

THE INFLUENCE OF PHYSICAL DISTURBANCE ON RECOLONIZATION PATTERNS OF A MAYFLY COMMUNITY IN A TROPICAL MOUNTAIN STREAM

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Field experiments on the influence of physical disturbance on Ephemeroptera community recolonization patterns in the Naro Moru River, Kenya, were undertaken from June 1993 to January 1994. Temporal and spatial experimental approaches based on continuous disturbance and extreme short-term, medium short-term and long-term disturbances were used on randomly selected subsites. *Afronurus* sp. and *Choroterpes* (*Euthraulius*) sp. were the most dominant taxa representing 49.4% and 25.6%, respectively, of the total mayfly taxa collected in the medium short-term experiments. The recolonization process was mostly erratic on the subsites with high disturbance frequency compared to those with low disturbance frequency. Disturbance frequency could either have an initial enhancement or depression of the recolonization process. Disturbance disorganized the community maturity class structure which, depending on the taxon, could be rebuilt to pre-disturbance maturity structure within 6 to 8 hours of post-disturbance.

INTRODUCTION

Environmental disturbance has been taking place since decades and may be defined in terms of effect and cause (RYKIEL, 1985). Since the seminal paper of CONNELL (1978), the study of disturbance increased awareness and has been recognized as one of the major factors influencing community structure in streams (FLECKER & FEIFAREK, 1994). Mayflies are known to be sensitive to disturbance and have frequently been used in water quality studies (e.g. FREMLING & JOHNSON, 1990). However, little is known about disturbance in the tropics and mayfly responses to disturbance in Kenya are yet unknown. This study was undertaken from June 1993 to January 1994. Physical disturbance involved overturning, stirring and local shifting of substrates by hand within demarcated subsites on the stream bed of the Naro Moru River in central Kenya. The overall objective was to examine pattern in the recolonization of disturbed subsites in relation to varied physical disturbance intervals, in order to determine whether different mayfly taxa respond to disturbance frequency in different ways. Densities, species richness and maturity structure were the characters used to describe the patterns.

MATERIALS AND METHODS

The Naro Moru River and the study site

The Naro Moru River (Lat. 0° 03'S, 0° 11'S; Long. 36° 55'E, 37° 19'E) is a 2nd-order river, with the North and South Naro Moru Rivers as its main tributaries. It flows from the

western side of Mt. Kenya and rivulets from Teleki Tam (4270 m a.s.l.), Tyndall Tam (4475 m), Hut Tam (4488 m) and from the remnants of the Darwin and Lewis Glaciers supply its tributaries with water throughout the year. High water discharge corresponds strongly with the wet seasons, with the discharge diminishing gradually with the progression of the dry seasons which occur twice a year. The months with the highest discharge are April-May and October-November and these are the months with the highest amount of rainfall. During these four months, approximately half the annual amount of water (46-53%) is discharged (LEIBUNDGUT, 1983). The Naro Moru River discharges into the Ewaso Ngiro River, which subsequently discharges into the Lorian Swamp.

In its long profile, the river is characterized by riffle-pool sequences. This study was conducted on a 82 m-long riffle (0° 10'S, 37° 01'E; altitude 2035 m a.s.l.), with the stream bed dominated by disc-shaped or oblate spheroid substrates. The chemical and physical characteristics of the Naro Moru River at the study riffle are the followings: Water temperature 11.3 - 18.1°C, current velocity 0.10 - 1.48 ms⁻¹, discharge (July - Dec. 1993) 0.12 - 3.57 m³/s, pH 6.88 - 7.99, 87% canopy cover, length of the riffle 82 m. From the source down to the study site, the altitude drops by 2552 m. The catchment area above the study site is 83 km². Riparian vegetation consists of tropical rainforest species, particularly *Podocarpus gracilior* (PILGER) and *Syzygium guineense* (WILLD.) (DC), and forms a closed canopy (about 87% cover) over the study site.

Sampling procedures

Subsites were permanently set randomly on the streambed of the study riffle (Fig. 1) and samples always collected from the upper 10 cm of the sediment surface with a modified Hess sampler (area: 3.142 dm², 80µm mesh-size). Experimental approaches involved disturbance duration (DUR), extreme short-term (ESTD), medium short-term (MSTD) and long-term (LTD) disturbances. Physical disturbances in all these experiments involved local displacement, shifting and stirring of the substrates within the sampled area for three minutes except for the DUR experiments where samples were taken every one minute for 14 minutes. The samples were preserved in 5% formaldehyde solution and later sieved through 250µm and 80µm mesh-

size nets to separate the debris and larger animals from the smaller ones. The ephemeropterans retained in both sieves were sorted, identified and enumerated. For the MSTD experiments, three subsites (MSTD1, MSTD2 and MSTD3) were set on Transect A on the study riffle and their locations marked with iron stakes in such a manner that the sampler fitted tightly between them. During each sampling occasion, physical disturbance was induced at 1200, 1300, 1500, 1900, 0100, 0900 and 1900hrs. On each collection time, three samples were also taken randomly from the undisturbed control area which was subdivided into ten 1.5x3.0 m strata to allow for randomly stratified sampling. Maturity of the mayfly larvae and nymphs collected from the MSTD subsites was discriminated into classes I, II, III, IV, V, VI, and VI* by visual examination of the wing pad developmental and hue states (Table 1).

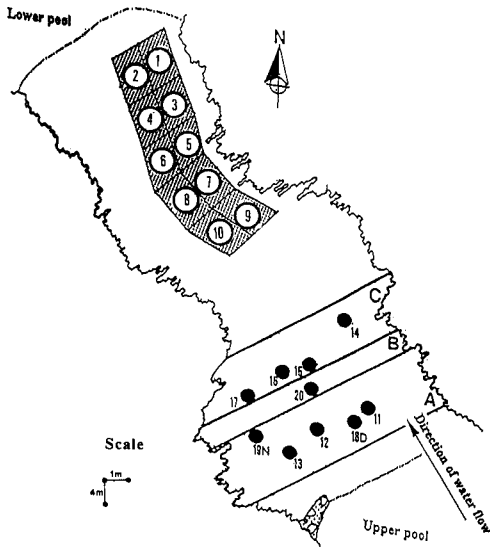
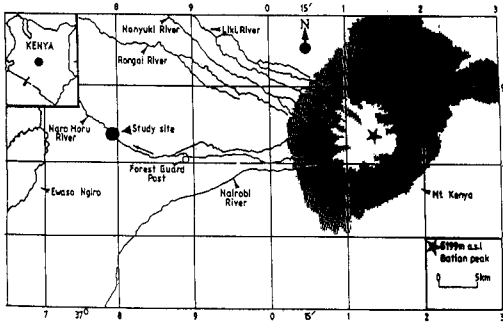


Fig. 1. Location of the Control and Experimental Sampling Transects A, B, & C) and subsites on the Naro Moru River study riffle. Inset shows the actual location of the study riffle. 1-10: Control area sampling strata; 11-13: Medium short-term disturbance (MSTD) subsites; 14-17: Long-term disturbance (LTD) subsites; 18D & 19N: Extreme short-term disturbance (ESTD) subsites. 18D-ESTD (Day), 19N-ESTD (Night); 20: Disturbance duration DUR subsite.

Table 1. Maturity categorization of mayfly larvae and nymphs in the current study. Categorization was based on visual examination of the mesothorax wing pad lengths and their hue.

Maturity class	Development stage	Wing pad development
I	Larvula, young larva	No wing pads.
II	Larva	Mesothorax wing pads small.
III	Late larva	Mesothorax wing pads covering half of the metathorax.
IV	Early nymph	Mesothorax wing pads cover the whole metathorax.
V	Moderately mature nymph	Mesothorax wing pads cover metathorax and first abdominal segment
VI	Mature nymph	Mesothorax wing pads cover metathorax and first two abdominal segments. Brown hue frequent.
VI*	Emerging nymph	Mesothorax wing pads cover metathorax and beyond the first two abdominal segments. Black wing pads observed at this stage.

Some appropriate adjustments on, for instance, the number of abdominal segments covered by the mesothorax wing pads were undertaken depending on the taxon in consideration.

ESTD (Day) and ESTD (Night) subsites were also marked as in MSTD experiments on Transect A to examine diel recolonization patterns. In these experiments, physical disturbance was induced at an interval schedule of 0, 10, 10, 20, 20, 40 and 40 minutes. One subsite for disturbance duration (DUR) experiment was similarly marked on Transect B and cumulatively disturbed from 1 minute to 14 minutes to simulate the effect of continuous disturbance on abundance and species richness.

Long-term disturbances, in which physical disturbance was induced after every 2-6 weeks, involved four subsites (LTD1, LTD2, LTD3 and LTD4) set on Transect C. LTD1 and LTD4 were disturbed after 33-43d interval and LTD2 and LTD3 after 13-28d interval.

RESULTS

The most abundant taxa included *Afronurus* sp. (49.4% of the MSTD total (17369), *Choroterpes (Euthraulius)* sp. (25.6%), *Baetis s.l.* (13.1%), *Afroptilum sudafricanum* (3.8%), *Baetis (Nigrobaetis)* sp. 1 (3.0%), *Baetis*

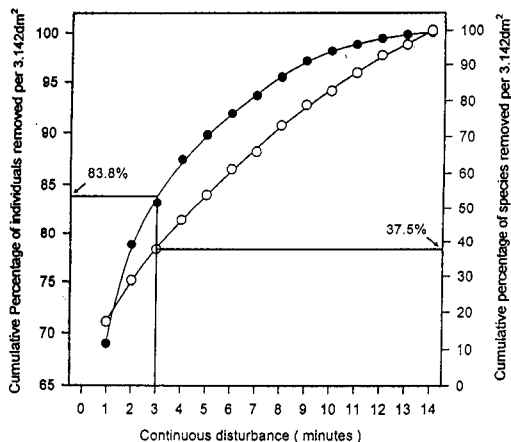


Fig. 2. Cumulative percentage curves for densities and species removed during the continuous disturbance experiments. Inside percentages indicate cumulative percentages removed for the first three minutes: ●— Cumulative % densities (Ind./3.142 dm²); ○— Cumulative % species richness (No. species/3.142 dm²).

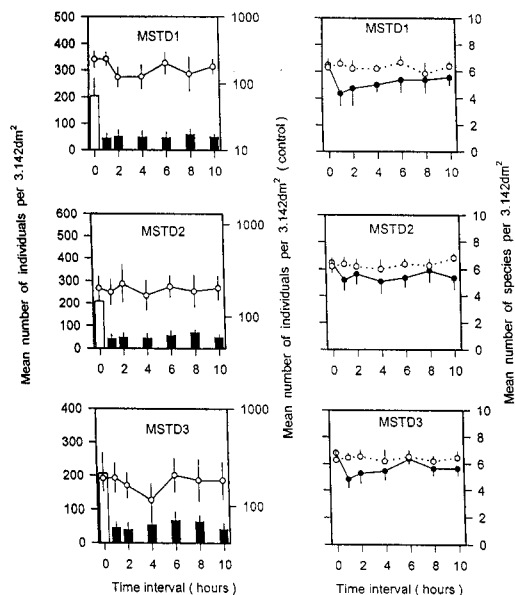


Fig. 3. Variations of the densities of recolonizers and species richness in the MSTD subsites and the controls. Bars indicate densities in the MSTD subsites: ●— Species richness (MSTD); ○— Densities (control); ○— Species richness (control); Pre-disturbance (i.e. 0 hour) bars and dots are all open. Vertical lines: ±95% CL.

(*Nigrobaetis* sp. 2 (3.0%) and *Caenis* sp. (2.1%). However, the total number of mayfly species in the Naro Moru River is unknown. Continuous disturbance had a distinct depressing effect on faunal densities as well as species richness. Cumulatively, 83.8% and 37.5% of the ephemeropteran density and species were removed from the streambed within the first three minutes of continuous disturbance, respectively (Fig. 2). There was a near-complete defaunation of the disturbed subsite within the 14 minutes' continuous disturbance. All the control densities and species richness showed trends contrasting the disturbed subsites which showed sharp decreases in densities but stabilized species richness (Fig. 3). There was a significant variation

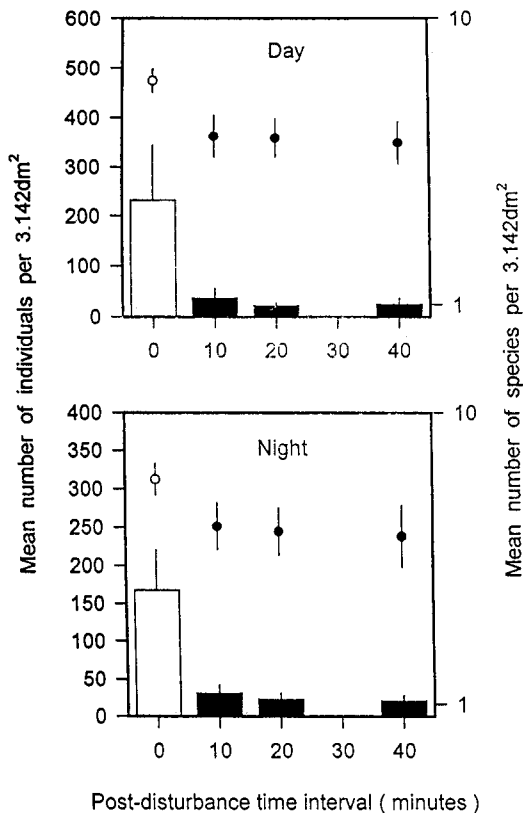


Fig. 4. Day and night variations of the densities of recolonizers and species richness in the extreme pre-disturbance density and species. Open bars and dots indicate pre-disturbance density and species, respectively. Vertical lines: ±95% CL. ■— Densities (Ind./3.142 dm²); •— Species richness (No. species/3.142 dm²).

between the densities of the recolonizers and the disturbance intervals in the MSTD experiments for *Afroptilum sudafricanum* (3-way ANOVA, $F_{6,230} = 28.24$, $p < 0.001$), *Afronurus* sp. ($F_{6,230} = 62.15$, $p < 0.001$), *Choroterpes* (*Eu.*) sp. ($F_{6,230} = 48.66$, $p < 0.001$) and *Caenis* sp. ($F_{6,230} = 20.97$, $p < 0.001$). The same trend was also shown by *Baetis* (*Nigrobaetis*) sp. 1 and 2 and by *Baetis s.l.* (ANOVA, $p < 0.001$). Disturbance also depressed faunal densities but stabilized species richness in the extreme short-term experiments (Fig. 4). Consideration of individual taxon in the long-term experiments indicated interspecific differences to varying disturbance frequencies (Fig. 5). The recolonization process was most erratic in the subsites with 11 disturbances as opposed to those with six disturbances over the entire study duration. Inter-subsite differences were also discernible between some of the taxa. Densities were

significantly different for *Afronurus* sp. between LTD1 and LTD3 (t -test = 3.17, $p < 0.01$), LTD1 and LTD2 ($t = 2.99$, $p < 0.01$) and LTD1 and LTD4 ($t = 3.36$, $p < 0.01$), for *Caenis* sp. between LTD1 and LTD2 ($t = 3.09$, $p < 0.01$) and between LTD1 and LTD3 ($t = 5.17$, $p < 0.001$). This trend was also manifested by *Baetis* (*Nigrobaetis*) sp. 1 between LTD2 and LTD4 ($t = 2.45$, $p < 0.05$) and LTD1 and LTD2 ($t = 2.16$, $p < 0.05$). These results show that there is a strong evidence that disturbance, irrespective of its frequency, could either have an initial enhancement or depression of the recolonization process. The enhancement, however, was not maintained for a long time as in depression which was more pronounced over a long time. This is exemplified in subsites 2 and 3 for *Baetis* (*Nigrobaetis*) sp. 2 and *Baetis s.l.* and subsites 1 and 4 for *Baetis* (*Nigrobaetis*) sp. 1. (see Fig. 5). Figs 6A, B, C show a sequential

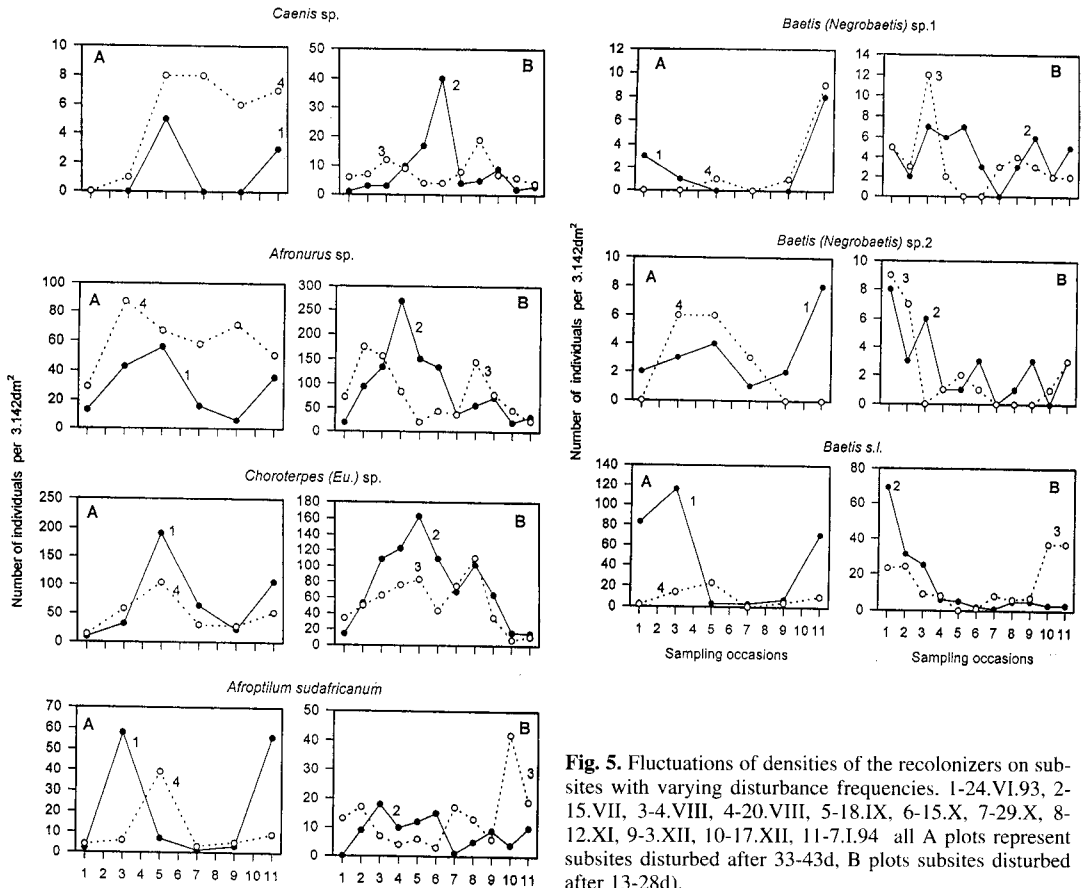


Fig. 5. Fluctuations of densities of the recolonizers on subsites with varying disturbance frequencies. 1-24.VI.93, 2-15.VII, 3-4.VIII, 4-20.VIII, 5-18.IX, 6-15.X, 7-29.X, 8-12.XI, 9-3.XII, 10-17.XII, 11-7.I.94 all A plots represent subsites disturbed after 33-43d, B plots subsites disturbed after 13-28d).

build-up of densities and species richness for all experiments combined. Generally, the community recovered fully in both density and species richness within 456 hours (19d) of post-disturbance (Fig. 6C), after that a sharp decline occurred possibly due to increases in water discharge (Fig. 6D).

The individual-species approach of using maturity class structure could reveal which maturity classes are able to take advantage of changing resources as a result of disturbance. Generally, post-disturbance distribution of recolonizing maturity classes shows no distinct trend (Fig. 7), implying that disturbance disorganizes the pre-disturbance population. Nevertheless, some taxa like *Choroterpes* (*Eu.*) sp. and *Afronurus* sp. have the ability to recover the pre-disturbance maturity structure within 6 to 8 hours. This restructuring was relatively rapid probably due to the proximity of colonists in the surrounding streambed and other source pools.

DISCUSSION

Relative importance of stochastic and deterministic processes which shape

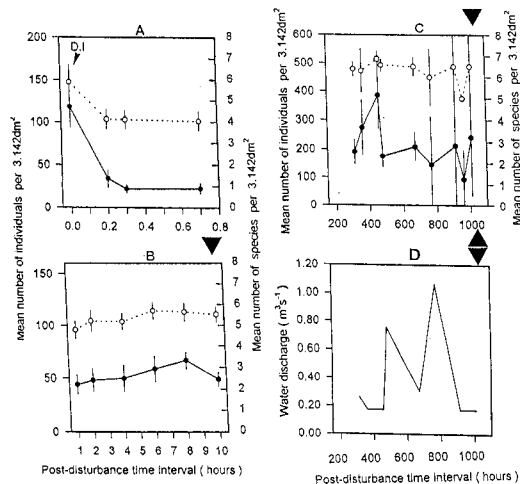


Fig. 6. Sequential presentation of combined experiments over the post-disturbance intervals (A, B, C). D relates discharge with the trends shown in C. D.I = Disturbance induction. Vertical lines: 95% CL. ●—● Densities (Ind./3.142 dm²); ○—○ Species richness (No. species/3.142 dm²).

community structure have been explored through disturbance and several methods have been used to induce disturbance in lotic ecosystems such as turning stones (BOULTON *et al.*, 1988) and kicking and raking (MARCHANT *et al.*, 1991). The initial physical disturbance intensity, which usually involves dramatic abundance and diversity reductions, and the individual taxon recolonization rate are important in determining subsite recovery rate. In general, mayflies are noted for their rapid colonization of new surfaces (e.g. LAKE & DOEG, 1985). In the current study, mobile animals had only to move a distance of 20 cm onto the disturbed subsite to be within sampling range the next sampling interval or occasion. Maximum recolonization of the subsites conspicuously took place after 19d of post-disturbance, confirming results obtained by other ecologists (range: 10-30d) considering total invertebrate densities (e.g. LAKE & DOEG, 1985; PECKARSKY, 1986). This fast recolonization process might be due to drift processes and the formation of biofilm. Heterotrophic epilithic community has been found to resemble that of the undisturbed substrates within 13d (OSBORNE, 1983). Moreover, artificial substrates used in the sediment of the Naro Moru River were maximally recolonized after about 10d (MATHOOKO & MAVUTI, 1992). Extreme short-term turning of stones normally maintains periphyton biomass at low levels. In the DUR and ESTD experiments, no recovery to the pre-disturbance density and species richness occurred, probably due to the short time lag which did not allow the fauna to re-establish itself. Reductions in abundance of individual taxa as disturbance intensity (frequency) increased are evident in the current study, concurring with results by REICE (1985), LAKE & DOEG (1985) and BOULTON *et al.* (1988). Furthermore, recolonization of MSTD subsites within 1 to 10 hours of post-disturbance may not be as a result of biofilm development since no substantial development could have taken place within such a short time. Thus it may be plausible that drifting organisms may take advantage of the relatively bare subsites.

BROOKS & BOULTON (1991) stated that the size (in this case also implies maturity) of a species could have a major effect on its rate of post-disturbance recovery and that slow recolonists

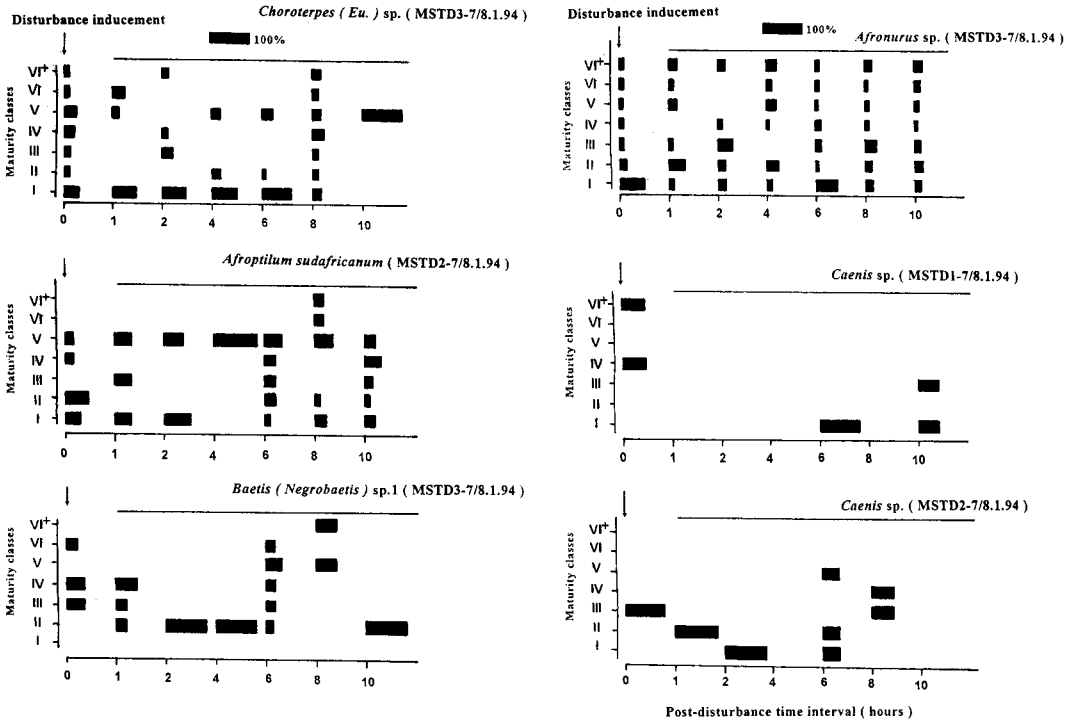


Fig. 7. Maturity class frequency histograms by disturbance time intervals for some of the taxa in MSTD subsites (7/8.1.94).

were usually small individuals. In this study small nymphs were as active in recolonizing disturbed subsites as the more mature nymphs. Recolonizers could be found within the subsites even after 1 hour after disturbance and could achieve a maturity class structure similar to the pre-disturbance community within 6 to 8 hours. In conclusion, physical disturbance is a factor with a depressant effect on mayfly densities depending on the disturbance interval. Apparently, the shorter the interval below the expected maximal recolonization time, the greater the depressant effect. The existence of erratic recolonization over the entire study duration could have been due to other factors such as immigration/emigration processes and hydrological regimes rather than by physical disturbance alone. No clear recolonization pattern for the individual taxon maturity classes was discernible, indicating that all maturity classes had equal opportunity to recolonize the subsites.

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REFERENCES

ANDREWS, E.D. 1983. Entrainment of gravel from naturally sorted riverbed material. Geol. Soc. Amer. Bull. 94: 1225-1231.
 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.
 BROOKS, S.S. & BOULTON, A.J. 1991. Recolonization dynamics of benthic macroinvertebrates after artificial

- and natural disturbances in an Australian temporary stream. *Aust. J. Mar. Freshwat. Res.* 42: 295-308.
- CONNELL, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.
- FLECKER, A.S. & FEIFAREK, B. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. *Freshwat. Biol.* 31: 131-142.
- FREMLING, C.R. & JOHNSON, D.K. 1990. Recurrence of *Hexagenia* mayflies demonstrates improved water quality in Pool 2 and Lake Pepin, Upper Mississippi River. In: CAMPBELL, I.C. (Ed.) *Mayflies and Stoneflies*, pp. 243-248, Kluwer Academic Publishers, Dordrecht.
- KRUMBEIN, W.C. 1941. Measurement and geological significance of shape and roundness of sedimentary particles. *J. Sedimentary Petrology* 11: 64-72.
- LAKE, P.S. & DOEG, T.J. 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. *Hydrobiol.* 126: 199-212.
- LEIBUNDGUT, C.H. 1983. Runoff regime of a tropical high mountain region: Hydrology of humid tropical regions with particular reference to the hydrological effects of agriculture and forestry practice (Proceedings of the Hamburg Symposium, August 1983). IAHS Publ. no. 140.
- MARCHANT, R., LAKE, P.S. & DOEG, T.J. 1991. Longitudinal variation in recolonization rates of macroinvertebrates along an upland river in south-eastern Australia. *Freshwat. Biol.* 25: 349-356.
- MATHOOKO, J.M. & MAVUTI, K.M. 1992. Composition and seasonality of benthic invertebrates, and drift in the Naro Moru River, Kenya. *Hydrobiologia* 232: 47-56.
- OSBORNE, L.L. 1983. Colonization and recovery of lotic epilithic communities: a metabolic approach. *Hydrobiologia* 99: 29-36.
- PECKARSKY, B.L. 1986. Colonization of natural substrates by stream benthos. *Can. J. Fish. Aquat. Sci.* 43: 700-709.
- REICE, S.R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* 67: 90-97.
- RYKIEL, E.J., JR. 1985. Towards a definition of ecological disturbance. *Aust. J. Ecol.* 10: 361-365.