Temporal and spatial distribution of the baetid *Afroptilum sudafricanum* in the sediment surface of a tropical stream

Jude Mutuku Mathooko

Department of Zoology, Egerton University, P.O. Box 536, Njoro, Kenya
E-mail: jmmathooko@egerton.ac.ke

Abstract

Spatial and temporal distribution patterns of *Afroptilum sudafricanum* (Lestage), a baetid from the Naro Moru River, Kenya, are analyzed and discussed. The seasonal distribution patterns of density and biomass were dissimilar, mosaic-like and stochastic. The distribution of *A. sudafricanum* density was patchy, especially during wet season 1 (June–July) and the dry season (August–October). The distribution of biomass showed more concentration patches during wet season II (November–January) and the dry season than in the wet season I. The density/biomass (D/B) ratio, as a measure of recruitment and also an important descriptor of the distribution of the biomass and density concentration patches, indicated that much of the recruitment occurred during wet season I (D/B = 78.2), in contrast with wet season II (D/B = 37.1) and the dry season (D/B = 61.7). The seasonal size-spectrum of the individuals inferred from the D/B ratios, starting from the smallest to the largest sizes was as follows: wet season I <dry season<wet season II, corresponding to the natural alternation of the seasons. Estimates of the negative binomial parameter k showed that 18.2% of all density samples showed strong aggregation ($0 < k < 1.0$), 36.4% quasi-random patterns ($k > 2.0$ but not $k < 0$) and 45.5% weak aggregation ($1.0 < k < 2.0$). One hundred percent of all biomass samples showed quasi-random patterns ($k < 0$). It was evident that weak density aggregations and quasi-random patterns of biomass were integral features of the *Afroptilum sudafricanum* population in the Naro Moru River. Further research on the population dispersion could reveal the underlying causes of this contrasting scenario between density and biomass.

Introduction

Faced with the complexity of nature, ecologists have long sought broad patterns as a means of drawing order from variety (Clarke & Johnston, 1999). In particular, ecologists have long been intrigued by the spatial and temporal distribution patterns of a population. It is because of this that a plethora of ecologists are still seeking to understand how species are 'packed' into patchy, unstable or stable habitats. The habitat, acting as a templet, normally dictates the kinds, numbers and population distribution patterns that describe the stream benthic community structures (Poff & Ward, 1989, 1990). However, this is complicated by the existence of habitat heterogeneity which is described as a pervasive characteristic of natural environments. This implies that benthic animal populations persist in a mosaic of occupied and unoccupied sites. Within this context, streams as dynamic unidirectional flow hydrosystems experience a wide streambed structural diversity with consequent extreme spatial and temporal fluctuations in benthic biota abundances. Distribution and abundance patterns across a habitat complex are fundamentally influenced by how individuals within a population move and reproduce, and by factors limiting populations at various scales (Bevers & Flather, 1999), including other factors that operate both within, and externally to, the population (Elliott & Hurley, 1998). The organism–environment relationships are, therefore, important in explaining spatial and temporal

distribution of benthos whilst between-site heterogeneity contributes to benthos diversity (Sheldon & Haick, 1981).

Investigations of the Naro Moru River have so far been based on invertebrate drift (Mathooko, 1988), colonization of artificial substrates by benthos (Mathooko, 1995), effect of artificial physical disturbance on mayflies and species diversity (Mathooko, 1996a, 1998, 1999a), fish diet (Van Someren, 1952; Mathooko, 1993, 1996b), and shredders-coarse particulate organic matter interactions (M. Dobson, A.M. Magana, J.M. Mathooko & F.K. Ndegwa, unpublished data). The present paper, in contrast, deals with the population dynamics of a single baetid species, *Afroptilum sudafricanum*, in time and space. This species has previously been described by taxonomists and stream ecologists (e.g. Gillies, 1992, 1999a; Mathooko, 1996a), but its distribution in streams is poorly known. In Kenya, *Afroptilum sudafricanum* has so far been collected from the Rift Valley in the vicinity of Lake Naivasha beside rivers Gilgil, Malewa and Murindati (Barnard & Briggs, 1988), and also from the high altitude streams of East Africa (e.g. in the Naro Moru River by Mathooko, 1988, 1996a; in the Isigi River by Gillies, pers. comm.). The reasons why this baetid was of particular interest for this study include the following:

(a) its abundance at the stream sediment surface suggests that it is an important component of the food web (cf. *Centroptilum sudafricanum*: Electivity index (Ivlev, 1961) value in the diet of rainbow trout: +0.9 (Mathooko, 1988)).

(b) its rapid population fluctuations as a response to physical disturbance on the streambed (e.g. Mathooko, 1996a, 1999b) implies that it could be used in stream quality assessment.

(c) its use as an organism for testing ecological hypotheses (e.g. development asynchrony hypothesis, J.M. Mathooko, unpublished data).

Although the quantitative biology of this baetid is scantily known, regular sampling of its larval population in the Naro Moru River from June 1993 through January 1994 permitted the description of its spatial and temporal distribution in the streambed. Temporal patterns of abundance were examined not only to provide life history information, but also to address a central problem of ecology that deals with population dynamics of a single species. It was the objective of this study to examine the patterns in terms of densities and biomass.

Materials and methods

Study site

The study site was on the Naro Moru River (Figure 1), a fast flowing gravel stream situated in central Kenya. As the stream was described in details by Mathooko (1988, 1996a, 1998, 1999a), only features relevant to the present investigation are given (Table 1). The streambed substrates are generally oblate spheroid with a sorting coefficient of >2.0, indicating that the substrates are very poorly sorted. The stream has a width of about 8.4 m and mean daily discharge of $0.431 \text{ m}^3/\text{s}$. Glaciers on Mt. Kenya supply its tributaries with water throughout the year. The Naro Moru River discharges into the Ewaso Nyiro, which subsequently discharges into the Lorian Swamp. From its source to the study site, the altitude drops by 2552 m. Riparian vegetation in its middle and upper reaches consists of tropical rainforest species which form a closed gallerial canopy (~87% cover). The benthic fauna of the stream is very diverse and mayflies (Ephemeroptera) form about 25% of the macrozoobenthos (Mathooko & Mavuti, 1992).

Collection and processing of the benthic samples

Quantitative benthic samples were randomly collected from the upper 10 cm of the sediment surface of a riffle in the Naro Moru River, using a Hess sampler (Ø 2.0 dm, 80 μm mesh-size). The exact sample positions were marked on a well-prepared outline map of the study site during each sampling occasion to allow for the plotting of surficial distribution profiles of the *Afroptilum sudafricanum* densities and biomass in the sediment. The collection of a sample from each sample position lasted for 3 min. In the present study, a total of 231 data sets (i.e. 21 replicates×11 sampling occasions) were collected and analyzed. After collection, the samples were preserved in 5% formaldehyde solution and later rinsed with water through a series of nets of differing mesh-sizes to separate the animals from the debris. The *Afroptilum sudafricanum* individuals retained in the sieves were then sorted under a stereo microscope and enumerated.

Ash-free dry weight (AFDW) of the *A. sudafricanum* individuals was determined by using the conventional method whereby the difference between dry weight and the weight after ashing of an individual is obtained. 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
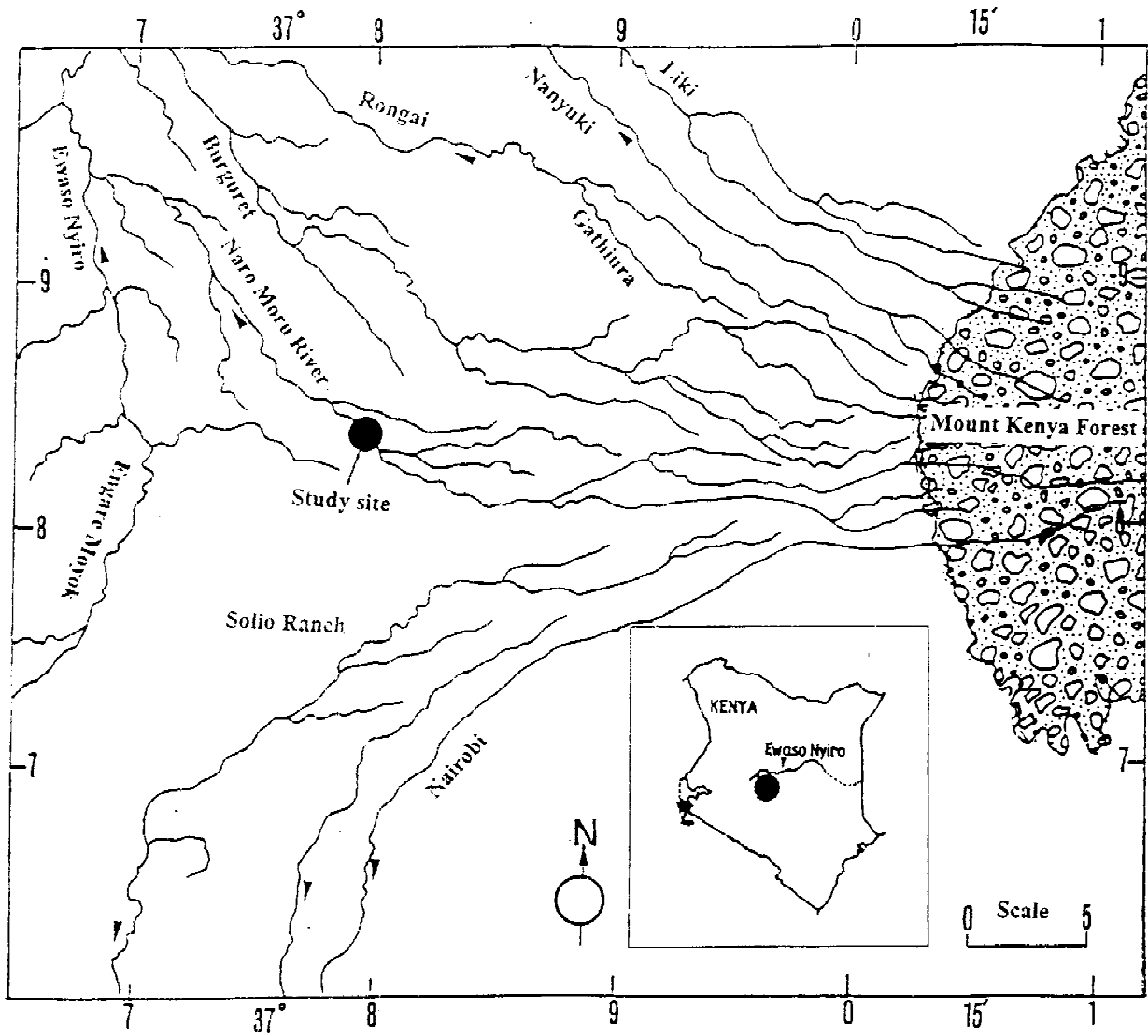
Figure 1. The Naro Moru River and the location of the study site. Inset shows the location of Naro Moru River in Kenya. Arrow heads refer to the direction of water flow. Scale in kilometres.

and then weighed on a UM3 microbalance to obtain the dry weight. They were then ashed at 500 °C for 1 h, desiccated for 1 h, and reweighed. When this procedure was not possible, the total body length (TBL) of the individual was determined, and the following formula used to derive the AFDW:

$$AFDW = 0.0024e^{0.50[TBL]}$$ (Mathooko, 1996a).

The total body length was obtained by measuring the individual from the tip of the head to the base of the cerci under a dissecting microscope fitted with an ocular micrometer. Total biomass of all the individuals in a given sampling occasion was calculated as follows:

$$B_{tot} = \Sigma AFDW_i,$$

where B_{tot} is total biomass and $AFDW_i$ is the ash-free dry weight of the ith *Afroptilum sudafricanum* individual. The density/biomass (D/B) ratio was used as an index of recruitment of individuals into the existing *Afroptilum sudafricanum* population and also as a descriptor of the nature of the concentration patches.

Although the biological basis of the use of the negative binomial distribution has been criticized (e.g. Williams, 1964), it is still the most applicable theoretical frequency distribution and has been used to de-

Table 1. Physicochemical characteristics of the Naro Moru River at the study site

Location:
Naro Moru River: (Latitude: $0°\ 03'$ S, $0°\ 11'$ S;
Longitude: $36°\ 55'$ E, $37°\ 19'$ E)
Study site: $0°\ 10'$ S, $37°\ 01'$ E
Altitude (m): 2035
Air temperature (°C): 10.8–23.5
Water temperature (°C): 11.3–18.1
pH: 6.88–7.99
Water depth (cm): 2.4–43.2
Water velocity (m/s): 0.10–1.48
Turbulence intensity: 0.05–0.24
Exposed streambed area (m^2): 0.0–56.0
Total monthly rainfall (mm): 0.0–166.7
Total monthly rainfall days: 0–21
Substrate characteristics
Shortest axis (cm): 1.50 ± 0.25 ($\pm$SD)
Intermediate axis (cm): 2.41 ± 0.43
Longest axis (cm): 3.27 ± 0.54
Sphericity (ψ): 0.70 ± 0.02
Classification of substrates: Disc-shaped or oblate spheroid
Discharge characteristics
River Gauging Station (RGS): 5BC2
Location of RGS: $0°\ 09'\ 55''$ S, $37°\ 01'\ 30°$ E
Mean discharge (m^3/s): 0.755
Discharge range: 0.121–3.571
Total hectare metre: 57.0–197.5
Total discharge/day: 6.6–22.9

scribe the degree of aggregation in aquatic organisms (e.g. Tokeshi, 1995). Contagiousness in the *Afroptilum sudafricanum* population density and biomass were analysed using the exponent k of the negative binomial distribution which was estimated according to Tokeshi (1995) thus: $k = m^2/(s^2-m)$, where m is the arithmetic mean and s^2 is the variance. Small values of k (<1.0) are taken to indicate strong aggregation whilst larger values indicate weak aggregation that approaches randomness. A negative k value shows that a pattern is tilting towards a regular dispersion.

Results

The population of *Afroptilum sudafricanum* was fluctuating spatially and seasonally. The total population ranged from 36 ind/dm^2 to 214 ind/dm^2 whilst total
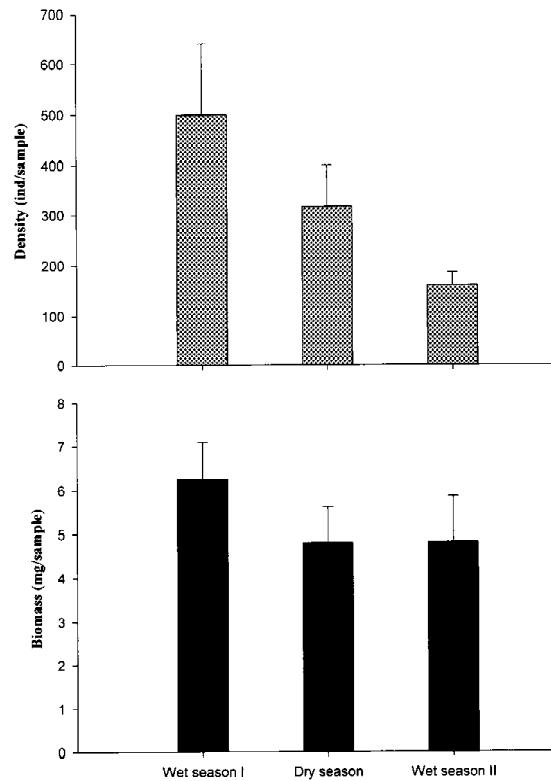

Figure 2. Density and biomass of *Afroptilum sudafricanum* in the wet and dry seasons. wet season I (June–July), dry season (August–October), and wet season II (November–January). Vertical lines: ± standard error.

biomass ranged from 0.0238 to 0.2850 mg/dm^2. Density was lowest during wet season II, with wet season I (June–July) producing the highest density and biomass (Figure 2). Dry season and wet season II biomass was similar in quantity.

The patterns of the horizontal distribution of density and biomass of the *Afroptilum sudafricanum* individuals on the study riffle are shown in Figures 3 and 4, respectively. As expected, the seasonal distribution patterns of density and biomass did not mirror each other and both distribution patterns were mosaic-like. The highest density and biomass concentrations were 43 ind/dm^2 and 106×10^{-3} mg/dm^2 and were observed during wet season I and the dry season, respectively. The distribution of *A. sudafricanum* was generally patchy, especially during wet season I (June–July) and the dry season (August–October). The distribution of biomass showed more concentration patches during the dry season and wet season II (November–January) than in the wet season I. To determine the nature of the distributions, values of k of the negative binomial were
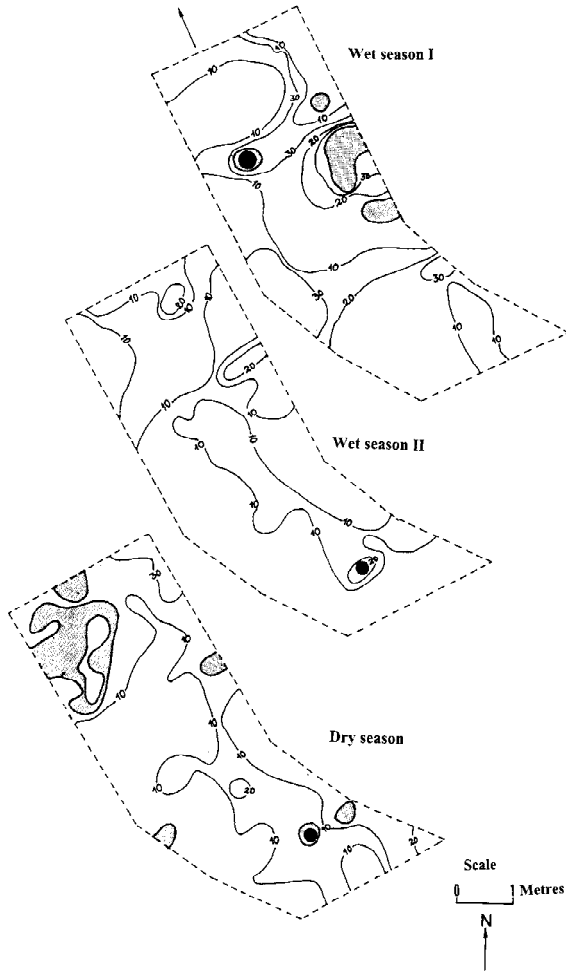
Figure 3. Isolines showing the seasonal horizontal distribution of *Afroptilum sudafricanum* densities at the streambed surface of the Naro Moru River. Tints show areas with densities ≥40 ind/sample. Black dots indicate areas of the highest concentration of density. Arrow shows the direction of water flow.
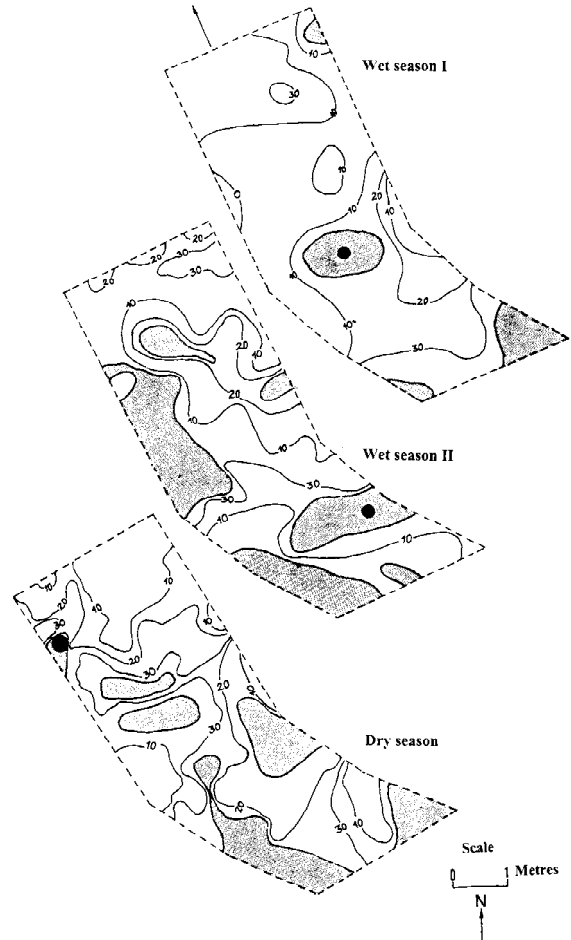
calculated for all samples and examined graphically as in Figure 5. Based on Tokeshi (1995), cases of $k > 2.0$ were considered to represent near randomness (quasi-randomness), $1.0 < k < 2.0$ weak aggregation, while $0 < k < 1.0$ corresponded to truly aggregated situations. The k values calculated for the density and biomass of *Afroptilum sudafricanum* from June 1993 to January 1994 (i.e. during each of the 11 sampling occasions) ranged from 0.43 to 4.47, and from −1.14 to −0.01, respectively. Close scrutiny of Figure 5 revealed the following distribution patterns: Density: true aggregation makes up 18.2% of all the cases, quasi-random patterns 36.4%, and weak aggregation 45.5%; biomass: quasi-random pattern 100% and all the other
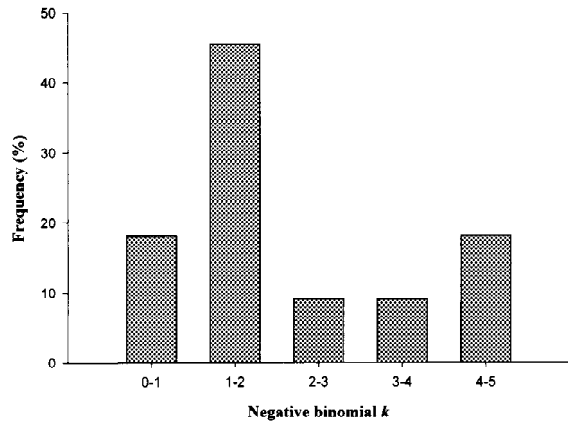

Figure 4. Isolines showing the seasonal horizontal distribution of *Afroptilum sudafricanum* biomass at the streambed surface of the Naro Moru River. Tints show areas with biomass $\geq 40 \times 10^{-3}$ mg/sample. Black dots indicate areas of the highest concentration of biomass. Arrow shows the direction of water flow.

Figure 5. Frequency distribution of the negative binomial of exponent k in the *Afroptilum sudafricanum* population of the Naro Moru River.
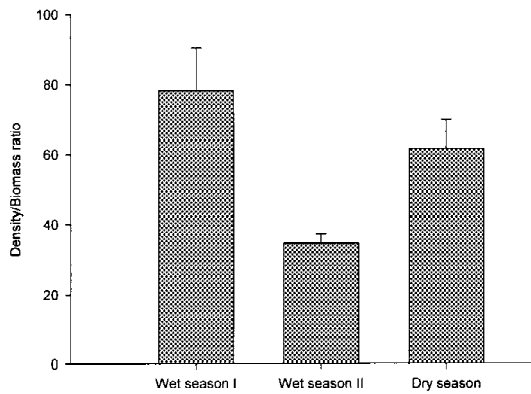
Figure 6. The distribution of the density/biomass (D/B) ratio in the wet and dry seasons. Vertical lines: ± standard error.

distribution descriptors 0%. The distribution patterns of the densities and biomass of *A. sudafricanum*, therefore, contrasted each other. In the wet seasons I, II and dry season, the mean k (±SD) values for density were 1.18 (0.45), 2.75 (1.31) and 1.83 (1.55), respectively. Similarly, in the wet seasons I, II and dry season, the mean k values for biomass were –0.02 (0.002), -0.03 (0.01) and –0.24 (0.50), respectively. This meant that the densities of the wet season I and dry season generally showed weak aggregations and the wet season II quasi-random pattern. All the seasons showed quasi-random biomass patterns. It is, therefore, evident that weak density aggregations and quasi-random patterns of biomass were integral features of the *Afroptilum sudafricanum* population in the Naro Moru River.

Density/biomass (D/B) ratio was used as a measure of recruitment and essentially gives the total number of individuals required to weigh 1.0000 mg. The larger the D/B ratio the smaller the weight and size of the individuals. It was observed that the highest recruitment occurred during wet season I (Figure 6). This meant that the small individuals attained large sizes progressively from wet season I, through the dry season to the wet season II. Intuitively, the number of individuals required to weigh 1.0000 mg decreased as follows: wet season I>dry season>wet season II, following the natural alternation of seasons. Recruitment into the already existing population, therefore, decreased in wet season II (November–January) as depicted by the low D/B ratio and the few individuals needed to weigh 1.0000 mg. Therefore, this ratio could also be an important descriptor of the distribution of the biomass as well as the density concentration patches.

Discussion

Time and space function together to shape lotic population patterns of abundance and biomass. Much speculation has been proffered on the extent to which these patterns reveal the underlying processes responsible for population structure. Random patch formation (*sensu* Tokeshi & Townsend, 1987) envisages aggregation to be stochastically variable rather than being largely fixed throughout the life cycle of an organism. The surficial density and biomass distribution isolines showed that the distributions of density and biomass of *Afroptilum sudafricanum* shifted with seasons and were dynamic. Biomass and density distributions in the two wet seasons (I & II) were different, although the patterns were expected to be similar. This contrasting scenario could be due to differences in stream hydraulic regimes and life-history characteristics of the *Afroptilum sudafricanum* individuals. During wet season II, resources were probably widely and uniformly distributed due to the high discharge of about 0.71 m^3/s which increased the wetted area of the stream channel and therefore the individuals could have been provided with a wider diversity of habitats to exploit. This could be the most plausible explanation for the regular density distribution pattern during this season. Since the dry season flow is normally low (i.e. 0.17 m^3/s) and does not wet the entire stream channel, organisms tend to concentrate in the reduced wetted area where food and/or oxygen concentration might be high. These, together with other factors, could explain the existence of density concentration patches on the streambed during the dry season.

The horizontal distribution of the densities and biomass of *Afroptilum sudafricanum* showed weak aggregation and quasi-random patterns, respectively. Hatching of the eggs into larvulae and the subsequent migrations and colonization of the sediments by larvae may have led to quasi-random distributions in wet season II. During this season the baetid distribution could have also been widespread due to the already mentioned high discharge that wetted a large streambed area compared with the low discharge of 0.44 and 0.24 m^3/s for the wet season I and dry season, respectively. It could, therefore, be concluded that aggregation in the *Afroptilum sudafricanum* population density was generally weak. There was a gradient of dispersion patterns ranging from quasi-randomness (near random) ($k > 2.0$) to strong contagion ($0 < k < 1.0$) for the baetid population density over the entire study

duration. This was in agreement with the trends observed by Tokeshi (1995) in a chironomid community.

Few large-sized individuals as depicted by the low D/B ratio were collected during wet season II (November–January). Two things might have happened during this time: firstly, there might have been emergence during the previous dry season (August– October) and the few large individuals collected in wet season II could have been relics of the previous population which was still maturing and emerging, and which survived erosion by the high discharge experienced during this time of the year. Secondly, the small larvulae might have acquired traits that cue them to move to deeper hyporheic interstitial spaces to avoid the increasing discharge as observed by Mathooko (1988), thus leaving the large-sized individuals in the upper layers of the sediment. Whichever is the case, this author collected subimagos and imagos of mayflies during wet season II in 1995 of which 60% were females. This could have been the time of emergence and oviposition, apparently supporting the first postulation. The recruitment of the *Afroptilum sudafricanum* individuals was high during the wet season I (June–July) as shown by the D/B ratio of 78.2. This was in accord with the findings of Mathooko (1996a) who found increases of small-sized individuals of mayflies during wet seasons and concluded that the survival strategy of the mayfly community in the Naro Moru River is for most of the population to mature and emerge during the wet seasons.

In conclusion, spatial and temporal distribution of *Afroptilum sudafricanum* in the streambed of the Naro Moru River is highly dynamic. The assertion by Tokeshi (1995) that 'aggregation cannot easily be maintained and patches of individuals are formed in a quasi-random fashion' might be the rule rather than the exception for the *Afroptilum sudafricanum* population inhabiting a hydrosystem experiencing stochastic physicochemical and biological processes. Perhaps one of the most interesting result of my study, although without comparison with any other known study, was the manifestation of quasi-random patterns ($k<0$) of biomass which lacked the gradient of dispersion depicted by density. Further research on the population dispersion could reveal the underlying causes of such contrasting scenario.

References

Barnard, P. C. & J. Biggs, 1988. Macroinvertebrates in the catchment streams of Lake Naivasha, Kenya. Rev. Hydrobiol. Trop. 21: 127–134.

Bevers, M. & C. H. Flather, 1999. The distribution and abundance of populations limited at multiple spatial scales. J. anim. Ecol. 68: 976–987.

Clarke, A. & N. M. Johnston, 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J. anim. Ecol. 68: 893–905.

Elliott, J. M. & M. A. Hurley, 1998. Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a Lake District stream. J. anim. Ecol. 67: 280–286.

Gillies, M. T., 1992. A new synonym and distribution records of *Afroptilum sudafricanum* (Lestage) (Baetidae: Ephemeroptera) from the East African highlands. J. ent. Soc. Sth. Afr. 55: 33–38.

Gillies, M. T., 1999. Reinstatement of *Afroptiloides* as a genus (Baetidae, Ephemeroptera). Aquatic Insects 21: 197–203.

Ivlev, V. S., 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, Liverpool: 302 pp.

Mathooko, J. M., 1988. Downstream drift of invertebrates in the Naro Moru River, a tropical river in central Kenya. MSc thesis, University of Nairobi: 199 pp.

Mathooko, J. M., 1993. Availability and selection of mayfly, *Caenis kungu* Kimm. (Ephemeroptera: Caenidae as a natural source of food by rainbow trout, *Oncorhynchus mykiss* Walb., in a tropical river. Afr. J. Ecol. 31: 58–65.

Mathooko, J. M., 1995. Colonization of artificial substrates by benthos in a second-order high altitude river in Kenya. Hydrobiologia 308: 229–234.

Mathooko, J. M., 1996a. Artificial physical disturbance at the sediment surface of a Kenyan mountain stream with particular reference to the Ephemeroptera community. Doctoral thesis, University of Vienna: 224 pp.

Mathooko, J. M., 1996b. Rainbow trout (*Oncorhynchus mykiss* WALBAUM) as a potential natural 'drift sampler' in a tropical lotic ecosystem. Limnologica 26: 245–254.

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., 1999a. Effects of differing inter-disturbance intervals on the diversity of mayflies recolonizing disturbed sites in a tropical stream. Arch. Hydrobiol. 146: 101–116.

Mathooko, J. M., 1999b. The effects of physical disturbance on *Afroptilum sudafricanum* (Ephemeroptera: Baetidae) population

densities in a Kenyan mountain stream. Sth. Afr. J. aquat. Sci. 24: 11–23.

Mathooko, J. M. & K. M. Mavuti, 1992. Composition and seasonality of benthic invertebrates, and drift in the Naro Moru River, Kenya. Hydrobiologia 232: 47–56.

Poff, N. L. & J. V. Ward, 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can. J. Fish. aquat. Sci. 46: 1805–1818.

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

Sheldon, A. L. & R. A. Haick, 1981. Habitat selection and association of stream insects: a multivariate analysis. Freshwat. Biol. 11: 395–403.

Tokeshi, M., 1995. Randomness and aggregation: analysis of dispersion in an epiphytic chironomid community. Freshwat. Biol. 33: 567–578.

Tokeshi, M. & C. R. Townsend, 1987. Random patch formation and weak competition: coexistence in an epiphytic chironomid community. J. anim. Ecol. 56: 833–845.

Van Someren, V. D., 1952. The Biology of Trout in Kenya Colony. Nairobi, Govt. Print: 114 pp.

Williams, C. B., 1964. Some experiences of a biologist with R. A. Fisher and statistics. Biometrics 20: 301–306.