The sizes, maturity stages and biomass of mayfly assemblages colonizing disturbed stream bed patches in central Kenya

Jude Mutuku Mathooko

Department of Zoology, Egerton University, PO Box 536, Njoro, Kenya

Abstract

The sizes, maturity stages and biomass of mayfly species colonizing disturbed patches on the stream bed surface of the Naro Moru River, Kenya, were determined from June 1993 to January 1994. All maturity stages I–VI^{+} were present in the pre-disturbance mayfly assemblages. Colonization of the disturbed patches by mayflies of different maturity stages was continuous, but slow or fast depending on the season and species. The overall post-disturbance maturity structure of the mayflies colonizing the disturbed patches did not demonstrate any distinct pattern. The majority of *Caenis* nymphs colonizing the patches in wet season II (November–January) were in emerging maturity stage VI^{+}, whilst the majority of the individuals of *Afronurus* and *Choroterpes* (*Euthraulus*) populations matured from stage I in the wet seasons to stage VI^{+} in the dry season. Furthermore, the majority of the individuals of *Baetis* (*Nigrobaetis*) sp.1 were maturing to stages IV–VI during the wet seasons. Small-sized mayfly individuals (body length <3.0 mm) of all mayflies colonized the disturbed patches in the majority of numbers. However, although having the highest densities, they contributed a very low biomass compared with the fewer large-sized nymphs. There was no size gradation in the colonization of the disturbed patches, since all sizes were sampled at all times but in differing proportions. Colonization of the patches by mayflies was not size- or maturity stage-specific. Size distribution patterns could be useful in assessing which mayfly size-spectra are more or less susceptible to disturbance in streams.

Key words: Ephemeroptera, colonization, disturbance, biometrics, stream, Kenya

Correspondence: E-mail: jmmathooko@egerton.ac.ke/zoology@egerton.ac.ke

Résumé

De juin 1993 à janvier 1994, on a déterminé la taille, les étapes du développement et la biomasse des espèces d'éphémères qui colonisaient des zones perturbées de la surface de la rivière Naro Moru, au Kenya. Toutes les étapes du développement, de I à VI^{+}, étaient présentes dans les assemblages d'éphémères avant les perturbations. La colonisation des endroits perturbés par des éphémères à différents stades de maturité était continue, mais lente ou rapide selon la saison et les espèces. La structure générale après perturbation des stades de développement des éphémères qui colonisaient les endroits perturbés ne présentait pas de schéma distinct. La majorité des nymphes de *Caenis* colonisant ces endroits en saison des pluies II (novembre-janvier) en étaient au stade de maturité VI^{+}, alors que la majorité des individus des populations de *Afronurus* et de *Choroterpes (Euthraulus)* évoluaient du stade I en saison des pluies au stade VI^{+} en saison sèche. De plus, la majorité des individus de *Baetis (Nigrobaetis)* évoluaient vers les stades IV à VI pendant la saison des pluies. Les éphémères de petite taille (longueur corporelle <3,0 mm) de toutes les espèces colonisaient les endroits perturbés en nombre plus élevé. Toutefois, bien que présentant les plus fortes densités, ils contribuaient très peu à la biomasse comparés aux moins nombreuses nymphes de grande taille. Il n'y avait pas de progression de la taille dans la colonisation des endroits dérangés puisqu'on a récolté chaque fois toutes les tailles, encore que dans des proportions différentes. La colonisation des endroits perturbés par les éphémères n'était pas spécifique de la taille ni du stade de développement. Les schémas de distribution de la taille pourraient être utiles pour évaluer quel spectre de taille d'éphémère est plus sensible à la perturbation des cours d'eau.

Introduction

Stream substratum, a very important template of community structure (Minshall, 1984; Dudley & D'Antonio, 1991), is often modified by many abiotic and biotic factors. One of the abiotic factors often cited is physical disturbance, which, in the present study meant displacement, stirring, shifting and relocation of stream bed substrates, either artificially by humans (Mathooko, 1996, 1998; Bely & Berg, 2000) or naturally by hydraulic force (see, for example, Palmer, 1992). Repeated disturbances at a stream bed site could either deteriorate or improve habitat quality, and some fauna may be eliminated. A disturbance that results in the erosion of macrozoobenthos from a site will, depending on its intensity and frequency, initiate a localized colonization process. If such a disturbance does not permanently change the physical properties of the habitat, one may expect that it will cause the system to revert to an earlier state, in a sequence of colonization phases. The vagility of the macrozoobenthos through aerial transport, drift and upstream and hyporheic movement (Williams & Hynes, 1976), including the presence of nearby source populations (Sheldon, 1984; Cushing & Gaines, 1989) are important for the colonization process.

Much of the colonization process has been studied in terms of the densities of macrozoobenthos found on a disturbed patch at a particular time (see, for example, Boulton, Spangaro & Lake, 1988; Wallace, Huryn & Lugthart, 1991; Johnson & Vaughn, 1995) and the morphological details of the individuals are rarely taken into consideration. Very few studies have ever considered the structure of the mayflies colonizing disturbed patches in terms of their sizes, maturity stages and biomass (see, for example, Mathooko, 1996). Mayflies are characteristically very heterogeneous in growth, morphological development and instar number (see, for example, Clifford, Hamilton & Killins, 1979). In heterogeneous development, individuals of different instars overlap widely in size and morphology, making discrete instars undetectable. The size distributions of organisms are potentially useful metrics of community and ecosystem structure, because they simplify comparisons among assemblages formed from different species (Hanson, Prepas & MacKay, 1989). A fundamental question which has occupied stream ecologists, and which is rarely studied, is whether the sizes and maturity stages of a species population colonizing disturbed patches are different from those of the pre-disturbance situation. The distribution of sizes, maturity stages and biomass of mayflies colonizing disturbed patches at different temporal intervals in Kenyan streams is not known. This lack of information provided the basis for this study, which was undertaken in the Naro Moru River, Kenya, from June 1993 to January 1994. This study demonstrates that sizes, maturity stages and biomass of the mayfly assemblages are useful descriptors of the temporal patterns that accrue during the colonization process of disturbed patches. Seasons (dry and wet) and interdisturbance intervals will be considered as factors that may influence the colonization of the disturbed patches by mayflies, and hence the accruing size, maturity and biomass patterns.

Materials and methods

Study site and experimental procedures

This study was conducted on a 82 m-long riffle zone (0°10′S, 37°01′E; elevation 2035 m above sea level) on the Naro Moru River, a gravel, second-order stream in central Kenya (Fig. 1a). The riffle was divided into two areas: one for colonization studies with three replicate patches (patches 1–3, Fig. 1b) and the other a control area which was >30 m downstream of the colonization patches. The locations of the three replicate colonization patches were permanently marked on the stream bed with iron stakes in such a manner that a Hess sampler (surface sampling area of 3.142 dm^2; 80 μm mesh size) could always fit tightly between them without changing position during the sample collection.

To open up the patches for the colonization process, the Hess sampler was placed on the sediment of the patches and a 3-min artificial physical disturbance, which involved continuous local displacement, shifting and stirring of the stream gravels by hand, was administered to the upper 10 cm of the sediment surface. This was also an act of sampling. The sample collection dates were as follows: 24–25 June 1993 (initial disturbance), 15–16 July (wet season I), 4–5 August, 20–21 August, 18–19 September, 15–16 October, 29–30 October (dry season), 12–13 November, 3–4 December, 17–18 December and 7–8 January 1994 (wet season II). Each sampling occasion took place over 2 days and artificial physical disturbance was administered at 12.00, 13.00, 15.00 and 19.00 hours (first day), and 01.00, 09.00 and 19.00 hours (second

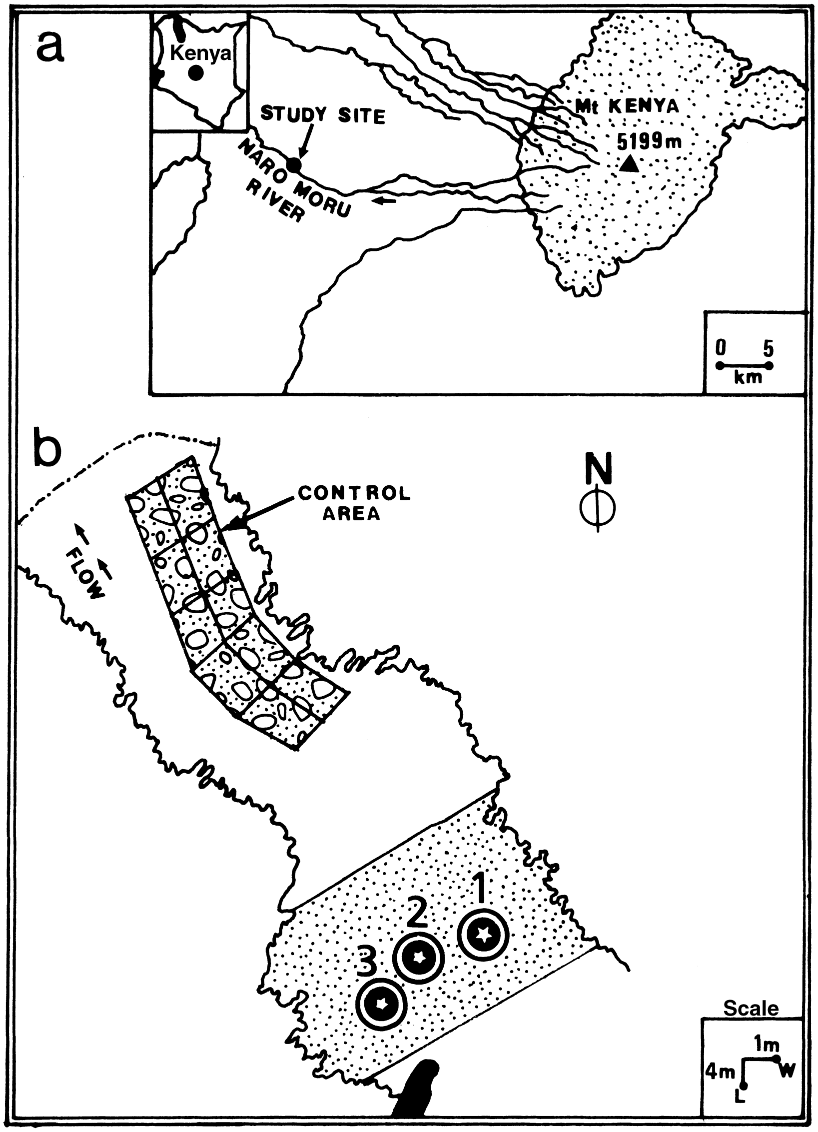

Fig 1 (a) The Naro Moru River and the location of the study site. The inset shows the location of the study area in Kenya. (b) The study riffle with the three replicate patches shown as 1, 2 and 3

day). This created interdisturbance intervals of 1, 2, 4, 6, 8 and 10 h. At each interdisturbance interval, three replicate quantitative samples were first collected from the control area and then three further replicate samples from the experimental patches. The collection of a sample from each site lasted for 3 min. After collection, the samples for size, maturity stage and biomass determinations were preserved in 5% formaldehyde solution. The mayflies were then sorted under a stereo microscope, identified and enumerated.

Mayfly body size, maturity stage and ash-free dry weight estimates

Mayfly individuals sorted from the samples for each sampling occasion and interdisturbance interval were randomly selected and their sizes and maturity stages determined, particularly for individuals of the seven dominant mayfly species, viz. *Afronurus* sp., *Afroptilum sudafricanum*, *Baetis* s.l., *Baetis* (*Nigrobaetis*) spp.1 and 2, *Caenis* sp. and *Choroterpes* (*Euthraulus*) sp. A full identification of the taxa to the species level was not possible because of the existing inadequacies in the systematics of afrotropical mayflies. The general discrimination of each mayfly individual into either maturity stages I–VI^{+} was made by a visual examination of the wing pad developmental and hue states. Maturity stage VI^{+} (the emerging nymphs), for instance, was assigned to mayfly nymphs with black mesothorax wing pads covering the metathorax and extending beyond the first two abdominal segments (for details, see Mathooko, 1997).

Body metrics of the mayfly individuals were estimated to the nearest 0.1 mm under a dissecting microscope fitted with an ocular micrometer. The total body length (TBL) was measured from the tip of the head to the base of the cerci. To obtain their dry weight, individual mayflies were placed separately in pre-heated and pre-weighed aluminium cups and oven-dried to a constant weight at 60°C for 24 h, cooled to room temperature and then the cups with the animal contents were re-weighed on a UM3 microbalance. They were then placed into a muffle furnace and burnt to ash at 500°C for 1 h, desiccated for 1 h, and re-weighed to obtain the ash weight. The ash-free dry weight (AFDW) of an individual mayfly was obtained by subtracting the ash weight after ignition from the dry weight.

Statistical analysis

All statistical analyses were performed using the Statistical Package for Social Science (SPSS for Windows, 1992). Probabilities were always two-tailed for tests, and in accordance with conventional statistical practice and procedures, probability values of $P < 0.05$ were used to denote statistical significance. The data were first tested for homogeneity of variances using F_{max} tests (Sokal & Rohlf, 1995) as follows: $F_{max} = s^2_{max}/s^2_{min}$, where s^2_{max} is the largest group variance and s^2_{min} is the smallest group variance. Data that did not meet this assumption were transformed to homogenize the variances. For instance, the ash-free dry weight data were transformed as $\log_{10}(x + 0.1)$. For multiple comparisons between the means, Tukey's honestly significance difference test (HSD, $\alpha = 0.05$) was used. This test statistic was used whenever a significant F-value resulted from the analysis of variance. The Kruskal–Wallis one-way analysis of variance by ranks test (Zar, 1984), a nonparametric test, was used to test for differences in the ash-free dry weight of the mayfly individuals between seasons.

Results

It was evident that all maturity stages (I–VI^{+}) were present in the pre-disturbance mayfly assemblage, as depicted by the structures of *Baetis* (*Nigrobaetis*) sp.2, *A. sudafricanum* and *Choroterpes* (*Euthraulus*) sp. (Fig. 2). With a few exceptions, however, there was a subsequent disproportionate representation of maturity stages of mayflies colonizing the disturbed patches. The overall post-disturbance distribution of mayflies classified according to maturity stages did not show any distinct pattern. In the wet season I (June–July), dry season (August–October) and wet season II (November–January), variations in the abundance of mayflies in each maturity stage were evident among the different mayfly species populations colonizing the disturbed patches (Table 1). A maturity structure, with stage I dominating, was shown by the *Afronurus* population in all seasons. A similar structure was shown by the *Choroterpes* (*Euthraulus*) population. Consequently, both the *Afronurus* and *Choroterpes* (*Euthraulus*) populations had reduced numbers of individuals comprising the subsequent maturity stages.

The majority of the individuals of *Baetis* (*Nigrobaetis*) sp.1 colonizing the disturbed patches were generally in maturity stages IV–VI during the wet seasons (see Table 1). In addition, a drastic shift of the majority of the individuals of this species to stages V–VI^{+} was observed during wet season II. The maturity structures of *Baetis* (*Nigrobaetis*) spp.1 and 2 populations were similar during the dry season. The *Baetis* s.l. population had a maturity structure which was similar to that of the *Afronurus* and *Choroterpes* (*Euthraulus*) populations throughout the dry and wet seasons, having the majority of the individuals in maturity stage I. Maturity stage I dominated the other stages in the *Caenis* population. The majority of *Caenis* nymphs (22.7%) colonizing the disturbed patches in wet season II were in the emerging maturity stage VI^{+}. The *A. sudafricanum* population showed a distinct shift from the young stages to the mature stages (V–VI^{+}) during wet season I.

Regressions of ash-free dry weight (AFDW) against total body length (TBL) of the four dominant species of the mayfly assemblages in the Naro Moru River are shown in Fig. 3. When the biomass of the mayflies at the various interdisturbance intervals was considered, it was evident that there was no discernible pattern portrayed by the biomass of the different size-classes. This was well

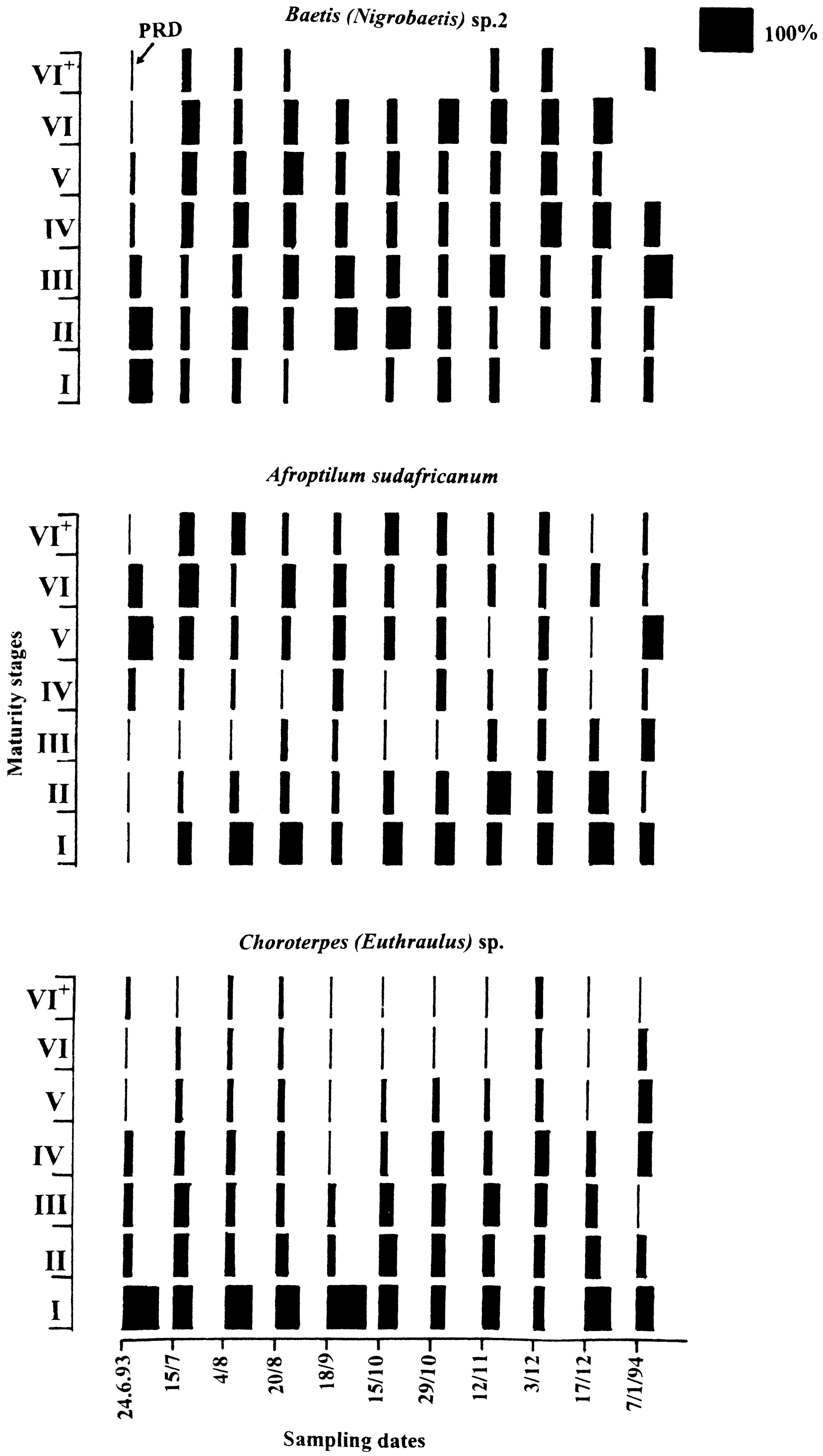

Fig 2 Maturity class distribution histograms by sampling occasions for the major taxa of the mayfly community of the Naro Moru River from June 1993 to January 1994. PRD = pre-disturbance population maturity structure

Table 1 Percentage proportions of the abundances of mayflies in the different maturity stages according to season. Wet season I (June–July), wet season II (November–January), dry season (August–October). N = total number of mayfly individuals randomly selected for maturity stage determinations in each season

	Maturity stages							
Taxa	I	II	III	IV	V	VI	VI^{+}	N
Afronurus sp.								
Wet season I	57.4	8.5	5.7	6.9	6.9	5.8	9.0	1017
Dry season	48.8	9.2	8.2	9.7	7.9	6.5	9.8	3162
Wet season II	34.1	12.6	10.4	11.7	9.1	7.8	14.3	2107
A. sudafricanum								
Wet season I	10.6	3.5	2.2	6.0	30.8	25.0	22.1	246
Dry season	31.4	14.4	4.4	6.2	13.3	15.7	14.5	494
Wet season II	28.0	22.8	12.4	7.2	13.7	8.5	7.6	224
Baetis s.l.								
Wet season I	49.9	12.5	10.2	17.9	4.2	1.6	4.0	188
Dry season	73.2	6.9	5.0	4.9	3.6	2.8	3.5	193
Wet season II	68.7	8.0	3.1	9.1	2.1	4.6	4.5	189
Baetis (*Nigrobaetis*) sp.1								
Wet season I	1.7	6.9	17.6	20.8	22.8	22.3	8.2	121
Dry season	3.8	8.4	16.7	27.7	18.1	17.8	7.5	121
Wet season II	0.7	1.9	5.6	15.3	24.5	26.4	25.7	132
Baetis (*Nigrobaetis*) sp.2								
Wet season I	23.5	24.7	10.9	8.9	11.4	14.2	6.5	185
Dry season	8.6	25.8	16.5	14.4	15.5	16.8	2.4	200
Wet season II	9.8	10.8	22.0	22.7	10.1	18.0	6.7	55
Caenis sp.								
Wet season I	37.9	20.7	19.3	10.0	0.0	8.6	3.6	24
Dry season	48.7	13.0	5.4	7.3	5.1	6.6	13.9	141
Wet season II	37.2	6.3	12.4	4.3	6.6	10.7	22.7	130
Choroterpes (*Euthraulus*) sp.								
Wet season I	46.8	13.0	15.4	11.9	4.2	3.5	5.3	415
Dry season	43.2	18.6	14.4	10.3	6.5	3.7	3.3	1797
Wet season II	31.4	16.6	16.3	16.2	9.3	5.4	4.9	826

depicted by the distribution of the biomass of *Choroterpes* (*Euthraulus*) in the various size classes (Fig. 4). Small-sized mayfly larvae (<2.0 mm) of *Choroterpes* (*Euthraulus*) sp. dominated in the disturbed patches. Conversely, the small-sized larvae contributed a very low biomass compared to the few large-sized nymphs. There was an inverse relationship between the size frequencies and the biomass of the *Afronurus* population colonizing the patches (Fig. 5), with a crowding of biomass in the large-sized mayfly colonizers.

The ash-free dry weight of the colonizing *Choroterpes* (*Euthraulus*) sp. individuals did not differ between the dry season (August–October) and wet season II (November–January) (Kruskal–Wallis (K–W) one-way ANOVA = 1.04, d.f. = 2, $P > 0.05$). The AFDW of *Afronurus* sp. individuals colonizing the disturbed patches was significantly higher in wet season II than in the other seasons (K–W = 53.12, d.f. = 2, $P < 0.001$). Furthermore, the AFDW of *Baetis* s.l. and *A. sudafricanum* individuals colonizing the disturbed patches differed significantly between seasons (*Baetis* s.l. K–W = 21.16, d.f. = 2, $P < 0.001$; *A. sudafricanum*: K–W = 8.27, d.f. = 2, $P < 0.05$), with the highest values achieved in wet season I (W1, June–July) and wet season II, respectively. There was no significant difference between the AFDW of *A. sudafricanum* individuals colonizing the disturbed patches and those in the control sites (t-value = 1.26, d.f. = 41, $P > 0.05$). The AFDW of *Choroterpes* (*Euthraulus*) sp. individuals colonizing the disturbed patches was significantly different from that in the control sites (t-value = 4.67, d.f. = 41, $P < 0.001$), with

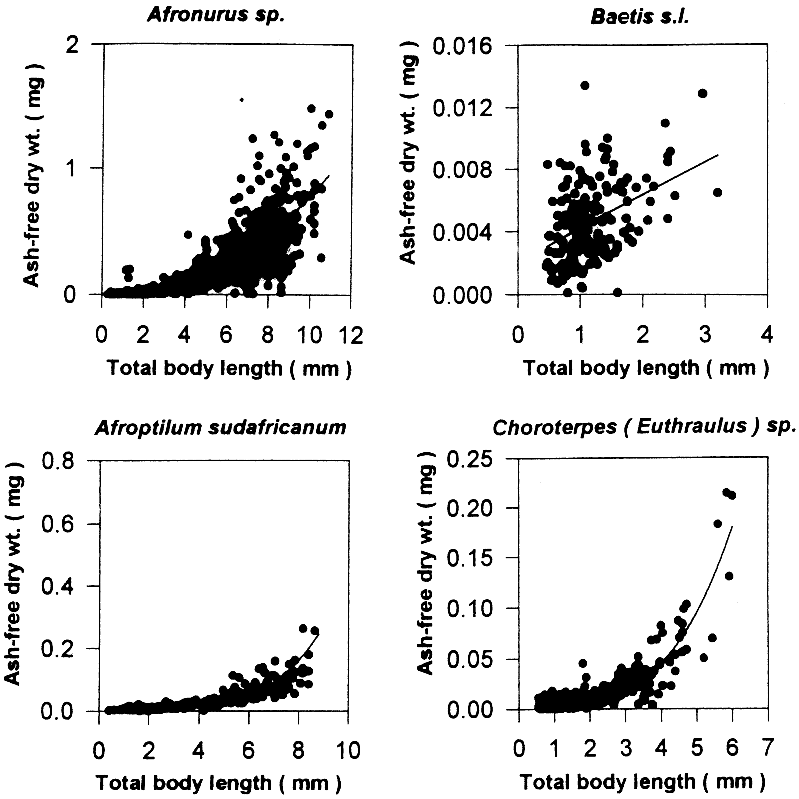

Fig 3 Relationship between ash-free dry weight and total body length of the major mayfly species colonizing the disturbed patches in the Naro Moru River, Kenya. Equations: *Afronurus* sp. AFDW = $0.0028e^{0.66[\mathrm{TBL}]}$, r^2 0.83, F-ratio = 7096.29***; *A. sudafricanum*: AFDW = $0.0024e^{0.50[\mathrm{TBL}]}$, $r^2 = 0.80$, F-ratio = 1047.31***; *Baetis* s.l. AFDW = 0.0020 + 0.0022[TBL], $r^2 = 0.17$, F-ratio = 34.17***; *Choroterpes* (*Euthraulus*) sp. AFDW = $0.0010e^{0.96[\mathrm{TBL}]}$, $r^2 = 0.57$, F-ratio = 461.13***

the disturbed patches having the highest AFDW. *Post hoc* comparisons of the AFDW by season showed that the weights of *Afronurus* individuals colonizing the disturbed patches were higher during wet season II than during the other two seasons (Tukey's HSD test, $\alpha = 0.05$).

Discussion

In general, the results show that physical disturbance in streams may create a surfeit of space upon which organisms can colonize. It alters the structure of the interstitial spaces which are pathways for invertebrates colonizing disturbed patches. A lull in physical disturbance may initiate the colonization of the disturbed patches by macroinvertebrates. However, the colonization of disturbed patches may be influenced by the proximity of refugia (Sedell *et al.*, 1990), the spatial-temporal heterogeneity of physical and biological structures (Poff & Ward, 1990; Reice, Wissmart & Naiman, 1990) and by other processes regulating secondary production (Fisher, 1990). Different life stages of aquatic organisms are less likely to be affected in the same way by any particular kind of disturbance (Marten & Zwick, 1989). Indeed, mayflies colonizing the disturbed patches showed a developmental variability in terms of sizes and maturity stages. This could have been due to differences in their phenology and also to seasonal changes in environmental variables. The magnitude of seasonal effects on the sizes, maturity stages and biomass differed with each mayfly species. The mayfly species did not respond to seasonal changes and disturbances in the same manner. Some life stages took advantage of the less populated patches faster than others. For instance, individuals of maturity stage I of *Baetis* s.l. and *Caenis* populations colonized the disturbed patches faster than the more mature individuals of stages V–VI$^+$. This suggests that the mature mayflies were either more susceptible to streambed disturbance than the small young larvae or they were not responsive to the conditions existing on the disturbed patches. The reconstitution of the pre-disturbance maturity stages structure by all species in the subsequent post-disturbance sampling occasions was discerned, with the exception of *Baetis* (*Nigrobaetis*) spp.1 and 2. The absence of a definitive maturity pattern of the mayflies colonizing the disturbed

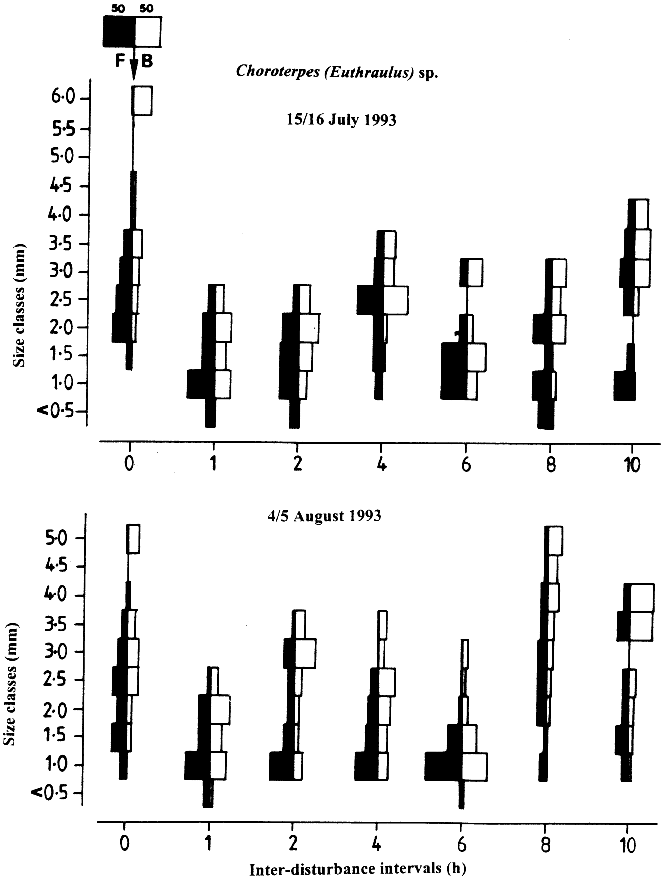

Fig 4 The structure of biomass and sizes of *Choroterpes* (*Euthraulus*) sp. in relation to interdisturbance time intervals. *F* (black bars): %frequency of individuals in the particular size class; *B* (open bars): %biomass corresponding with the number of individuals in the particular size class

patches indicated that mayflies of all maturity stages were present in the environment, either as drifters or as crawlers in the sediment, and had an unimpeded opportunity to colonize the disturbed patches.

The size of the organisms plays an important role in determining the rate of colonization of disturbed stream bed patches. Organisms colonizing a disturbed patch may set up size, maturity stage and biomass structures which may contrast totally with the pre-disturbance structures. The size-spectra and weight of the mayflies colonizing the disturbed patches in the current study were different from those of the pre-disturbance community. Fernando (1958; cited in Williams & Hynes, 1976) stated that colonization from aerial sources, via oviposition, may occur all year round in tropical streams and rivers. Wallace *et al.* (1991) and Yasuno, Ohkita & Keyama (1982) reached similar conclusions, that the immigration of aerial adults is probably the predominant mechanism of re-colonization in streams. The absence of a distinct size structure of the colonizing mayflies may be due to factors such as rapid development, continuous emergence, and oviposition, and the downstream drift of mayflies of all sizes. This probably explains the persistence of the small-sized mayfly larvulae in the Naro Moru River. The larvulae might have been able to escape into crevices below the disturbed surface from where they rapidly colonized newly opened surficial habitats. The under-representation of the larger sizes of mayflies colonizing the disturbed patches was therefore probably due to the rapid growth and emergence of late instars between sampling dates.

In conclusion, colonization of the disturbed patches in the Naro Moru River was a stochastic and continuous process. There was no size-graded response to the colonization of the disturbed patches, since all sizes were sampled at all times but in differing proportions. Size graduation was only apparent – with smaller size-classes dominating – when the size frequency distributions of all species individuals collected during the entire study duration were considered (Fig. 5). Since no

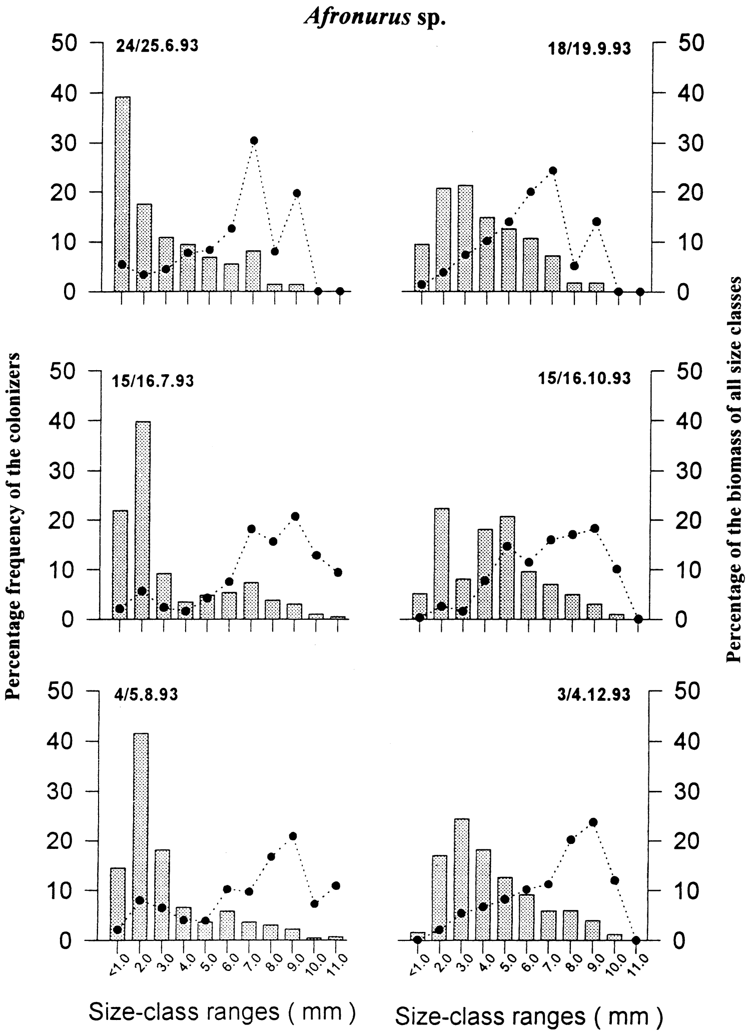

Fig 5 Size frequencies and biomass distribution of *Afronurus* sp. populations during selected sampling occasions. Only the upper limits of the size classes are shown on the *x*-axis (1.0 mm interval). %abundance (tinted bars), %biomass (●)

distinct size/maturity structure was discernible in this study, it is plausible to speculate that all sizes/maturity stages of the mayfly species population had an equal opportunity to colonize the disturbed patches. The results of this study, although without any other comparable results, have therefore demonstrated that the colonization of disturbed patches by mayflies was not size- or maturity stage-specific. The relevance of the findings in understanding more about the colonization of disturbed patches in streams will be undoubtedly contingent on further testing of the assumption that the rate of entry into the patches by the different mayfly species is regulated by the size and maturity of the individual mayflies.

Acknowledgements

I thank Dr Peter E. Schmid and Dr Jenny Schmid-Araya (Queen Mary & Westfield College, University of London, U.K.) and Prof. Dr Gernot Bretschko (Biological Station Lunz, Austria) for advice and guidance during this work. Sincere thanks also to the late Jamhuri N. Mathooko for his assistance in the field, and to the late Dr M. T. Gillies (Whitfeld, Sussex, UK) who assisted with the identification of the mayfly specimens. The Department of Zoology (Egerton University, Kenya) and the Biological Station Lunz (Austria) provided working space. I acknowledge ÖAD (Austria) for the financial support through the Nord-Süd Dialogue Programme (EH-Project 894/92).

References

Boulton, A.J., Spangaro, G.M. & Lake, P.S. (1988) Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance: an experimental approach. *Arch. Hydrobiol.* **113**, 551–576.

Clifford, H.F., Hamilton, H. & Killins, B.A. (1979) Biology of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae). *Can. J. Zool.* **57**, 1026–1045.

Cushing, C.E. & Gaines, W.L. (1989) Thoughts on recolonization of endorheic cold desert spring-streams. *J. N. Am. Benthol. Society* **8**, 277–287.

Dudley, D.L. & D'Antonio, C.A. (1991) The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology* **72**, 297–309.

Fernando, C.H. (1958) The colonization of small freshwater habitats by aquatic insects. I. General discussion, methods and colonization in the aquatic Coleoptera. *CeylonJ. Sci. Biol. Sciences.* **1**, 117–154.

Fisher, S.G. (1990) Recovery processes in lotic ecosystems: limits of successional theory. *Environ. Mngt* **14**, 725–736.

Hanson, J.M., Prepas, E.E. & MacKay, W.C. (1989) Size distribution of the macroinvertebrate community in a freshwater lake. *Can. J. Fish. Aqua. Sci.* **46**, 1510–1519.

Johnson, S.L. & Vaughn, C.C. (1995) A hierarchical study of macroinvertebrate recolonization of disturbed patches along a longitudinal gradient in a prairie river. *Freshwat. Biol.* **34**, 531–540.

Marten, M. & Zwick, P. (1989) The temperature dependence of embryonic and larval development in *Protonemura intricata* (Plecoptera, Nemouridae). *Freshwat. Biol.* **22**, 1–14.

Mathooko, J.M. (1996) *Artificial Physical Disturbance at the Sediment Surface of a Kenyan Mountain Stream with Particular Reference to the Ephemeroptera Community.* Doctoral Thesis, University of Vienna, Austria.

Mathooko, J.M. (1997) The influence of physical disturbance on recolonization patterns of a mayfly community in a tropical mountain stream. In: *Ephemeroptera and Plecoptera: Biology-Ecology-Systematics* (Eds P. Landolt and M. Sartori) Mauron and Tinguely & Lachat SA, Moncor, Fribourg.

Mathooko, J.M. (1998) The effect of continuous physical disturbance on mayflies of a tropical stream: an experimental approach. *Hydrobiologia* **362**, 209–216.

Mathooko, J.M. (2000) Artificial physical disturbances on streambed sites of a Kenyan mountain stream: effects of inter-disturbance intervals on mayfly densities. *Limnologica* **30**, 331–339.

Mathooko, J.M. & Kariuki, S.T. (2000) Disturbances and species distribution of the riparian vegetation of a Rift Valley stream. *Afr. J. Ecol.* **38**, 123–129.

Minshall, G.W. (1984) Aquatic insect-substratum relationships. In: *The Ecology of Aquatic Insects* (Eds V. H. Resh and D. M. Rosenburg). Praeger, New York.

Palmer, M.A., Bely, A.E. & Berg, K.E. (1992) Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia* **89**, 182–194.

Poff, N.L. & Ward, J.V. (1990) Physical habitat template of lotic ecosystems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environ. Mngt.* **14**, 629–645.

Reice, S.R., Wissmar, R.C. & Naiman, R.J. (1990) Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environ. Mngt.* **14**, 647–659.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A. & Hawkins, C.P. (1990) Role of refugia in recovery from disturbance: modern fragmented and disconnected river systems. *Environ. Mngt.* **14**, 711–724.

Sheldon, A.L. (1984) Colonization dynamics of aquatic insects. In: *The Ecology of Aquatic Insects* (Eds V. H. Resh and D. M. Rosenburg) pp. 401–429. Praeger, New York.

Sokal, R.R. & Rohlf, F.J. (1995). *Biometry.* Freeman, New York.

Spss (1992) *Spss for Windows. Base System User's Guide.* SPSS, New York.

Wallace, J.B., Huryn, A.D. & Lugthart, G.J. (1991) Colonization of a headwater stream during three years of seasonal insecticidal applications. *Hydrobiologia* **211**, 65–76.

Williams, D.D. & Hynes, H.B.N. (1976) The recolonization mechanisms of stream benthos. *Oikos* **27**, 265–272.

Yasuno, M., Ohkita, J. & Keyama, S.H. (1982) Effects of temephos on macrobenthos in a stream of Mt. Tsukuba. *Jap. J. Ecol.* **32**, 29–38.

Zar, J.H. (1984). *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs, New Jersey.

(Manuscript accepted 21 May 2001)