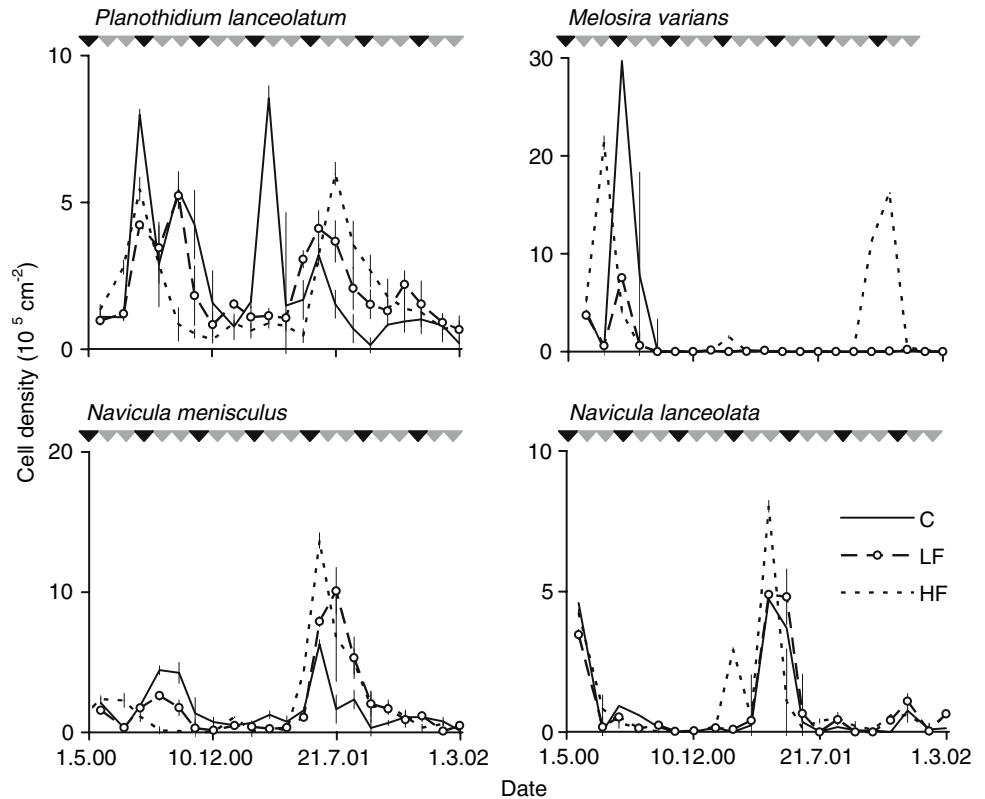
A fourth partial RDA demonstrated statistically significant directional change in community structure that was dependent on treatment (analysis 4, Table 2; Fig. 7). Thus, abundances of 11 diatom species, notably *P. lanceolatum*, *M. varians*, *N. menisculus*, *N. lanceolata*, *N. perminuta* and *S. elliptica*, either peaked in high-disturbance patches and/or decreased in controls and low-disturbance patches late in the sequence (Fig. 2). For these filamentous mat species, differences in numerical abundance among disturbed treatments and controls were statistically significant in mid-2000 and or mid-late 2001 (Tukey HSD,  $P < 0.05$ ; Figs. 1, 2), with the greatest overall percentage change in mat diatom densities occurring in the HF treatment (Fig. 6).

## Discussion

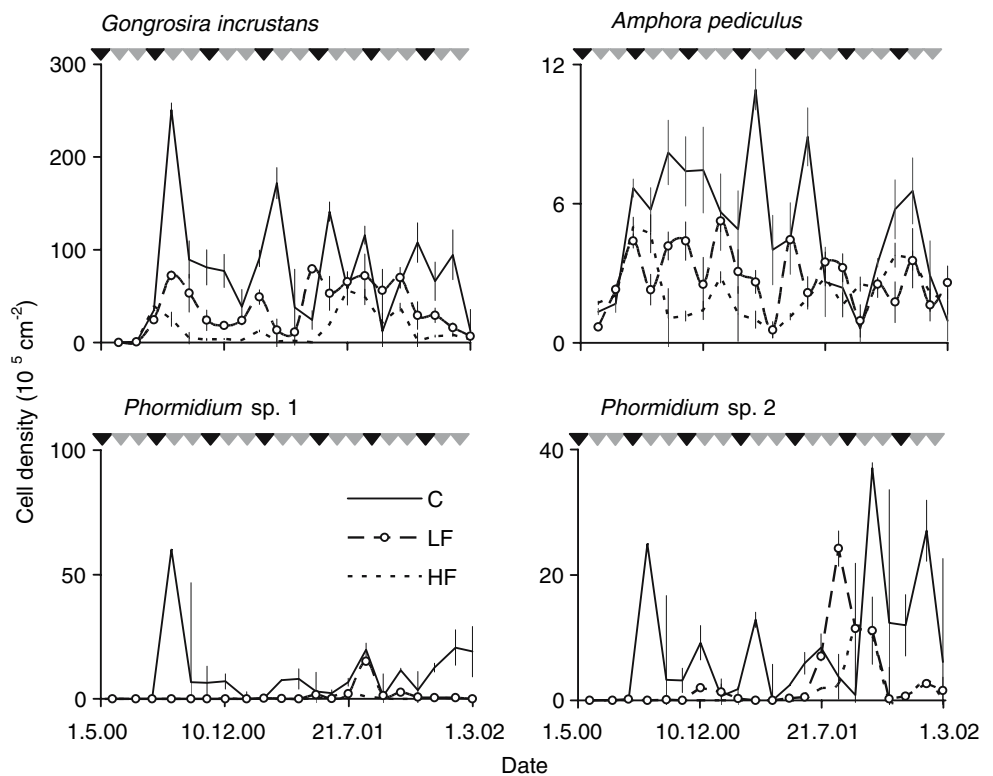
### Temporal dynamics

Algal community structure changed markedly during the experiment, with a species-poor crust assemblage, dominated by the green alga *Gongrosira incrustans* and associated epiphytes, replacing a more diverse diatom mat in the absence of the dewatering disturbance. The substantial proliferation of diatoms observed early in this study is characteristic of chalk streams (Marker 1976) during periods when high nutrient concentrations coincide with periods of high multiplication (Casey et al. 1981). Diatoms have *r*-selected traits, notably rapid recruitment, large reproductive output and short generation times, which enable the rapid exploitation of epilithic space (Steinman and McIntire 1990; Biggs 1996). Our observations indicate that the chain-forming species *Melosira varians* was initially an

**Fig. 2** Mean ( $\pm 1$  SE) densities of dominant mat diatoms in mesocosms disturbed at high frequency (*HF*) and low frequency (*LF*) and in the controls (*C*) over a 21-month period. Note different scaling on the y-axes. Triangles indicate onset of disturbances (see Fig. 1 caption for explanation)

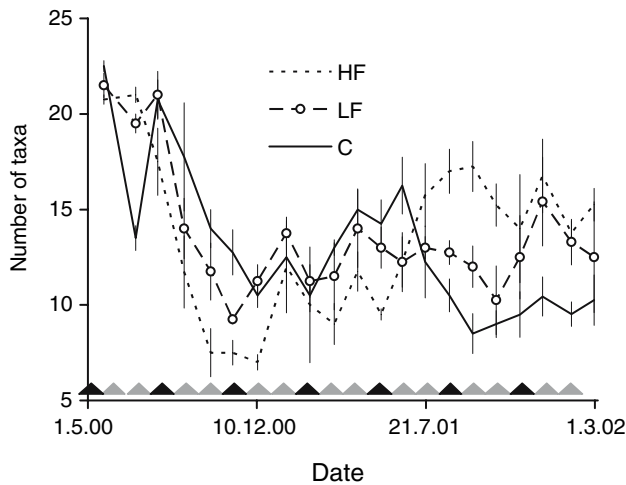


**Fig. 3** Mean ( $\pm 1$  SE) densities of dominant crust-associated algae in mesocosms disturbed at high frequency (*HF*) and low frequency (*LF*) and in the controls (*C*) over a 21-month period. Note different scaling on the y-axes. Triangles indicate onset of disturbances (see Fig. 1 caption for explanation)



important structuring component of the diatom mat, providing a habitat for various unicellular ‘passengers’, notably species of *Navicula* and *Nitzschia*. Chain-formation probably enhances areal production for these weak competitors

by facilitating the capture of light and dissolved nutrients (see Round et al. 1990; Sickogoad and Andresen 1991). However, *Melosira* lacks durable attachment to the substratum (Crawford 1978), and sloughing of dense senescing



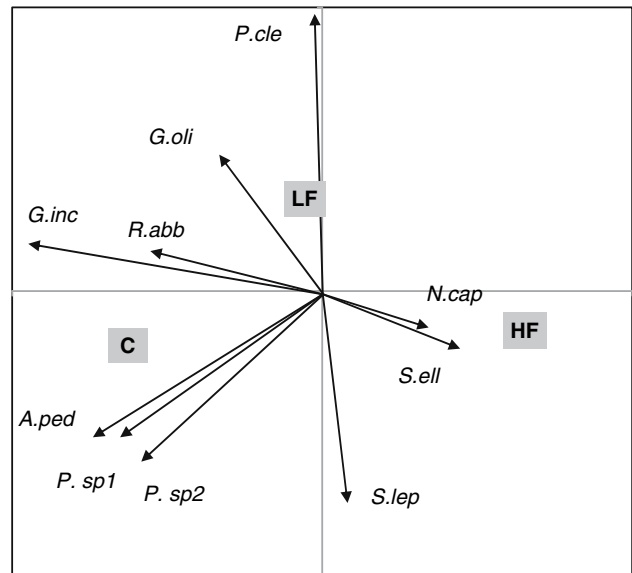
**Fig. 4** Taxon richness ( $\pm 1$  SE) of epilithic algae in mesocosms disturbed at high frequency (HF) and low frequency (LF) and in the controls (C) over a 21-month period. Triangles indicate onset of disturbances (see Fig. 1 caption for explanation)

**Table 3** Repeated-measures ANOVA testing the effect of disturbance treatment, time and their interaction on the densities of benthic crusts and mats, and of the dominant component algal and cyanobacterial taxa

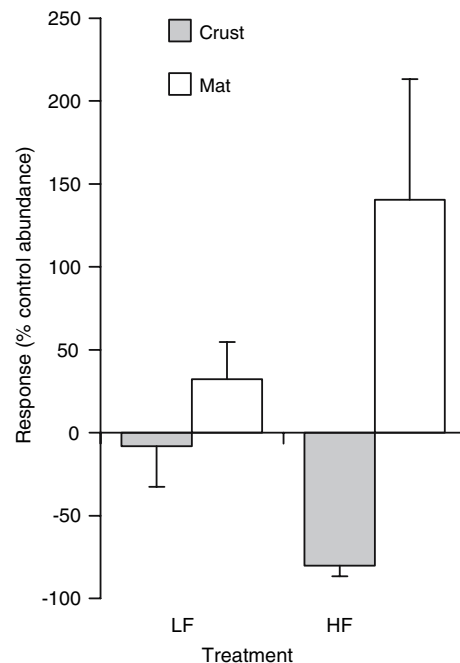
	Treatment (df 2,6)	Time (df 20,120)	Interaction (df 40,120)
Crust	<0.0001*	<0.0001*	<0.0001*
<i>Gongrosira incrustans</i>	<0.0001*	<0.0001*	<0.0001*
<i>Amphora pediculus</i>	0.001*	<0.0001*	0.007*
<i>Phormidium</i> sp. 1	<0.0001*	<0.0001*	0.013
<i>Phormidium</i> sp. 2	0.004*	0.004*	0.004*
Mat	0.956	<0.0001*	<0.0001*
<i>Planothidium lanceolatum</i>	0.310	<0.0001*	0.005*
<i>Melosira varians</i>	<0.0001*	<0.0001*	0.138
<i>Navicula menisculus</i>	0.121	<0.0001*	<0.0001*
<i>Navicula lanceolata</i>	0.387	<0.0001*	0.019

\* Significant at an alpha of 0.05 after non-sequential Bonferroni correction. Numbers are ANOVA P values

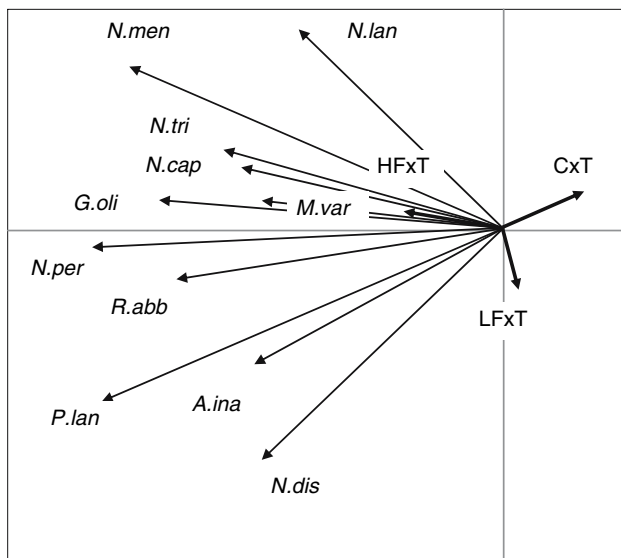
mats during the first summer of the experiment reduced taxon richness in all treatments. Thereafter, algal crusts, predominantly of *Gongrosira*, developed on the mineral surfaces in the control channels. This green alga propagates vegetatively, forming hard calcified hemispherical crusts of erect and prostrate uniseriate filaments (John 2002). Spatial and temporal variation in the thickness of the crusts accounted for the fluctuating abundances observed on stones. *Gongrosira* colonies are slow-growing and long-lived and can persist for a year or more (Pentecost 1988). In our study, crusts dominated undisturbed stone surfaces for approximately 18 months. This longevity facilitated the efficient capture and control of epilithic space and inhibited the invasion of potential competitors. Our visual inspections



**Fig. 5** Partial redundancy analysis (RDA) ordination diagram demonstrating overall differences in algal community structure among treatments where drying disturbances were applied at high (HF) and low frequency (LF). C Control. Grey boxes indicate position of treatment centroids. The direction and length of species vectors indicate differences in abundance among treatments. Taxa are abbreviated on vector labels: *A. ped* *Amphora pediculus*, *S. ell* *Staurosira elliptica*, *S. lep* *Staurosirella leptostauron*, *G. inc* *Gongrosira incrustans*, *G. oli* *Gomphonema olivaceum*, *N. cap* *Navicula capitata*, *P. cle* *Placoneis clemantis*, *P. sp1* *Phormidium* sp. 1, *P. sp2* *Phormidium* sp. 2, *R. abb* *Rhoicosphenia abbreviata*



**Fig. 6** The mean ( $\pm 1$  SE) effect of disturbances applied at low frequency (LF) and high frequency (HF) on abundances of crust and mat algae, expressed as the percentage difference from control abundance



**Fig. 7** Partial RDA ordination diagram demonstrating directional changes in algal community structure in treatments. The *direction and length* of species vectors indicate the trend and extent of increase in abundance specific to particular treatments. The interactions between each treatment (C, HF, LF) and time (T) are shown by *arrows*. Taxa abbreviations: *A. ina* *Amphora inariensis*, *P. lan* *Planothidium lanceolatum*, *N. lan* *Navicula lanceolata*, *M. var* *Melosira varians*, *N. tri* *Navicula tripunctata*, *N. dis* *Nitzschia dissipata*, *N. per* *Nitzschia perminuta*. Other abbreviations are given in the caption to Fig. 5

suggest that epilithic space is a limiting resource for mat-forming algae in undisturbed patches, with between 90 and 100% of bare surfaces occupied by crusts. Both the curtailed development of diatom mats in mid-late 2001 and a sustained decline in algal species richness on undisturbed stones were consistent with the monopolisation and dominance of space by crustose algae. While our observations suggest mat diatoms do not overgrow *Gongrosira*, a range of epiphytes, notably small unicellular diatoms (*Rhoicosphenia*) and blue-greens (*Phormidium*), coexist with the green alga. These taxa may avoid competition for epilithic space by attaching instead to the colony surface, as has been shown for diatoms on marine crusts (Airoldi 1998, 2000). Although few studies have examined the dynamics of crustose algae in streams, the taxonomy of the crust is similar to that described previously in the same catchment (Marker 1976) and in other calcareous systems in Europe (Pentecost 1988, 1991; Sabater 1990)

#### Disturbance effects

Recurrent disturbances altered the structure and temporal dynamics of benthic algae in the mesocosms. Crustose algae were particularly vulnerable to drying, and the abundances of *Gongrosira* and associated epiphytes usually decreased with increasing disturbance frequency. Logistic constraints prevented algal sampling at the end of each

disturbance event. However, crusts were consistently bleached during emersion and either deteriorated, losing bulk, or disintegrated completely, exposing clean mineral surfaces. Many benthic algal species can adapt physiologically to withstand desiccation by developing thick cell walls or forming propagules (Steinman and McIntire 1990), but emersion can nevertheless destabilise the architecture of colonies and cause sloughing (Peterson 1987; Robson 2000). Following disturbance, *Gongrosira* re-growth occurred within damaged crusts and spread into open space from remnant prostrate filaments. Our endpoint data indicated that crusts regenerated slowly, achieving partial recovery where disturbances were applied at low frequency, with the effect that crusts were thinner and less extensive than the controls. High-frequency disturbance exceeded the resilience of *Gongrosira*, and crusts were either eliminated, or they persisted as small isolated nodules several millimetres in diameter on stones, increasing the availability of space for colonisation by other opportunistic species of algae.

Disturbance effects on mat diatoms shifted strongly during the experiment, shaping algal taxon richness on stones. In the spring of 2001, responses of mat assemblages were weak, and there was little evidence for a strong depletion of abundance or taxon richness, nor was there any apparent exploitation of empty space. However, marked responses were observed in HF treatments during the summer and autumn, with decreased and increased presence and abundance of mat diatoms in 2000 and 2001 respectively. These contrary responses were associated with directional changes in the taxonomic composition and physiognomy of the diatom mat. In 2000, extensive sloughing of loosely adhering mats of *Melosira* and associated diatoms reduced abundances and eliminated some taxa. Diatom species differ in their resistance and resilience to emersion (Peterson 1996), and loosely attached mats are particularly vulnerable to disturbance (Peterson 1987; Biggs and Thomsen 1995). Localised sloughing can, in turn, yield a paucity of remnants and new colonists, limiting post-disturbance recovery and the exploitation of empty space (Moore 1977; Biggs and Thomsen 1995; Peterson 1996). In 2001, by contrast, *Melosira* was scarce during the summer, and mats were more closely adhering, being mixtures of unicellular species with physiognomies more resistant to disruption, and we speculate that a greater proportion of cells persisted through disturbances, multiplying to exploit epilithic space exposed by the erosion of *Gongrosira*. The closely adhering physiognomy of the mat enhanced the persistence of diatoms in disturbed patches during 2001, producing richer, more abundant layers than in the controls. Thus, over the course of the experiment, directional change in assemblage composition increased the stress tolerance of diatom mats, and disturbances promoted coexistence with the dominant



green alga, as predicted by Sousa (1979) and others. The reversals in disturbance effects revealed by our relatively prolonged study emphasise the important influence of disturbance timing and history on the responses of populations. Our observations support the proposition of Robson and Matthews (2004) that responses to disturbances in the past influence the taxonomy and physiognomy of algal layers; as such, they may thereby govern future responses to disturbance events.

Trade-offs in the species-specific abilities to colonise and compete are essential components of theoretical models of community structure (Petraitis et al. 1989; Tilman 1990). According to these models, disturbances promote the persistence of species by preventing the exclusion of weak competitors by dominant and/or long-lived species (Connell 1978; Sousa 1979). The results of our study are consistent with the existence of contrasting species traits among the benthic algae. The crust-forming alga *Gongrosira* effectively acquires and retains benthic space but lacks a high resistance or resilience to disturbance and is therefore strongly reduced by recurrent emersion. By contrast, competitively inferior mat-forming diatoms lack traits that enable the retention of space, but some possess resilience traits that promote the rapid exploitation of patches opened by drought, although – in our study – this was contingent upon disturbance timing and initial mat species composition.

This study was based on the premise that the frequency of physical disturbance can vary spatially across the river bed, depending on the local topography of the substratum (Ruetz et al. 2005). The results of our experiment indicate that patchy disturbances create heterogeneity in the structure and temporal dynamics of attached algal communities, one of the key elements of patch dynamics theory (Pickett and White 1985). The patch dynamics perspective, which regards communities as mosaics of patches of contrasting successional ages, was developed for terrestrial plants (Clements 1916; Pickett and White 1985), coral reefs (Connell 1978) and marine rocky shores (Sousa 1979). The application of models of coexistence to rivers and streams (see Townsend 1989) has been controversial, however, with the development of theory incorporating highly mobile invertebrates (Frid and Townsend 1989; Downes 1990; Matthaei and Townsend 2000). However, the dynamics of benthic algae are more comparable to those of terrestrial plant or marine rocky shore assemblages, being dependent upon attachment space (Frid and Townsend 1989; Townsend 1989). Previous studies have shown that the interplay of algal succession with disturbance creates a patchwork of primary producers on the river bed (Fisher et al. 1982; Power and Stewart 1987). In our study, mat diatoms rapidly exploit disturbed patches but are displaced by encrusting green algae, thereby driving down taxon richness on stones. These

dynamics are consistent with the concept of dominance-control (Yodzis 1986), whereby competitive dominants exclude good colonists locally. Mat diatoms coexist with *Gongrosira* by exploiting “probability refuges” (Shorrocks and Rosewell 1987; Townsend 1989), patches of empty space opened by disturbance in the environment. Localised disturbances caused by local flow fluctuations impart heterogeneity in the structure of benthic algae, with successional age inversely related to disturbance frequency. Patchy disturbance could therefore promote the diversity of riverine landscapes by providing refuges for opportunistic algal species.

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