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Artificial Physical Disturbances on Streambed Sites of a Kenyan Mountain Stream: Effects of Inter-disturbance Intervals on Mayfly Densities

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With 4 Figures and 9 Tables

Key words: Ephemeroptera, disturbance intervals, stream, tropics, Kenya

Abstract

Field experiments to determine the effects of inter-disturbance intervals on the densities of mayflies recolonizing disturbed sites in the Naro Moru River, Kenya, were undertaken from June 1993 to January 1994. Stirring, shifting and relocation of streambed substrates by hand was used to define artificial physical disturbance within the randomly selected sites. The sites were exposed to differing inter-disturbance intervals, i.e. short, intermediate and long inter-disturbance intervals. Mayfly species abundances were more similar within the disturbed subsites than between disturbed versus control sites. Individual experiments showed that maximal recolonization of the different sites was relatively short (< 8 h) but highly variable. When the three experiments were systematically combined, densities of mayflies recolonizing the disturbed sites were highest on day 19, followed thereafter by a sharp density decline. Mayfly densities on the control sites were highest on days 20 and 40. The effects of short, intermediate and long inter-disturbance intervals on densities of mayflies recolonizing the disturbed sites was bifaceted, which included slight increases and strong declines in the densities.

Introduction

The impact of any type of disturbance on stream fauna is complex. Disturbance may have either detrimental or desirable effects on macrozoobenthic species. In lotic ecosystems, there are several sources for recolonizers of the disturbed sites which include drift (Allan 1984; Williams & Hynes 1976), crawling from the surrounding substrates (Giller & Cambell 1989), and movements from deeper hyporheic sediment layers (Palmer et al. 1992). Doeg et al. (1989) suggested that drift contributed 36% of the individuals that recolonized gravelly sediments in the Acheron River in Australia, while Richards & Minshall (1988) estimated that about 40–50% of *Baetis* larvae reach the substrates by crawling from surrounding areas. Whichever mechanism is used, macroorganisms will eventually find their way to the disturbed sites which they either exploit for a short or long time depending on the habitability of the site and their competitive status relative to other potential colonizers. Several recent studies have demonstrated that recovery of macroinvertebrates in streams after disturbance is dependent upon the physical characteristics of the disturbed stream (Robinson et al. 1993), the nature of the disturbance (Niemi et al. 1990; Mathooko 1996), proximity of refugia (Cushing & Gaines 1989; Sedell et al. 1990), vagility and life history specifics of the habitat biocoenosis (Wallace 1990; Mackay 1992) and processes regulating secondary production (Fisher 1990). Artificial physical disturbances in stream hydrosystems have been induced variously, including kicking and shuffling of the sediments (Matthaei et al. 1996), scraping (Johnson & Vaughn 1995) and stirring and shifting of the sediments by hand (Mathooko 1998). The frequency of these disturbances determines the type of community structure found on the streambed (Mathooko 1996).

Earlier studies have failed to define the extent of disturbance frequency on the temporal scale (e.g. Whiles & Wallace 1995; Mulholland et al. 1991). Due to this failure, inter-disturbance intervals have been reported in minutes, hours, months (Mathooko 1996, 1998) and/or in years (Collins et al. 1975). The wide inter-disturbance intervals might not integrate most of the intervening processes, especially the recolonization events that take place between the sampling occasions. A fundamental question in this study is whether different inter-disturbance intervals have any effect on the densities of mayflies recolonizing disturbed stream surface sites. Three field experiments with differing inter-disturbance intervals, i.e. short, intermediate and long, were designed to address this question. This study therefore presents an experimental approach describing the spatial and temporal changes in the structure of the mayfly community in the Naro Moru River, with a view to advance our knowledge on inter-disturbance intervals and the recolonization process by an aquatic community. It examines the inter-disturbance interval when the highest recolonization occurs in the three experiments and when the experiments are systematically rearranged in a time series. This will be aimed at elucidating the discrepancies that exist when short and prolonged inter-disturbance intervals are considered in assessing the densities of recolonizing biota in lotic hydrosystems.

Descriptions of the Naro Moru River and study site

The Naro Moru River (Fig. 1a, b) is a fast flowing gravel lotic hydrosystem in central Kenya that erodes volcanic sediments. Its two main tributaries, the North and South Naro Moru Rivers, meet at 2180 m above sea level after flowing between deeply incised banks. In the upper forested areas the watercourses are completely overgrown. The main Naro Moru River has year-round flow, a width of ≈8.4 m and mean daily discharge of ≈0.431 m^3/s. Rivulets from Mt. Kenya tarns and glaciers supply its tributaries with water throughout the year. Based on water discharge records at River Gauging Station (RGS; National Reference Number 5BC2; ≈1 km upstream the study site), the discharge regime of the Naro Moru River strongly reflects the rainfall pattern, being high during the wet seasons (March–May; October–December) and low during the dry season (June–September).

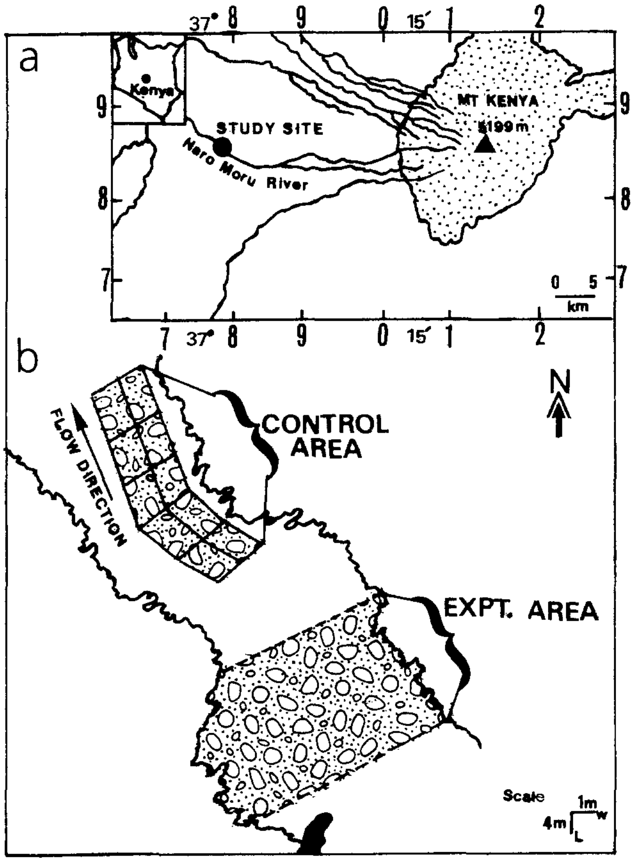

Fig. 1. The Naro Moru River and the location of the study site (**a**). Inset shows the location of the study area in Kenya. Location of the experimental (EXPT.) and control sampling areas on the study site

About 25% of the macrozoobenthos and 65% of the macrobenthic drift in the Naro Moru River is composed of Ephemeroptera (Mathooko & Mavuti 1992). Four families are particularly dominant: Heptageniidae, Baetidae, Caenidae and Leptophlebiidae. Seven species make up 99.5% of the mayfly community by abundance and were chosen as the focal mayfly species for this study. These are *Afronurus* sp. (Heptageniidae), *Afroptilum sudafricanum* (Lestage), *Baetis s.l.*, *Baetis (Nigrobaetis)* sp.1, *Baetis (Nigrobaetis)* sp.2 (Baetidae), *Caenis* sp. (Caenidae) and *Choroterpes (Euthraulus)* sp. (Leptophlebiidae) (Mathooko 1996).

The study site was on a 82 m-long riffle zone (0°10'S, 37°01'E; elevation 2035 metres above sea level). The catchment area above the study site was 83 km^2. The majority of the streambed substrates in the study riffle and within the disturbed experimental subsites had sphericity ranging from 0.67 to 0.72 [as determined by the method of Krumbein (1941)] and were poorly sorted (sorting coefficient: >2.00). This indicated that the sediment interstitial spaces were well developed and could form pathways for vertical and horizontal recolonization of the disturbed sediment surface by macroinvertebrates. The study site was divided into two sections, an experimental area and a control area. The control area, located 33 m downstream from the experimental area, was subdivided into ten (1.5 by 3.0 m) strata. The distance between the two areas was considered adequate since mayflies drift for short distances (< 20 metres) before landing on another "hold" (personal observation). Furthermore, samples were first collected from the downstream control sites and then from the experimental subsites.

Materials and Methods

Routine sampling protocol

In both the experimental and control sites, quantitative benthic samples were collected from the upper 10 cm of the sediment surface from June 1993 to January 1994 using a Hess sampler (sampling area: 0.03 m^2; 80 µm mesh-size). The locations of the experimental subsites were permanently marked on the streambed with iron stakes in such a manner that the Hess sampler was fixed between them during sampling. Artificial physical disturbances involved local displacement, shifting and stirring of the substrates within the sampled area by hand for three minutes. Artificial physical disturbance was therefore the same as the act of sampling. Collection of samples from the control sites also lasted for three minutes on each sampling

Table 1. Sampling and inter-disturbance intervals on the experimental sites in the Naro Moru River, Kenya. ^{a}Sampled between 1200–1500 h, ^{b}Sampled between 1900–2200 h, ^{c}Actual sampling times during each sampling occasion: 1200, 1300, 1500, 1900, 0100, 0900 & 1900 h. * Sampling intervals used for the collection of the control samples. Subsites with ¶ and § symbols were sampled 6 and 11 times, respectively, during the study duration.

Disturbance levels	Subsites	Sampling intervals/dates
Short	Day^{a} & Night^{b}	0, 10, 20 & 40 minutes
Intermediate	1^{c}–3^{c}	0, 1, 2, 4, 6, 8 & 10 hours*
Long	1¶ & 4¶	24/6/93, 4/8, 18/9, 29/10, 3/12 & 7/1/94
	2§ & 3§	24/6/93, 15/7, 4/8, 20/8, 18/9, 15/10, 29/10, 12/11, 3/12, 17/12 & 7/1/94

position. The inter-disturbance interval schedules for the experimental subsites were as indicated in Table 1. After the initial disturbance of 24/6/93 experimental subsites subjected to the short and intermediate disturbance levels were also sampled on 15/7, 4/8, 20/8, 18/9, 15/10, 29/10, 12/11, 3/12, 17/12 and 7/1/94. The intervals used during the sampling of the subsites subjected to the intermediate disturbance levels were also used for the collection of control samples. After collection of the samples from both the experimental and control sites, they were preserved in 5% formaldehyde solution and later rinsed with water through 250 µm and 80 µm mesh-size nets to separate the debris and larger animals from the smaller ones. The ephemeropterans retained in both sieves were then sorted under a stereomicroscope, identified and enumerated.

Inter-disturbance interval experimental designs

- Short inter-disturbance intervals

The design of this experiment was to assess the effect of an inter-disturbance interval of between 10 and 40 minutes on the densities of mayflies. Two subsites, i.e. daytime (between 1200–1500 h) and nighttime (between 1900–2200 h) subsites, were sampled to assess whether there were differences in diurnal and nocturnal densities of mayflies recolonizing the disturbed subsites. Quantitative samples from the day and night subsites were collected at inter-disturbance intervals shown in Table 1, with sample collection at each interval lasting for three minutes.

- Intermediate inter-disturbance intervals

Three subsites were sampled to determine the effect of intermediate inter-disturbance intervals (between 1 and 10 hours) on mayfly densities. Each sampling occasion was spread over two days, with artificial physical disturbance administered at 1200, 1300, 1500, 1900 hr (first day), 0100, 0900 and 1900 hr (second day). This created inter-disturbance intervals of 0, 1, 2, 4, 6, 8 and 10 hours (see Table 1). On each sample collection time, three random samples were also taken from the control area.

- Long inter-disturbance intervals

Long inter-disturbance interval experiments were designed to assess the effect of low disturbance frequency on the densities of mayflies recolonizing disturbed subsites. In this experiment, four subsites were disturbed on 24/6/93 and thereafter five samples were collected at 33–43 d inter-disturbance intervals from two of the four subsites over seven months and ten samples from the remaining two subsites at 13–28 d inter-disturbance intervals.

- Combined experimental design

The short, intermediate and long inter-disturbance interval experiments were systematically combined to determine the overall effect of varying inter-disturbance intervals on mayfly densities and species richness. This combination effectively spread the inter-disturbance intervals over a wider range than the individual experiments, rearranging the experiments in a "time continuum". The shortest inter-disturbance interval was therefore 0.2 h (i.e. the 10 minutes in the short inter-disturbance interval experiments) and the longest inter-disturbance interval was 1032 h (i.e. the 43 d disturbance interval of the two subsites exposed to six disturbances in the long inter-disturbance interval experiment). The times of the other inter-disturbance intervals from the various experiments were appropriately placed within these two extremes.

- Statistical analysis

Statistical Package for Social Sciences (SPSS® for Windows 1992) was used for statistical analysis in this study. Density datasets were subjected to $\log_{10}(x+1)$ transformation prior to analysis. One of the null hypotheses (H_o) was that densities of the mayflies recolonizing the disturbed subsites were not different among the different inter-disturbance intervals and therefore the densities should be similar among subsites. Densities were compared among inter-disturbance intervals (short: 0, 10, 20, 40 minutes; intermediate: 0, 1, 2, 4, 6, 8, 10 hours), seasons (wet season I: June–July; wet season II: November–January; dry season: August–October) or sampling dates (11 sampling dates) by two-way analysis of variance (ANOVA). Tukey's honestly significance difference (HSD) test ($\alpha = 0.05$) for multiple comparisons among means (Zar 1984) was carried out whenever a significant F-value resulted from the analysis of variance. To test the null hypothesis that the means of species densities were equal in the disturbed versus undisturbed sites, the t-test was used following Sokal & Rohlf (1995). It was performed on day versus night mayfly densities and control versus experimental mayfly densities. Spearman's rank correlation coefficient (r_s) was used to correlate species richness in the experimental subsites with inter-disturbance intervals up to the time of maximum recolonization in the combined experiments.

Similarity in species abundance on the disturbed versus control sites was quantified using the proportional similarity index (PSI) (Schoener 1968):

$$PSI_{xy} = 1 - 0.5\,(\textstyle\sum |P_{xi} - P_{yi}|),$$

where P_{xi} and P_{yi} are the proportional abundances of species i in samples x and y. Values range from 0 (no species in common) to 1 (species present and relative abundance identical).

Results

The relative abundance of the seven dominant mayfly taxa, and statistical comparison between the densities of mayflies recolonizing the intermediate inter-disturbance interval sub-

Table 2. Relative abundance (% composition) of the dominant mayfly species collected in all experimental and control sites, and paired *t*-test results comparing mayfly densities in the control sites and in the intermediate inter-disturbance interval sites. $df = 230$. ***$p < 0.001$.

	Inter-disturbance intervals			Control	*t*-value
Taxa	Short	Intermediate	Long		
Baetidae					
Baetis (Nigrobaetis) sp.1	1.44	2.96	1.74	2.30	8.91***
Baetis (Nigrobaetis) sp.2	1.71	2.94	1.46	1.18	0.97
Afroptilum sudafricanum	4.11	8.05	7.17	7.11	8.39***
Baetis s.l.	6.90	8.77	10.78	11.79	11.22***
Heptageniidae					
Afronurus sp.	45.82	49.02	39.02	22.35	4.29***
Leptophlebiidae					
Choroterpes (Eu.) sp.	35.45	25.46	35.35	52.47	28.36***
Caenidae					
Caenis sp.	3.04	2.11	3.66	2.48	13.88***
Others	1.53	0.69	0.08	0.32	–

Table 3. Proportional similarity index (PSI) values of the densities of mayflies recolonizing the experimental subsites and densities in the control sites.

Inter-disturbance Intervals	Short (night)	Intermediate	Long	Control
Short (day)	0.95	0.88	0.92	0.75
Short (night)		0.89	0.93	0.75
Intermediate			0.86	0.70
Long				0.81

sites and control sites are indicated in Table 2. *Afronurus* sp. and *Choroterpes (Euthraulus)* sp. were numerically dominant in all sites. Apart from *Baetis s.l.* and *Afroptilum sudafricanum*, the other mayfly species occurred in low numbers (< 5%) in both the experimental and control sites. Analysis of the datasets indicated that, with the exception of the densities of *Baetis (Nigrobaetis)* sp.2, all mayfly species densities in the control sites were significantly higher than those in the intermediate inter-disturbance interval sites (see Table 2). Further, mayfly abundances were more similar between the disturbed subsites (PSI range: 0.86–0.95) than between those of the disturbed versus control sites (PSI range: 0.70–0.81) (Table 3).

Short inter-disturbance intervals distinctly reduced the densities of mayflies recolonizing the day and night subsites as shown by *Afronurus* sp. and *Choroterpes (Euthraulus)* sp. (Fig. 2). The densities were lowered below the pre-disturbance density levels. Further, the post-disturbance densities of the recolonizing mayflies were well below the control mayfly densities. Pre-disturbance mayfly densities were significantly higher than the mayfly densities of the control site during the day (*t*-value = 3.61; $df = 42$, $p < 0.001$). Statistical details on mayfly density differences between the various inter-disturbance intervals in the day and night experiments are given in Table 4 for the mayfly community and three representative mayfly species. Densities of five of the dominant mayfly species in the day short inter-disturbance interval subsite varied significantly between inter-disturbance intervals and also between seasons (two-way ANOVA, $p < 0.05$) (Table 5).

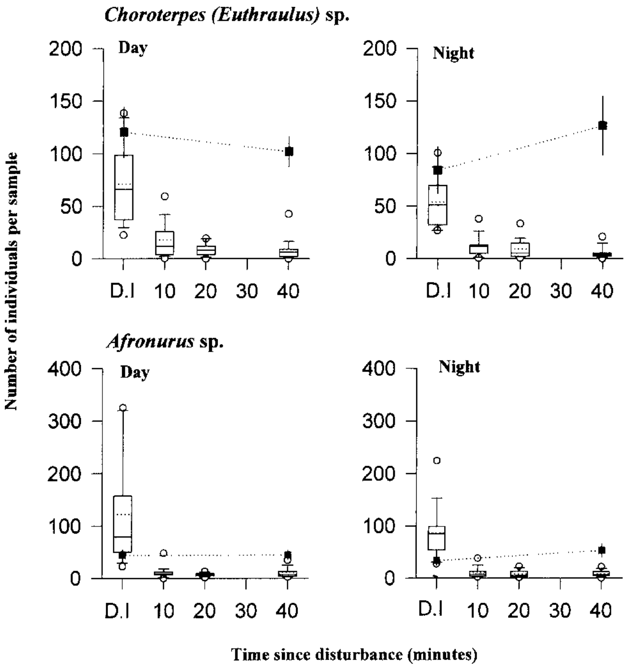

Fig. 2. Tukey box-plots for day and night density variations of *Choroterpes (Euthraulus)* sp. and *Afronurus* sp. recolonizing the short inter-disturbance interval subsites. The box itself encompasses the 25th through the 75th percentiles. The 5th and 95th percentiles are shown as symbols (○) below and above the 10% and 90% caps, respectively. The median and mean are indicated as complete and dotted lines within the box, respectively. D.I. is the initial disturbance inducement time 0 minute. Control mean densities (■—■), vertical lines: ±95% confidence limits.

Table 4. Summary of t-tests for the analysis of mayfly densities in the short inter-disturbance interval day (D) and night (N) subsites and control densities. E_0: initial disturbance, E_{10}, E_{20} & E_{40}: inter-disturbance intervals of 10, 20 & 40 minutes, respectively; C_0: initial control sampling, C_{10} & C_{40}: control inter-sampling intervals of 10 and 40 minutes, respectively. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. The directions of difference are given in the text.

Intervals	Mayfly community		*Afronurus* sp.		*Choroterpes (Euthraulus)* sp.		*Afroptilum sudafricanum*	
	D	N	D	N	D	N	D	N
E_0/E_{10}	5.64***	10.19***	6.96***	7.91***	4.73***	5.60***	5.39***	3.77***
E_0/E_{20}	10.02***	7.69***	9.85***	8.79***	7.68***	6.76***	6.01***	4.80***
E_0/E_{40}	8.42***	8.26***	7.99***	8.17***	7.43***	9.29***	7.46***	3.98***
E_0/C_0			3.61***	4.47***	5.86***		2.87**	
E_0/C_{40}	6.70***		3.70***	2.27***	5.67***	3.04**		
E_{10}/E_{20}			2.98***					
E_{10}/E_{40}					2.35*	2.72**		
E_{20}/E_{40}								
E_{40}/C_{40}	16.21***	14.07***	7.29***	8.17***	8.11***	15.03***	8.24***	5.51***
C_0/C_{40}		3.20***		2.40*		2.28*		

Table 5. Summary of two-way ANOVA comparing mayfly densities among the three seasons and inter-disturbance intervals in the short inter-disturbance interval (day and night) subsites. Significant levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Day				Night			
Source	SS	*df*	MS	*F*	SS	*df*	MS	*F*
Afronurus sp.								
Interval	9.36	6	1.56	17.32***	9.76	6	1.63	24.76***
Season	2.54	2	1.27	18.17***	3.60	2	1.80	27.43***
Interval × Season	0.87	12	0.07	0.84	0.70	12	0.06	0.89
Error	4.81	56	0.09		3.68	56	0.07	
Afroptilum sudafricanum								
Interval	4.42	6	0.74	13.68***	1.85	6	0.31	3.02***
Season	1.45	2	0.72	13.43***	0.98	2	0.49	4.79***
Interval × Season	1.18	12	0.10	1.82	0.43	12	0.04	0.35*
Error	3.02	56	0.05		5.72	56	0.10	
Baetis s.l.								
Interval	2.70	6	0.45	4.41***	1.29	6	0.22	2.49***
Season	4.87	2	2.43	23.87***	2.92	2	1.46	16.97***
Interval × Season	0.58	12	0.05	0.47	1.05	12	0.09	1.02
Error	5.71	56	0.10		4.82	56	0.09	
Baetis (Nigrobaetis) sp.1								
Interval	1.15	6	0.19	5.11***	1.69	6	0.28	7.44***
Season	0.19	2	0.10	2.54	0.40	2	0.20	5.28***
Interval × Season	0.54	12	0.05	1.20	0.98	12	0.08	2.16***
Error	2.07	56	0.04		2.12	56	0.04	
Baetis (Nigrobaetis) sp.2								
Interval	1.28	6	0.21	3.53**	0.53	6	0.09	1.26***
Season	0.98	2	0.49	8.13***	1.22	2	0.61	8.79***
Interval × Season	0.42	12	0.04	0.58	0.36	12	0.03	0.43*
Error	3.38	56	0.06		3.90	56	0.07	
Caenis sp.								
Interval	3.36	6	0.56	7.51***	2.74	6	0.46	8.19***
Season	0.08	2	0.04	0.54	0.58	2	0.29	5.21***
Interval × Season	0.23	12	0.02	0.25	0.92	12	0.08	1.37
Error	4.17	56	0.07		3.12	56	0.06	
Choroterpes (Eu.) sp.								
Interval	7.47	6	1.24	12.60***	8.50	6	1.42	22.17***
Season	4.15	2	2.08	21.02***	4.17	2	2.08	32.59***
Interval × Season	1.75	12	0.15	1.48	1.39	12	0.12	1.81*
Error	5.53	56	0.10		3.58	56	0.06	

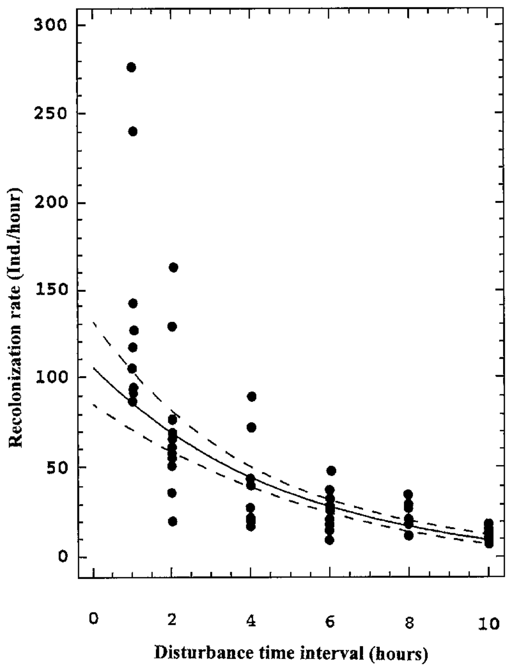

Fig. 3. Negative exponential curve of the recolonization rates per hour of the mayfly community recolonizing the intermediate inter-disturbance interval subsites. Dotted lines indicate ±95% confidence limits. Equation: [Recolonization rate] = $105.45e^{-0.21[\text{hours}]}$, $F_{(1.64)} = 134.04$, $r^2 = 0.68$, $p < 0.001$.

Fig. 3 depicts the relationship between the recolonization rates by the mayfly community and the intermediate inter-disturbance intervals. The recolonization rate per hour decreased exponentially with increase in inter-disturbance intervals ($F_{(1.64)} = 134.04$; $r^2 = 0.68$; $p < 0.001$). *Baetis (Nigrobaetis)* sp.1, *Baetis (Nigrobaetis)* sp.2, *Baetis s.l.* and *Afroptilum sudafricanum* had the highest densities after 6–8 h inter-disturbance intervals in the intermediate disturbance experiments whilst the other taxa had stable densities over the inter-disturbance intervals (Table 6). All post-disturbance densities of *Afronurus* sp., *Afroptilum sudafricanum*, *Caenis* sp. and *Choroterpes (Euthraulus)* sp. were lower than their respective pre-disturbance densities (Tukey's HSD test, α = 0.05). Comparison of mayfly densities in the inter-

Table 7. Summary of two-way ANOVA comparing mayfly densities among inter-disturbance intervals and sampling dates in the intermediate inter-disturbance interval subsites. Significant levels: $*p < 0.05$, $***p < 0.001$.

Source	*SS*	*df*	*MS*	*F*
Afronurus sp.				
Interval	10.50	6	1.75	44.27***
Date	4.62	10	0.46	11.68***
Interval × Date	3.28	60	0.05	1.38
Error	6.09	154	0.04	
Afroptilum sudafricanum				
Interval	10.11	6	1.68	28.64***
Date	6.53	10	0.65	11.10***
Interval × Date	5.57	60	0.09	1.58*
Error	9.06	154	0.06	
Baetis s.l.				
Interval	6.93	6	1.15	13.25***
Date	16.22	10	1.62	18.63***
Interval × Date	7.13	60	0.12	1.37
Error	13.41	154	0.09	
Baetis (Nigrobaetis) sp.1				
Interval	4.56	6	0.76	12.89***
Date	3.88	10	0.39	6.58***
Interval × Date	7.33	60	0.12	2.07***
Error	9.08	154	0.06	
Baetis (Nigrobaetis) sp.2				
Interval	2.73	6	0.76	7.16***
Date	10.73	10	1.07	16.88***
Interval × Date	5.72	60	0.10	1.50*
Error	9.79	154	0.06	
Caenis sp.				
Interval	6.98	6	1.16	21.71***
Date	2.24	10	0.22	4.18***
Interval × Date	4.35	60	0.07	1.35
Error	8.25	154	0.05	
Choroterpes (Euthraulus) sp.				
Interval	17.23	6	2.87	42.58***
Date	12.11	10	1.21	17.96***
Interval × Date	6.28	60	0.11	1.55*
Error	10.38	154	0.07	

Table 6. Duration when the highest density was observed for each mayfly species in the three intermediate inter-disturbance interval subsites and control sites. – means "none". Duration is given in hours.

Taxa	Subsite 1	Control	Subsite 2	Control	Subsite 3	Control
Afronurus sp.	–	–	–	–	–	–
Afroptilum sudafricanum	–	0	6	10	6	–
Baetis s.l.	–	0	–	0,10	–	10
Baetis (Nigrobaetis) sp.1	8	–	6	10	6	2
Baetis (Nigrobaetis) sp.2	6	–	4	2	6	–
Caenis sp.	–	1	–	–	6	0
Choroterpes (Euthraulus) sp.	–	6	–	–	–	6

Table 8. Summary statistics of the densities of mayflies recolonizing the long inter-disturbance interval subsites. Same superscripts indicate subsites with similar disturbance frequency: *a* is for subsites which were disturbed six times and *b* for subsites which were disturbed eleven times from June 1993 to January 1994. Density is expressed as individuals per sample (±95% confidence limits). Density ranges are presented below the means of each taxon.

Taxa	Subsite 1^a	Subsite 2^b	Subsite 3^b	Subsite 4^a
Afronurus sp.	28.33 (±20.59) 6–56	92.55 (±50.59) 19–268	80.00 (±37.01) 20–175	60.50 (±20.69) 29–87
Afroptilum sudafricanum	21.17 (±29.21) 1–58	8.45 (±3.74) 0–18	13.36 (±7.43) 3–42	11.00 (±14.56) 3–39
Baetis s.l.	47.17 (±51.64) 3–116	14.09 (±13.93) 1–69	14.55 (±9.04) 0–37	8.83 (±9.11) 0–23
Baetis (Nigrobaetis) sp.1	2.00 (±3.32) 0–8	4.18 (±1.56) 0–7	3.27 (±2.19) 0–12	1.83 (±3.72) 0–9
Baetis (Nigrobaetis) sp.2	3.33 (±2.63) 1–8	2.64 (±1.68) 0–8	2.18 (±2.06) 0–9	2.50 (±3.10) 0–6
Caenis sp.	1.33 (±2.27) 0–5	8.82 (±7.62) 1–40	7.82 (±2.97) 4–19	5.00 (±3.75) 0–8
Choroterpes (Euthraulus) sp.	70.67 (±71.85) 9–191	76.09 (±33.32) 14–163	53.55 (±21.28) 7–111	47.50 (±33.84) 13–104

Table 9. Responses of mayfly densities to different inter-disturbance interval levels. Increase (+) and decrease (–) in density.

Inter-disturbance intervals	Subsites	Density
Short	(a) Day & Night	(–)
Intermediate	(b) 1, 2 & 3	(+/–)
Long	(c) 1, 2, 3 & 4	(+/–)
Combined	(a) + (b) + (c)	(+)

mediate inter-disturbance interval subsites with sampling dates and inter-disturbance intervals (Table 7) revealed significant differences between densities in the various inter-disturbance intervals and sampling dates (two-way ANOVA, $p < 0.05$). The interactions of these two factors resulted to significant density variations for *Afroptilum sudafricanum, Baetis (Nigrobaetis)* sp.1, *Baetis (Nigrobaetis)* sp.2 and *Choroterpes (Euthraulus)* sp. Generally, inter-disturbance intervals and sampling dates had a strong effect on the mayfly densities.

Examination of the density ranges in the long inter-disturbance interval experiments showed that *Afronurus* sp. and *Caenis* sp. had the highest densities in subsite 2 which was disturbed eleven times whilst the highest density for *Choroterpes (Euthraulus)* sp., *Baetis s.l.* and *Afroptilum sudafricanum* occurred in subsite 1 (Table 8). In addition, *Baetis (Nigrobaetis)* sp.1 and *Baetis (Nigrobaetis)* sp.2 had their highest densities occurring in subsites 2 and 1, respectively. The responses by the mayfly community to variations in inter-disturbance intervals included slight increases (+) and strong declines (–) in the densities of mayflies recolonizing the disturbed subsites (Table 9). The short and long inter-

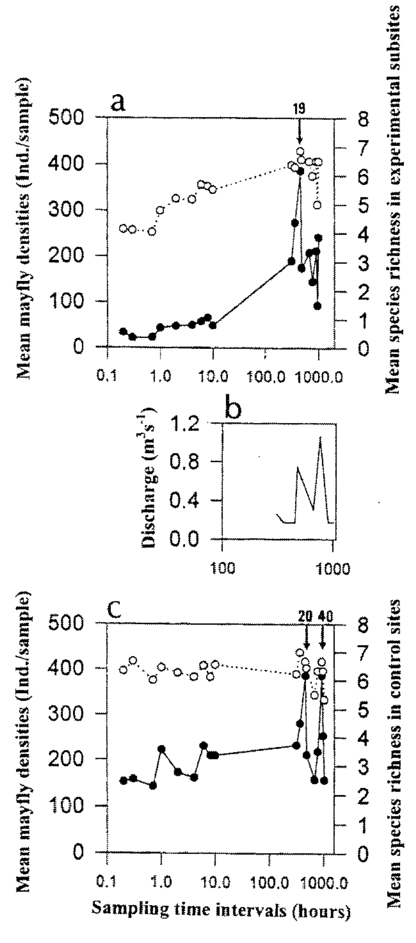

Fig. 4. Fluctuations of densities (●) and species richness (○) of mayflies recolonizing disturbed subsites in the combined experiments. Experimental subsites (**a**), daily discharge fluctuations in the Naro Moru River during 1993/1994 (**b**) and control sites (**c**). Arrows (⬇) indicate 19 d [experimental subsites (a)] and 20 d and 40 d [control sites (c)].

disturbance intervals had negative and positive effects on the mayfly densities, respectively. When the combined experimental design was considered, the densities of mayflies recolonizing the disturbed subsites were highest on day 19, followed thereafter by a sharp decline in densities (Fig. 4a), probably due to increase in discharge which peaked at 1.064 m^3s^{-1} after 13d (Fig. 4b). At the control sites, densities were highest after day 20 and 40 (Fig. 4c). Mayfly densities of the combined experimental design were significantly correlated with increase in inter-disturbance intervals up to day 19 (r_s = 0.94; $p < 0.01$; n = 12). Further, species richness was also significantly correlated with increase in inter-disturbance interval within the same period (r_s = 0.93; $p < 0.01$; n = 12) but species richness in the control sites was not correlated with sampling intervals (r_s = 0.32; $p > 0.05$; n = 12). It was apparent that species richness trend in the disturbed subsites followed that of the concomitant density changes.

Discussion

Short and intermediate inter-disturbance intervals reduced densities of mayflies recolonizing the disturbed subsites in the Naro Moru River. All the results suggest strong disturbance-related reductions in this site. They support similar results from previous studies. REICE (1985) found that > 60% of the total numbers of *Baetis* in the New Hope Creek in North Carolina were reduced due to stone-overturning disturbances. He found that many taxa had population size reductions ranging from 21% to 95%. Similarly, ROSSER & PEARSON (1995) found a decline in macrozoobenthos densities with increased disturbance of the sediment surfaces in Gorge and Birthday Creeks in Australia. A post-disturbance recovery time of 40 minutes in the short inter-disturbance interval experiments was too short to allow the mayfly community densities to rebound to the pre-disturbance density levels. Too frequent disturbances therefore lowered the mayfly densities below the control density levels, a situation that was evident in the densities of both day and night short inter-disturbance interval subsites in this study.

The recolonization rate per hour of mayflies on the intermediate inter-disturbance interval subsites decreased with increase in inter-disturbance intervals. This pattern indicated a fast recolonization of the disturbed habitats and a low residence time which contradicts day 19 of maximum colonization in the combined experiments. Immigration was higher than emigration in the initial stages of recolonization. As the subsite was recolonized, immigration became less pronounced until immigration possibly equaled emigration in the 10th hour of disturbance interval. This may possibly indicate that small patches only serve as net recolonization sites for a short time after which they resemble their surroundings. The succession of recolonization events shown by the mayflies in the intermediate inter-disturbance subsites, however, gave fine details of what could happen when a microsite is disturbed.

The increase and/or decrease in densities of the recolonizing mayflies and the patterns thereof, may reflect the mayfly species mobility, especially in foraging for food, search for habitat and refuge. The movement of the mayfly species in this study was so high that intra-specific competition for resources (e.g. habitat) might not have been an important feature in the structuring of the mayfly community. High mayfly densities could be achieved within 8 hours when individual experiments were considered. This is an extremely short time compared to 8–30 d reported by BOULTON et al. (1988) in the Taggerty River, Australia, and by PANEK (1991) in the Oberer Seebach, Austria, for different communities. However, the current results agree favourably with observations by SCHMID-ARAYA (pers. comm.) who found that sediments of the Oberer Seebach were maximally colonized by meiofauna within 2 hours. BOULTON et al. (1988) found that densities of *Baetis* sp. on the undersides of overturned stones rose up to day 8, exceeding the densities on the bottoms of control stones. The highest density of the mayflies recolonizing the disturbed sites on day 19 in the combined experiments coincided with the highest density in the environment. The decline in densities and species richness after day 19 in the current study could have been caused by an increase in discharge that eroded the mayflies from the subsites. Day 19 lies within the most frequently cited time spans (i.e. 8-30 days) for maximum recolonization of disturbed sites (BOULTON et al. 1988). This might be the more reliable time for achieving the highest recolonization densities on the disturbed subsites than the ones reported for individual experiments in the Naro Moru River. In comparison, MATHOOKO (1995) found that it took 10 days for artificial substrates to be maximally colonized in the same river. Therefore the peaks reported in the individual experiments could have been a progressive "ecological noise" in a build-up toward the major peak on day 19.

In conclusion, the mayfly community of the Naro Moru River was very resilient and "mobility-controlled" (*sensu* TOWNSEND 1989). The fast recolonization process evidenced high mobility pattern among the species. Only short inter-disturbance intervals (in the range of minutes) were able to delay the recovery of the disturbed subsites. The mayfly species that were most common in the pre-disturbance phase were also the most common in the post-disturbance phases. The effects of short, intermediate and long inter-disturbance intervals on densities of mayflies recolonizing the disturbed subsites appeared to be bifaceted. The most common pattern of response in all experiments was a general decline in mayfly density irrespective of the set inter-disturbance intervals. The inter-disturbance intervals in the combined experiments had a positive effect on mayfly density. It is therefore suggested that disturbance intervals reported in literature be reviewed to ascertain their temporal scales and their effects on macrozoobenthic densities. The colonization density peaks reported in most works are dynamic and could shift depending on the inter-disturbance time intervals used and the locale of the study.

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