Hydrobiologia **362:** 209–216, 1998.

The effect of continuous physical disturbance on mayflies of a tropical stream: an experimental approach

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Received 15 April 1997; in revised form 5 November 1997; accepted 19 November 1997

Key words: mayfly, artificial disturbance, stream, Kenya, tropics, biomass

Abstract

Field experiments to examine the effect of continuous physical disturbance on the Ephemeroptera of the Naro Moru River, Kenya, were undertaken from June 1993 to January 1994. Continuous disturbance was administered on a randomly selected subsite of the sediment surface. Artificial physical disturbance within the experimental subsite involved continuous local displacement, shifting and stirring of the streambed surface substrates (about 10 cm depth) by hand every one minute for 10 or 14 min. Three control samples were also taken randomly from the sediment surface of an undisturbed stratified area of the study riffle at the start of each disturbance occasion. All samples were collected using a Hess sampler (surface sampling area of 3.142 dm^2; meshsize 80 μm). Seven mayfly species were particularly abundant and these included *Afronurus* sp., *Afroptilum sudafricanum* LESTAGE, *Baetis s.l.*, *Baetis (Nigrobaetis)* sp. 1, *Baetis (Nigrobaetis)* sp. 2, *Caenis* sp. and *Choroterpes (Euthraulus)* sp.

About 83,8% of the total mayfly density and 88.1% of the biomass were removed from the streambed surface within the first three minutes of continuous physical disturbance. A mayfly biomass of 33.7391 mg dm^2 and total density of 1357.6 ind dm^2 were collected from the disturbed subsite during the study duration. Further, a biomass of about 42.8335 mg dm^{-2} and total density of 2366 ind dm^{-2} were collected from the control sites. There was a near-complete depletion of mayfly individuals from the topmost sediment layer within 14 min of continuous disturbance.

Introduction

An extensive field study of the impact of artificial physical disturbance on the Ephemeroptera community of the Naro Moru River by the author from 1993 to 1994 involved several experimental approaches of physical disturbance of similar intensity but varying frequency. This paper forms part of the field experiments that dealt with continuous artificial physical disturbance on the sediment surface. Seven species of mayflies were chosen as the focal invertebrates for this study. These included *Afronurus* sp., *Afroptilum sudafricanum* LESTAGE, *Baetis s.l.*, *Baetis (Nigrobaetis)* sp. 1, *Baetis (Nigrobaetis)* sp. 2, *Caenis* sp. and *Choroterpes (Euthraulus)* sp.

Since all streams, whatever their locale, are continuously disturbed, the intensity and frequency of these inherent disturbances coupled, in some cases, with random allogenic disturbances, determine the extent of their effect on the stream biota. The allogenic disturbances, whenever present, merely boost the effects of the autogenic natural disturbances on stream communities. One question which has occupied stream ecologists over the past decade is whether a disturbance intensity and frequency beyond the level of the stream at the time of observation could affect the zoobenthic community structure. In view of this, several methods, including turning/tumbling stones (Boulton et al., 1988; Reice, 1985) and shuffling, kicking and raking (Marchant et al., 1991; Brooks & Boulton, 1991) have been used in field studies in search of ecological answers. The effects of these physical disturbances have normally been defined in terms of results (i.e. removal of residents) (Dudgeon, 1991), and the results expressed in terms of patterns that accrue (Mathooko, 1996).

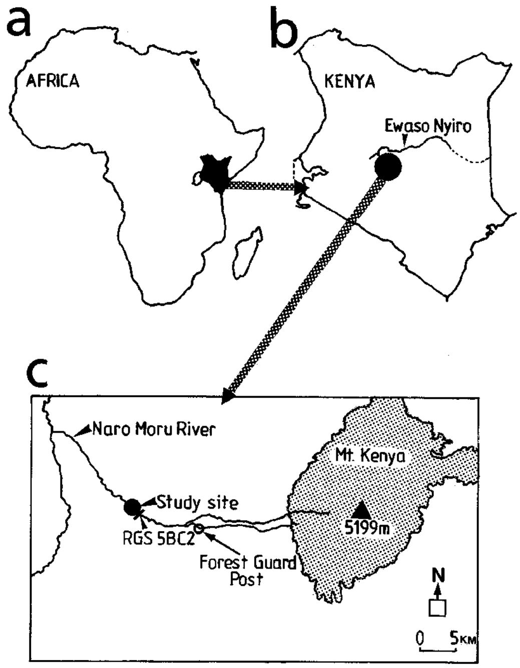

Figure 1. The Naro Moru River and the study site. (a) Location of Kenya in Africa, (b) location of the Naro Moru River in Kenya, and (c) location of the study site on the Naro Moru River.

Continuous disturbance does not defaunate sediments completely. A few relict organisms (*sensu* Townsend, 1989) may remain, especially those in the deeper sediments or hyporheic zone. In the Naro Moru River, macrozoobenthos tend to migrate to the deeper layers during the time of floods (pers. obs.), and these may form part of the pool that recolonizes the upper sediment layers. Nevertheless, a large proportion of the fauna and biomass is removed during disturbance. Shuffling and kicking of substrates have been shown to reduce the number of individuals by 97% (Brooks & Boulton, 1991). The change in abundance and biomass as a result of continuous disturbance is rarely studied. The main question being addressed here is whether or not continuous physical disturbance has any impact on a mayfly community. It is, therefore, the objective of this study to elucidate mayfly interspecific and species-specific responses to continuous physical disturbance in terms of densities and biomass. Since it is not possible to collect benthic samples from the streambed in bankfull situations, this study attempts to experimentally simulate the possible outcomes of such high disturbance intensity on the fauna densities and biomass.

Materials and methods

Site description

This study was conducted on a 82 m long riffle zone (0°C 10′ S, 37°01′ E, elevation 2035 m above sea level (m a.s.l.)) on the Naro Moru River (Figure 1), a gravel stream which flows from the western side of Mt. Kenya through the Mt. Kenya National Park in its upper reaches. The Naro Moru River is a 2nd-order stream formed when the North and South Naro Moru Rivers join at about 2180 m a.s.l. Rivulets from Teleki Tarn (4270 m a.s.l.), Hut Tarn (4488 m a.s.l.), Lewis Tarn (4574 m a.s.l.), Tyndall Tarn (4457 m a.s.l.), Naro Moru Tarn (4190 m a.s.l.) and, from remnants of the Darwin and Lewis Glaciers supply its tributaries with water throughout the year. The catchment area above the study site was 83 km^2, which comprised only 0.04% of the Ewaso Ngiro drainage area (drainage area: 56 980 km^2) of which the Naro Moru River is a subset.

Monthly rainfall amounts monitored at the Naro Moru Forest Guard Post (Stn. No. 9037064–0°11′ S, 37°07′ E–RDA 4A) from 1980 to 1993 show that the highest amount of rainfall occurs from March to May and from October to December, emphasizing a bimodal rainfall distribution. The months with the highest water discharge are April/May and October/November. During these months, approximately half the amount of water (46–53%) is discharged (Leibundgut, 1983). In some cases, the months of June and December are also part of the rainy season discharge, and 55- 68% of the annual amount is then discharged during these rain periods. Occasional intermittent spates may occur as a result of snow-melt or ‘mountain rain’ which occur irregularly irrespective of the season. Based on water discharge recorded at RGS 5BC2 ($\sim$ 1 km upstream the study site), the discharge regime of the Naro Moru River strongly reflects the rainfall intensity (Figure 2), showing two major peaks.

The Naro Moru River traverses a wide vegetational spectrum stretching from the arborescent species of *Senecio brassica* R.E. FR. & TH. FR. Jr and *Lobelia* at about 4000 m a.s.l., through the bamboo forest, remnants of the tropical rainforest, savanna woodlands to the semi-desert shrubs in its lower reaches. The riparian vegetation at the study site was dominated by *Podocarpus gracilior* PILGER, *Syzygium guineense* (WILLD.) DC and *Acokanthera longiflora* STAPF and a few exotic pines. About 87% of the study riffle was canopied.

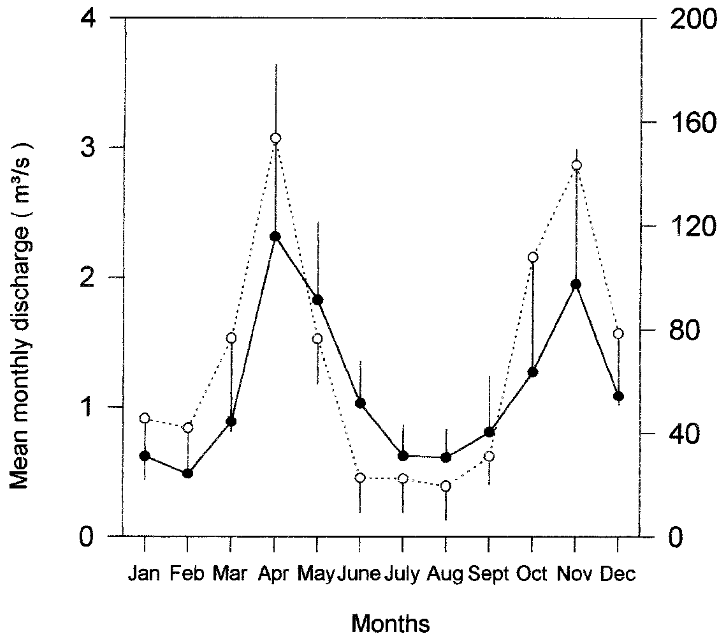

Figure 2. Mean monthly discharge of the Naro Moru River and rainfall amounts of the upper Naro Moru River catchment from 1980 to 1993. Discharge (•), rainfall (○). Only upper and lower limits, respectively, are shown. Vertical lines: $\pm$ 95% CL.

Experimental design

The study was carried out from June 1993 to January 1994 and involved eleven sampling occasions. The Naro Moru River was chosen for this study because it is relatively unperturbed by humans and has a mayfly community comprising 25% of the macrozoobenthos and 65% of the macrozoobenthic drift (Mathooko & Mavuti, 1992). Stirring, shifting and relocation of sediment substrates by hand was used to delimit artificial physical disturbance on the sediment surface. To avoid variations in disturbance intensity, same person induced disturbance throughout the experimental duration. The induced artificial physical disturbance and the inherent natural disturbances in the Naro Moru River were taken as complementary variables which structure the patterns of mayfly abundance as well as biomass. Since it is not easy to quantify the artificial disturbance to compare it with the effects of natural disturbances, it can only be inferred that the high erodibility of benthos by the artificial disturbance compares with the high erodibility of benthos by high discharge as found by Mathooko & Mavuti (1994) in the same river. This experimental design was therefore used to simulate physical disturbance of very high intensity, frequency and erodibility since it shifted and rearranged the substrates, a situation only encountered on streambeds during very high discharges. It examines the immediate effect of physical disturbance on the mayfly assemblage at a single sample position, especially its effect on mayfly densities and biomass.

The location of the experimental site was permanently marked with iron stakes in such a manner that the Hess sampler (surface sampling area of 3.142 dm^2, 80 μm meshsize) could always fit tightly between them without changing position. The samples were approximately collected from the upper 10 cm of the sediment surface. During each sampling occasion, the Hess sampler was placed in the delineated area and the enclosed sediment substrates disturbed by hand for one minute and the sample emptied within the shortest time possible ($\approx$ 7–10 sec). The exercise was then continuously repeated in the subsequent minutes until 10 to 14 one-minute samples were collected from the same disturbed position. The whole experimental exercise took $\approx$ 20 min. The samples were preserved in 5% formaldehyde solution and later sieved through 250 μm and 80 μm mesh-size nets to separate the debris and larger animals from the smaller ones. To obtain their abundance, the ephemeropterans retained in both sieves were sorted under a stereomicroscope, identified and enumerated. The individuals of each sample were stored separately for biomass determination.

Biomass determinations

Ash-free dry weight (AFDW) was determined for all the seven dominant mayfly species. Since specimens were preserved in formaldehyde solution for some time before analysis, changes in individual weight are expected (Donald & Paterson, 1977). In this study, the conventional method of determining the AFDW by subtracting ash content after ignition from dry weight was used without considering prior weight loss due to preservation. Samples were put in pre-heated and pre-weighed aluminium cups and oven-dried to constant weight at 60 ˚C for 24 h, cooled to room temperature and then weighed on a UM3 microbalance. They were then ashed at 500 ˚C for 1 h, desiccated for 1 h, and reweighed.

All the statistical analyses were done using the Statistical Package for Social Science (SPSS® for Windows™) 1992). The data were first tested for homogeneity of variances using F_{max} tests (Sokal & Rohlf, 1995). Density data that did not meet this assumption were transformed as $\log_{10}(x+1)$ and biomass as $\log_{10}(x+0.1)$.

Results

A mayfly biomass of 33.7391 mg/dm^2 and a total density of 1357.6 ind./dm^2 were collected during the study duration. At least six Ephemeroptera families and fifteen species were represented. Out of these, *Afronurus* sp. comprised 41.34% of the total individuals whilst *Choroterpes (Euthraulus)* sp. comprised 32.46%. *Baetis s.l.* contributed 14.41%, *Afroptilum sudafricanum* 5.02%, and *Baetis (Nigrobaetis)* sp. 1 and *Baetis (Nigrobaetis)* sp. 2 comprised 0.82% and 1.66%, respectively *Caenis* sp. contributed 2.52%. It was evident that *Afronurus* sp. and *Choroterpes (Eu.)* sp. numerically dominated the other mayfly species.

A large proportion of the mayfly individuals was removed from the streambed surface within the first few minutes of physical disturbance. About 83.8% of all ephemeropteran individuals and 88.1% of the biomass were removed within the first three minutes of continuous disturbance. After 14 min of continuous disturbance, nearly all mayfly individuals were removed from the disturbed subsite.

Neither interspecific nor species-specific responses to disturbance were evident in this study (Figure 3). All the species had a sharp decline in densities and biomass when physical disturbance was administered. There was no evidence of densities and biomass recovering to the pre-disturbance levels. The density removal rates of the mayfly species from the streambed surface indicated that the removal of *Afronurus* sp. was the highest and also provided a correspondingly high biomass removal rate (Table 1). Generally, the total density and biomass of the control samples were about two-fold higher on average than the density and biomass of the disturbed subsite samples (see Table 1). It was only *Afronurus* sp. which registered a lower density in the control site than in the disturbed subsite. *Caenis* sp. had also a lower biomass in the control site than in the disturbed subsite. The one-minute disturbance had a highly significant effect on the mayfly mean densities and biomass (Table 2). *Post-hoc* comparisons indicated that biomass removed in the first minute was significantly different from the biomass removed in the subsequent one-minute physical disturbances (Student-Newman-Keuls (SNK) test, $\alpha = 0.05$). *Afronurus* sp. densities removed within the first minute differed significantly from those of the subsequent disturbances (SNK test, $\alpha = 0.05$). Consequently, peak biomass removal for all mayflies occurred in the first minute of disturbance with the highest mean (± se) biomass removed per minute being 6.0103 (1.1471) mg for *Afronurus* sp., 0.4148 (0.0856) for *Afroptilum sudafricanum*, 0.1454(0.0368) for *Baetis s.l.,* 0.5471 (0.2464) for *Choroterpes (Eu.)* sp. and, 0.0905 (0.0177) and 0.1043 (0.0323) for *Baetis (Nigrobaetis)* sp. 1 and *Baetis (Nigrobaetis)* sp. 2, respectively. Mean weight per individual was not correlated with increase in disturbance time for all species (Spearman's rank correlation, r_2, $p > 0.05$).

Discussion

Disturbance is a phenomenon which is integrated in the physicochemical and biological characteristics of streams. Streams are subjected to daily, seasonal and annual increases or decreases in discharge. An increase in discharge beyond a theoretical threshold could lead to erosion of individuals from one or more points on the streambed. The sizes of disturbed areas on the sediment surface depend on several factors, including the intensity and frequency of the disturbance itself, and the nature of the substrate being acted upon. In particular, micro-scale natural disturbances (e.g. hydraulic jumps, eddies) are a common feature of lotic systems, and large-scale disturbances such as spates only expand the

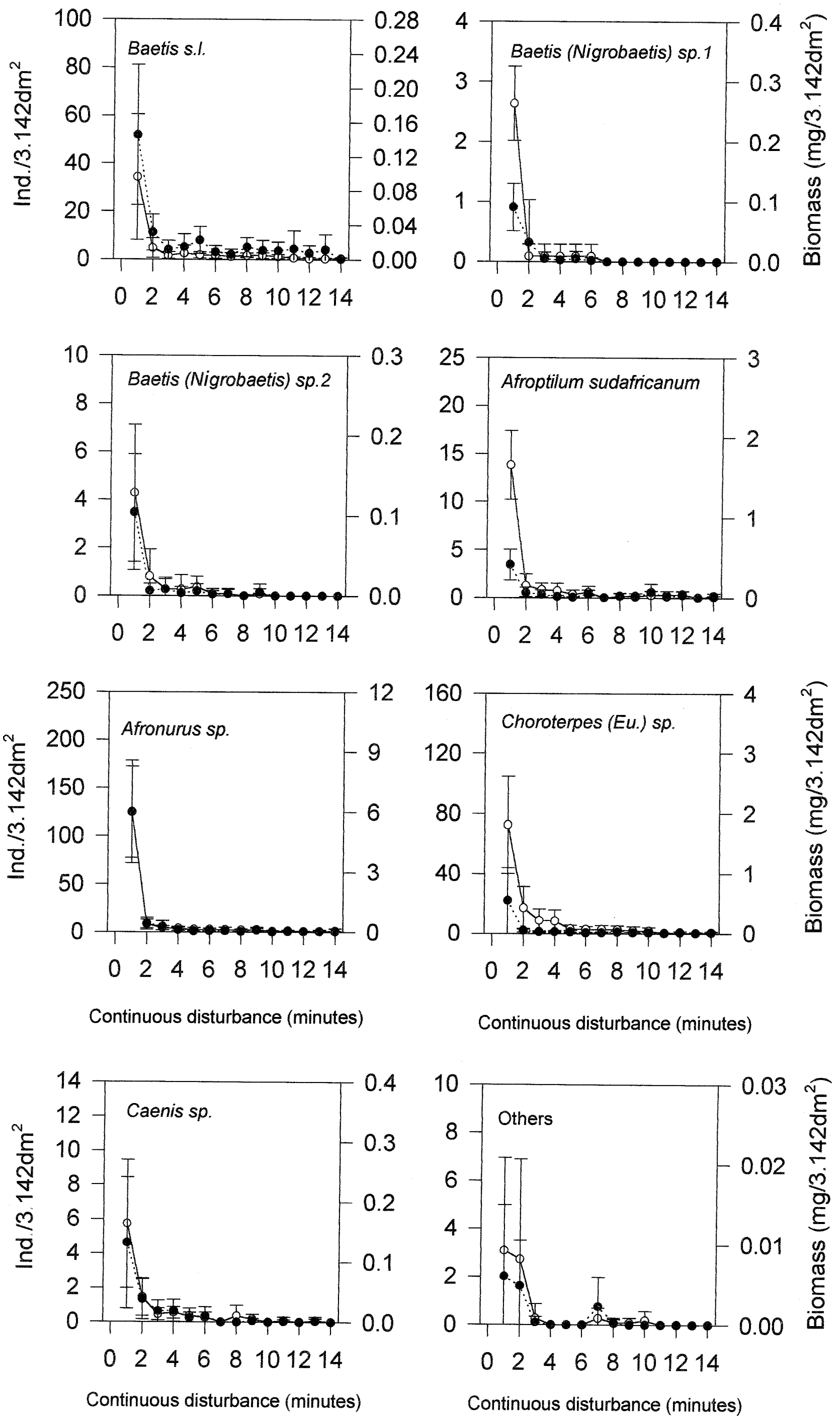

Figure 3. The fluctuations of density and biomass with continuous physical disturbance of the major mayfly species. Density (○), Biomass (●). Vertical lines: ± 95% CL.

Table 1. Mean densities, biomass and removal rates of the major mayfly species in the disturbed and control sites during the entire study duration. DRR = Density removal rates, BRR = Biomass removal rates, mean ± 95% CL, N = 11.

Taxa	Disturbed site				Control site	
	Mean density (Ind./dm^2)	Mean biomass (mg/dm^2)	Mean DRR (Ind./min/dm^2)	Mean BRR (mg/min/dm^2)	Mean density (Ind./dm^2)	Mean biomass (mg/dm^2)
Afronurus sp.	46.44 ± 16.08	2.3153 ± 0.8234	3.58 ± 1.44	0.1720 ± 0.0569	41.34 ± 13.83	2.8306 ± 1.2412
Afroptilum sudafricanum	5.84 ± 1.18	0.2338 ± 0.0787	0.42 ± 0.08	0.0180 ± 0.0067	15.54 ± 7.43	0.2346 ± 0.0984
Baetis s.l.	16.64 ± 11.71	0.0977 ± 0.0372	1.36 ± 1.01	0.0079 ± 0.0037	26.30 ± 19.97	0.1033 ± 0.0739
Baetis (Nigrobaetis) sp. 1	0.98 ± 0.29	0.0437 ± 0.0277	0.08 ± 0.02	0.0032 ± 0.0020	5.04 ± 2.23	0.1685 ± 0.1089
Baetis (Nigrobaetis) sp. 2	1.97 ± 1.20	0.0433 ± 0.0284	0.16 ± 0.10	0.0036 ± 0.0025	2.63 ± 1.89	0.0992 ± 0.1128
Caenis sp.	2.84 ± 1.46	0.0737 ± 0.0416	0.21 ± 0.10	0.0055 ± 0.0030	5.79 ± 2.51	0.0595 ± 0.0321
Choroterpes (Euthraulus) sp. 3	6.71 ± 16.94	0.2568 ± 0.1722	2.82 ± 1.39	0.0190 ± 0.0122	113.19 ± 29.88	0.3979 ± 0.1435

Table 2. Table of one-way analysis of variance testing for effects of continuous physical disturbance on pooled densities and biomass of the dominant mayfly species during the entire study duration. Disturbance df = 13, *** $p < 0.001$.

Taxa	Disturbed subsite		Control sites			
	MS_{error}	MS	F-ratio	MS_{error}	MS	F-ratio
Afronurus sp.	0.09	2.42	25.51***	0.06	2.03	35.89***
Afroptilum sudafricanum	0.03	0.89	27.57***	0.02	0.30	13.04***
Baetis s.l.	0.10	0.94	9.43***	0.01	0.08	9.79***
Baetis (Nigrobaetis) sp. 1	0.01	0.22	33.98***	0.004	0.05	12.23***
Baetis (Nigrobaetis) sp. 2	0.03	0.25	9.81***	0.004	0.05	11.52***
Caenis sp.	0.03	0.34	10.26***	0.01	0.06	7.50***
Choroterpes (Euthraulus) sp.	0.15	2.10	14.16***	0.02	0.26	15.67***

sizes of the existing disturbed microsites. An increase of discharge that leads to the stirring, scouring and relocation of the substrates in which the faunae live is not a daily phenomenon in streams, and may occur at least twice per year in the Naro Moru River (Mathooko, 1996). This small-scale experiment is, therefore, particularly important as it could provide considerable insight into the effects of high discharge and its continuous erosion of the stream fauna.

Physical disturbance on the streambed surface may decrease or increase interstitial spaces through relocation/rearrangement of the streambed substrates, and this physical restructuring has an immediate effect on mayfly densities. Reice (1984, 1985) found that tumbling rocky substrates in the New Hope Creek in North Carolina resulted in a greater than 60% reduction in the total fauna. Further, Brooks & Boulton (1991) showed that shuffling and kicking of substrates reduced the number of individuals by 97%. In Gorge and Birthday Creeks in Australia, Rosser & Pearson (1995) found a decline in macrozoobenthos densities with increased disturbance of the sediment surfaces. All these results are in agreement with strong disturbance-related reductions of zoobenthic densities in the current study. It is expected that with decline in densities, there will be a corresponding decline in biomass. A large number of the mayfly individuals (84%) and biomass (88%) were removed from the sediment surface within the first three minutes of continuous physical disturbance. Further, a distinct reduction of mayfly densities and biomass was observed with subsequent disturbances. Apparently, this was due to the high disturbance frequency, coupled with lack of ample time lag to enable the mayflies to re-establish themselves in a situation of high resource shifting. These resources may include space and the loosely-held food resources which could greatly be altered by the high subsite instability. The high disturbance frequency could not have reduced to a significant extent the firmly-held food resources, i.e. epilithon biomass, on the substrate surfaces. Karlström (1978) found that even scrubbing stones with a steel-wire brush failed to remove all the epilithon. In view of this, food could not have been a limiting factor for the recolonizing mayfly individuals. A plausible explanation could be the short time lag between one disturbance and the next as a consequence of the high disturbance frequency. Probably, the mayflies could not cope with a disturbance frequency of this magnitude which is rare in their environment. The possibility of annulling the effect of this disturbance could have been by retreating to the deeper sediment layers as observed by Mathooko & Mavuti (1992). A very high disturbance frequency delayed the recovery of the mayflies in the disturbed subsite to the pre-disturbance abundance levels.

Palmer et al. (1992) observed a dramatic reduction of the overall faunal abundance during spates in the sandy bottom Goose Creek because of substrate scouring. Floods occur at least twice a year in the Naro Moru River although there are occasional spates due to snow-melt and/or 'mountain rain'. Mathooko & Mavuti (1992) found that drift increased when discharge increased in the Naro Moru River. This could provide an evidence that high discharge, which does not even displace the substrates, could reduce densities of macrozoobenthos on the streambed. The accompanying high water velocities normally make resettling on the streambed by fauna extremely difficult. This means that the intensity of the induced disturbance in the present study was even beyond that level which was observed to increase drift since it shifted the substrates. Continuous disturbance reduced drastically the mayfly density but not the individual mean weight, although biomass was highly reduced. This could have been due to the continuous redistribution of the mayfly individuals of smaller sizes in the system through drift and/or due to the immigration of the relict mayfly individuals which contributed to continuous biomass input on the disturbed subsite. This could explain the lack of correlation between mean individual weight and disturbance time. Doeg et al. (1989) suggested that drift contributed 36% of the individuals that recolonized gravelly sediments in the Acheron River in Australia. In the Naro Moru River, Mathooko & Mavuti (1992) indicated that mayflies comprised 65% of the macrozoobenthic drift. Thus, drift could have been an important contributor of the continuous biomass input on the disturbed subsite.

In conclusion, several facts about continuous disturbance emerge from this study:

(a) Disturbance itself reduces both densities and biomass of the mayfly species.
(b) Continuous disturbance delays the recovery time of the disturbed site to the pre-disturbance density and biomass levels, thus lowering or eliminating resilience ability.
(c) In the absence of data on the actual effect of very high discharge on mayflies, it is extremely difficult to directly discern whether this study fully simulates the situation during high discharge.

Based on my previous research on drift and benthos in the same river (Mathooko, 1988), it is clear that this study to some extent simulates natural disturbance. Drift increased with increase in discharge indicating that some sections of the streambed were being depleted of their fauna as high discharge raged. Similarly, artificial physical disturbance decimated the fauna on the sediment surface. Further research, however, would be required, involving taking samples from the streambed during a high water discharge with a force to move, shift and relocate the stream substrates.

Acknowledgements

I thank Dr Peter Eric Schmid (Queen Mary College, University of London, U.K.) and Prof. Dr Gernot Bretschko (Biologische Station Lunz, Austria) for advice and guidance during this work. Sincere thanks also to Dr Jenny Schmid-Araya (Queen Mary College, U.K.) for advice and encouragement, and to Dr M. T. Gillies (Whitfeld, Sussex, U.K.) who assisted with the identification of the mayfly specimens. Two anonymous referees contributed valuable comments and criticism of the manuscript. Finally, I wish to acknowledge ÖAD (Austria) for its financial support through the Nord-Süd Dialogue Programme (EH-Project 894/92).

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