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Chironomid community structure deduced from larvae and pupal exuviae of a chalk stream

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Abstract

Species abundances of Chironomidae (Insecta: Diptera) have often been excluded from studies of benthic river communities because of difficulties associated with sampling and identifying larvae. Chironomid pupal exuviae are easier to collect and identify and could be used to determine community structure if shown to be representative of local larval assemblages. Larvae were sampled along a 20 m chain secured over mid-channel gravels, upstream of two collection points for pupal exuviae. Proportional taxa abundances of pupal exuviae and larvae sampled from 130 m of stream were directly compared by a χ^2 test of independence and also separately fitted to four models of species abundance distribution. Observed proportions of taxa were not independent of the life stage sampled. The greatest discrepancies occurred with species of pupal exuviae that were absent as larvae from the gravel. The log series model provided the best fit with both pupal and larval data. Collections of pupal exuviae had greater species richness and evenness than samples of larvae. This was considered to be a consequence of sampling larvae from the gravel habitat alone.

Introduction

The Chironomidae are considered the most widely distributed and abundant of aquatic insect families (Pinder, 1986). Chironomids contribute significantly to secondary production in temperate streams (e.g. Berg & Hellenthal, 1991) and have been used for characterising lakes (e.g. Saether, 1979) and rivers (e.g. Wilson & Bright, 1973). Quantitative sampling and species identification of larval Chironomidae are arduous tasks that often cause freshwater ecologists to ignore species of this family in their investigations. The surrogate use of discarded pupal exuviae to deduce information on local larval chironomid assemblages requires considerably less effort than direct sampling and is becoming more widespread (Coffman & Ferrington, 1984; Chutter, 1984; Boothroyd, 1988; Ashe, 1990). If pupal exuviae can be shown to provide an accurate assessment of the larval community structure in the vicinity of the sampling point then more researchers might include Chironomidae in river community studies.

Collections of chironomid pupal exuviae have been directly related to larvae in stream bed sediments by preventing extraneous exuviae entering the study area, using barriers to surface flow (Coffman, 1974) or small enclosures (Wartinbee & Coffman, 1976). Floating materials may pass beneath surface barriers, while enclosures can create several artefacts (Connell, 1975; Diamond, 1986; Peckarsky & Penton, 1990; Kohler, 1992). Using collections of pupal exuviae, Ruse (1993a) found indirect evidence that the structure of chironomid assemblages was correlated with substrata differences between three stream sites. In the present study, chironomid pupal exuviae and larvae were sampled from the same stretch of stream and their patterns of species assemblage compared.

Study area

The Pang is a third order stream situated at the eastern end of the Berkshire Downs in southern England. Almost the entire 30 km of channel are situated over Upper Chalk. The stream has a catchment area of 171 km^2 with a mean discharge into the River Thames of 0.609 m^3 s^{-1} (1969–1990). The annual mean discharge for October 1990 to September 1991 was 0.288 m^3 s^{-1}, the third successive year of below average flows. The catchment is primarily rural, the largest sewage discharge is 91 m^3 d^{-1} from a treatment works 6.5 km upstream of the study area. The sampling site was situated within the grounds of Pangbourne groundwater pumping station (National Grid reference SU 635 763). River width ranged from 5.0 to 5.6 m with approximately 3 m of central gravel (mean particle size – 2.04ϕ, sorting coefficient 2.78ϕ, skewness 0.42ϕ) and 1 m of silt with macrophytes at the margins. Below a depth of 8–10 cm of the gravel there was a compact grey clay which was impenetrable to chironomid larvae. Bushes on the left bank gave shade from the west, while the right bank had regularly maintained grass verges. Water chemistry data for the site during the period of this study are provided in Ruse (1994).

Methods

Core samples (surface area 95 cm^2) of gravel were taken to a depth of 5 cm at eight randomly selected positions along a 20 m chain secured in mid-channel on six occasions between October 1990 and September 1991. Chironomid larvae were separated from samples by live flotation in a solution of $MgSO_4$ (1.25 sg). Full details of sampling and sorting larvae are provided in Ruse (1994). Identification of larvae to genus was possible using the key of Wiederholm (1983), species identification of Orthocladiinae relied on the keys of Cranston (1982) and Hirvenoja (1973), species aggregates of Chironomini conform with descriptions in Moller Pillot (1984). Otherwise, larval identification was assisted by rearing to pupae or adults. Identification of early instars was assisted by descriptions in Mozley (1979), Soponis & Russell (1982), Williams (1985), Storey (1986) and Olafsson (1992).

Chironomid pupal exuviae accumulating with other floating debris were collected with a 250 μm mesh pond net from two positions, among vegetation 10 m downstream of the chain and behind a floating beam a further 100 m downstream. Six drift trials, using simulated pupal exuviae material, had indicated that 70–100% of exuviae in a sample would not have drifted further than 200 m with surface current velocities ranging from 13–46 cm s^{-1} (Ruse, 1993b). Pupal exuviae were collected monthly at each position from January to October 1991. Approximately 200 pupal exuviae were removed from each sample following the methods of Wilson & McGill (1979) which achieved random dispersion of pupal exuviae before subsampling (Ruse, 1993b). Pupal exuviae were identified according to the key of Langton (1991). Pupal data from all samples were combined to represent chironomid emergence from Pangbourne during 1991. Larval data were also amalgamated for the six surveys. Combining data for comparing community structure was considered most appropriate since variations in the appearance of the two life stages would be smoothed. The collection of pupal exuviae began three winter months after the first larval survey to accommodate the time required for larval development. Seasonal variations in larval and pupal exuviae abundances during this study are reported in Ruse (1995).

Direct comparison of pupal data with data for larvae was made using a χ^2 test of independence (Sokal & Rohlf, 1981). A contingency table of observed and expected abundances was constructed for each taxon of pupal exuviae and larvae. The null hypothesis was that proportions of each taxon collected were independent of the method of sampling.

According to Magurran (1988) a species abundance distribution uses all the information gathered in a community and is the most complete mathematical description of the data. Species rank versus abundance was plotted for both pupal exuviae and larval data to provide two separate descriptions of the chironomid community structure. The similarity of the pupal and larval distributions was assessed by comparing each with four models of species abundance; the geometric series, log series, log normal and broken stick. These models were chosen because of their common usage and relative ease of calculation, as described by Magurran (*op. cit.*). Predicted species abundances for each model were compared with observed abundances using a χ^2 goodness of fit test (Sokal & Rohlf, 1981). Diversity indices derived from three of these models were used to compare species evenness or richness deduced from pupal and larval data.

Results

A total of 3325 pupal exuviae from 78 taxa were identified (Table 1). These data were compared with the four models of species abundance. For the test of independence of sampling methods the abundances

Table 1. Abundances of chironomid taxa used for rank correlations between pupal exuviae and larval data

	Pupae	Larvae
Clinotanypus nervosus (Meigen)	1	0
Apsectrotanypus trifascipennis (Zetterstedt)	45	44
Macropelopia nebulosa (Meigen)	7	1
Procladius choreus (Meigen)	59	94
Ablabesmyia spp.	8	136
Arctopelopia spp.	0	26
Conchapelopia spp.	8	747
Larsia spp.	0	57
Zavrelimyia spp.	0	4
Tanypus punctipennis Meigen	1	0
Potthastia gaedii (Meigen)	103	424
Potthastia longimanus Kieffer	14	432
Prodiamesa olivacea (Meigen)	2	3
Brillia flavifrons Johannsen	6	3
Brillia modesta (Meigen)	2	0
Cricotopus albiforceps (Kieffer)	86	415
Cricotopus annulator Goetghebuer	164	1026
Cricotopus bicinctus (Meigen)	64	0
Cricotopus fuscus (Kieffer)	8	71
Cricotopus triannulatus (Macquart)	3	220
Cricotopus trifascia Edwards	1	0
Cricotopus sylvestris (Fabricius)	3	0
Cricotopus trifasciatus (Panzer)	5	34
Eukiefferiella/Tvetenia	25	14
Heterotrissocladius marcidus (Walker)	3	0
Nanocladius bicolor (Zetterstedt)	6	122
Nanocladius rectinervis (Kieffer)	90	363
Orthocladius fuscimanus Kieffer	2	0
Orthocladius luteipes Goetghebuer	1	0
Orthocladius rivulorum Kieffer	1	0
Orthocladius glabripennis (Goetghebuer)	5	0
Orthocladius pedestris Kieffer	92	0
Orthocladius rubicundus (Meigen)	241	2549
Orthocladius oblidens (Walker)	254	2274
Orthocladius obumbratus Johannsen	31	1
Paracladius conversus (Walker)	127	228
Paratrichocladius rufiventris (Meigen)	24	231
Rheocricotopus chalybeatus (Edwards)	9	366
'Rheorthocladius sp. A' Thiennemann 1944	1	0
Synorthocladius semivirens (Kieffer)	219	2506
Chaetocladius spp.	0	28
Corynoneura carriana Edwards	5	3
Corynoneura coronata Edwards	0	2
Corynoneura lobata Edwards	176	623
Epoicocladius flavens (Malloch)	19	1390
Heleniella ornaticollis (Edwards)	1	0
Limnophyes spp.	38	0
Metriocnernus obscuripes (Holmgren)	4	0
Parakiefferiella smolandica (Brundin)	5	40
Parakiefferiella bathophila (Kieffer)	36	905
Parametriocnetnus stylatus (Kieffer)	0	1
Paraphaenocladius impensus (Walker)	1	0
Paratrissocladius excerptus (Walker)	68	0
Thienemanniella spp.	96	108
Chironomus annularius (Degeer)	1	0
Chironomus commutatus Keyl	1	0
Cryptotendipes holsatus Lenz	3	0
Cryptotendipes pseudotener (Goetghebuer)	1	0
Demicryptochironomus vulneratus (Zetterstedt)	0	1
Dicrotendipes notatus (Meigen)	0	1
Microtendipes pedellus agg.	25	1584
Parachironomus spp.	0	51
Paracladopelma camptolabis (Kieffer)	2	0
Paratendipes spp.	1	21
Phaenopsectra spp.	5	60
Polypedilum breviantennatum Tshernovskij	0	10
Polypedilum laetum agg.	8	130
Polypedilum nubeculosm gp.	0	28
Cladotanytarsus vanderwulpi (Edwards)	77	1015
Microspectra spp.	54	17
Paratanytarsus spp.	121	1741
Rheotanytarsus curtistylus (Goetghebuer)	52	304
Rheotanytarsus pentapoda Kieffer	1	0
Rheotanytarsus photophilus (Goetghebuer)	7	69
Stempellina bausci (Kieffer)	12	20
Stempellinella minor (Edwards)	2	0
Tanytarsus spp.	782	3750

of some species of pupal exuviae were amalgamated. This was necessary because larvae, especially early instars, could not always be identified to species. To obtain pupal exuviae abundances in Table 1 the following species were combined, *Ablabesmyia longistyla* Fittkau and *A. monilis* (Linnaeus); *Conchapelopia melanops* (Meigen) and *C. pallidula* (Meigen); *Eukiefferiella claripennis* (Lundbeck) and *Tvetenia calvescens* (Edwards); *Thienemanniella* Pe 2b and *T. vittata* (Edwards); *Micropsectra apposita* (Walker)/*M. contracta* Reiss and *M. atrofasciata* Kieffer; *Paratanytarsus dissimilis* Johannsen and *P. lauterborni*

Kieffer; *Tanytarsus brundini* Lindeberg, *T. ejuncidus* (Walker), *T. eminulus* (Walker), *T. mendax* Kieffer, *T. palettaris* Velneaux, *T. pallidicornis* (Walker) and *T. longitarsis* (Kieffer).

Core sampling obtained 24 293 larvae from 67 taxa (Ruse, 1994: Table 3), these data were adapted in Table 1 for the contingency table. For example, abundances of early instars of *Cricotopus* spp. and *Orthocladius* spp. were apportioned to species according to their relative proportions as third and fourth instars while first instars of *Eukiefferiella/Tvetenia* were combined with *T. calvescens.*

In a χ^2 test of independence between proportions of taxa collected as pupal exuviae or larvae the null hypothesis was rejected ($\chi^2_{[36]} = 3696, P<0.001$). The test was restricted to 37 pairs of pupal/larval taxa with expected counts greater than 5. The three largest discrepancies between observed and expected counts were due to species identified from collections of pupal exuviae which were absent as larvae from gravel samples, these were *Orthocladius pedestris*, *Paratrissocladius excerptus* and *Cricotopus bicinctus*. There were eleven species of larvae that were not found as pupal exuviae but they were all rare ($\geq$0.2%) with expected counts below 5. All but two of these species (*Demicryptochironomus vulneratus* and *Dicrotendiupes notatus*) had been collected as pupal exuviae from Pangbourne in the previous two years (Ruse, 1993b: Table 5.1). The most significantly under-representated larval species in collections of pupal exuviae were *Microtendipes pedellus* agg. and *Epoicocladius flavens.*

Species abundance models

A goodness of fit (GOF) test between ranked lists of observed and predicted abundances of pupal exuviae species indicated a highly significant deviation from a geometric series (Fig. 1). The most significant discrepancies occurred with predictions for the five most abundant species and for several middle-ranking species. A better fit was found for larvae but a GOF test again indicated a highly significant departure from a geometric series (Fig. 2). Predictions for the first three dominant taxa were close to the observed abundances but several taxa among the first thirty had significant departures from those expected. The fixed proportion k pre-empted by successive species of pupal exuviae in a geometric model was 0.068 and for larvae it was 0.113.

Observed and expected data for the remaining three distribution models were compared by their species frequencies. Taxa were arranged into classes of abundance following a $\log_2$ sequence (octaves). Data for pupal exuviae showed no significant difference with expected frequencies for a log series, with a particularly good fit for rare species ($\chi^2 = 11.75$, $P = 0.1$–0.25, d.f. 8). Larval frequency distribution was also not significantly different from that expected for a log series ($\chi^2 = 16.80$, $P = 0.1$–0.25, d.f. 11). Species aggregates of early instars would create a distortion of the true larval abundance distribution if these instars belonged to species allocated to later instars. A revised larval distribution was obtained by apportioning abundances of first instar *Orthocladius/Cricotopus* and second instar *Orthocladius* spp. and *Cricotopus* spp. among species of these two genera, according to their relative proportions as third and fourth instar larvae. First instars of *Tanytarsus/Micropsectra* were assumed to be *Tanytarsus* because later instars of *Micropsectra* were rare. Their numbers were apportioned between the four most dominant species of *Tanytarsus*; *T. eminulus*, *T. pallidicornis*, *T. brundini* and *T. ejuncidus*, according to their relative proportions in the combined pupal exuviae collection. Larval abundance for *Tanytarsus* spp. (2^{nd}–4^{th} instars) was also distributed between the three species other than *T. brundini* (which was identifiable), according to their proportions in the pupal data. These modifications produced a revised larval distribution for 63 taxa which was tested against the two models that best fitted the original larval distribution, the log series and log normal. The revised larval distribution had a higher probability of fitting a log series model than the original data ($\chi^2 = 9.63$, $P = 0.5$–0.75, d.f. 11). The log series index of diversity (α) for pupal exuviae was 14.3 while for the original and revised larval distributions it was 8.4 and 7.8 respectively.

Ninety-two species of pupal exuviae were predicted by the log normal model. The additional 14 species over those observed represent rare species beyond the veil line, towards the left hand tail of a bell-shaped log normal distribution curve (Preston, 1948). Observed pupal exuviae frequencies did not fit the log normal model ($\chi^2 = 15.77$, $P = 0.01$–0.025 d.f. 6), the most abundant classes had some of the largest departures from predicted frequencies. The numbers of observed larval species were 4 less than predicted for a log normal model which fitted both original and revised distributions ($\chi^2 = 13.76$, $P = 0.1$–0.25, d.f. 9 and $\chi^2 = 10.08$, $P = 0.25$–0.5, d.f. 9 respectively). The poorest fitting octave for both larval lists was that for

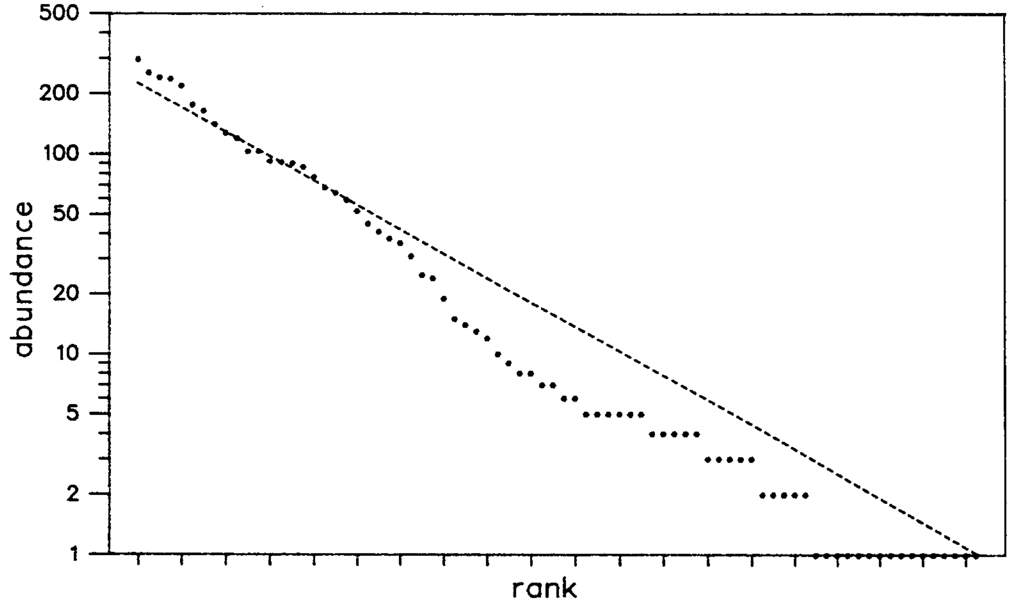

Fig. 1. Rank/abundance plot for pupal exuviae species. Observed abundances as dots, geometric series as broken line ($\chi^2 = 201.6$, $P < 0.001$, d.f. 77).

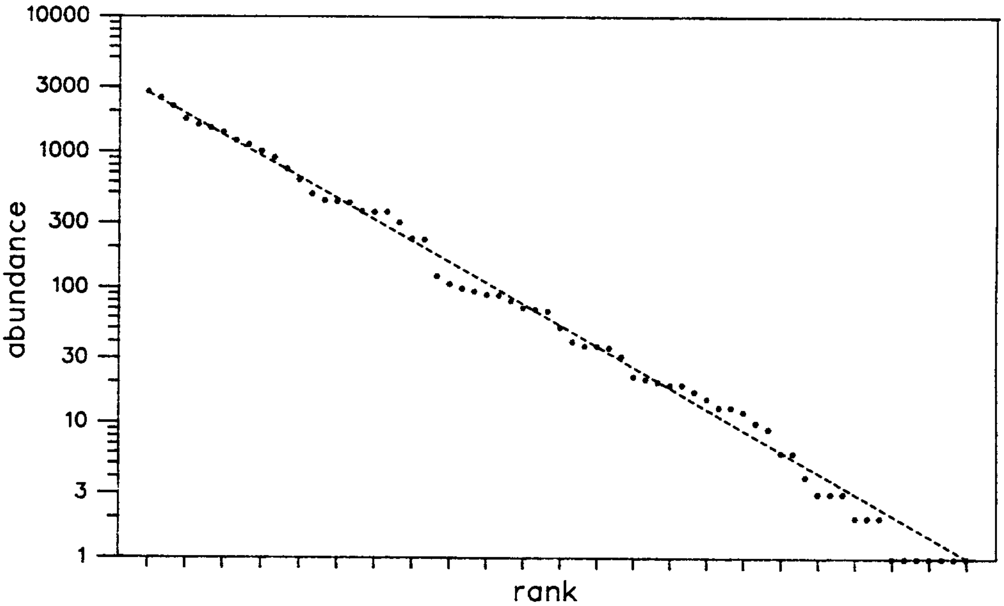

Fig. 2. Rank/abundance plot for larval species. Observed abundances as dots, geometric series as broken line ($\chi^2 = 188.74$, $P<0.001$, d.f. 66).

species with abundances between 1024 and 2048 individuals. Log normal diversity (λ) was 115.3 for pupal exuviae, 68.0 for the original larval data and 62.6 for the revised larval distribution. The broken stick model provided the poorest fit of those tested against pupal exuviae and larval distributions (both $P<0.001$).

Discussion

Proportional abundances of chironomid taxa deduced from collecting pupal exuviae or larvae were not independent of the method used. The most obvious discrepancy between the pupal and larval data sets was the greater diversity of the former. The log series α and log normal λ indices are most sensitive to species richness (Magurran, 1988) while the geometric index k is more sensitive to evenness (Tokeshi, 1993). Pupal exuviae exhibited greater species richness and evenness than larvae. The lack of correspondence with larval data in a contingency test was due to species recorded as pupal exuviae being absent, or under-represented, in samples of larvae from gravel. Drift trials had indicated that the majority of pupal exuviae collected from the two sampling positions would have been derived from 300 m of stream. The pupal exuviae collected were expected to include some species whose larvae spent all or most of their lives in habitats other than the gravels sampled. Pinder (1977) refers to the epiphytic chironomid community of chalk streams while Wright (1992) cites chalk stream studies that found greater invertebrate species richness among macrophytes compared to gravel and silt. The constraints of the core sampling area and frequency would reduce the probabilities of certain species present being sampled as larvae, particularly those associated with macrophytes at the stream margins. Referring to species highlighted in the results as examples, *Paratrissocladius excerptus* was absent as larvae from core samples despite its appearance as pupal exuviae during April, May and from July to October. Larvae of *P. excerptus* were collected in June from sand and silt deposited around bases of *Myosoitis scorpioides* (L.) (Ruse, 1993b). *Cricotopus bicinctus* was also absent from core samples while larvae were collected with a pond net from marginal stands of *M. scorpioides*, *Scirpus lacustris* (L.) and *Sparganium emersum* Rehm.

The peak emergence of species that were abundant as larvae but relatively poorly represented as pupal exuviae may have been missed by collections of pupal exuviae. Alternatively, the larvae of these species may have been concentrated within the mid-channel substratum relative to marginal habitats. This might be expected for larvae of *Epoicocladius flavens* which have a commensal association with nymphs of the mayfly *Ephemera danica* Müller (Tokeshi, 1986). A discrepancy between pupal and larval data could also arise from a differential mortality of larval species.

May (1975) summarises the broken stick, geometric and log series distributions as characteristic of simple communities whose dynamics are dominated by a single factor. The broken stick distribution is the most equitable, arising from a random apportionment of a resource. At the other extreme, the geometric series is a hierarchical, niche preemption model. May, *op. cit.* suggested that the geometric series could occur when species arrived at regular intervals to preempt unoccupied niches. If the length of time between species arrivals was random then the log series would be predicted. The log normal is a statistical distribution that can arise when species abundance in a large community results from several independent factors acting multiplicatively (May, *op. cit.*; Pielou, 1975). The almost linear rank/abundance plots, with high numbers of rare species (Figs 1 & 2), were an indication that the log series would fit pupal and larval data sets. It is not unusual for both the log series and log normal to fit the same data (Magurran, 1988). This occurred with the original and revised larval abundance distributions. The closeness of the observed and predicted number of larval species suggests that both data sets were sufficiently large to reveal most of the log normal distribution curve. If this is correct, the observed larval distributions were best represented by the log series rather than assuming a truncated form of the log normal. The closest fit to any model tested was between the revised larval data and the log series.

A log series can arise as an artefact of sampling too few individuals from a log normally distributed community (Preston, 1948). Comparisons with examples used by Preston, *op. cit.* to illustrate log normal distributions indicated that the number of larvae recorded from the mid-channel gravels was an adequate sample. In comparison to larvae, far fewer pupal exuviae were identified and these may have originated from several habitats along 300 m of stream. Rare species present in each pupal exuviae collection would be missed due to subsampling. Larvae were also subsampled and yet both data sets fitted the log series, which has a higher proportion of rare species compared with the log normal. Many chironomids have long emergence periods (Coffman, 1973; Wilson, 1977) which improves the possibility of species being represented in monthly samples of pupal exuviae. The 101 species of pupal exuviae collected from three years of samples at Pangbourne (Ruse, 1995) provide a good estimate of the total list of taxa available. The 78 species collected in one year were considered to be a large proportion of the species present that year.

Assuming that the sample sizes of pupal exuviae and larvae were adequate, what ecological implications of a log series species abundance distribution were possible? The chironomid assemblage at Pangbourne was strongly inequitable, possibly stressed or at an early successional stage (hence immigration of a large number of rare species) and regulated by one or a few influences. Despite a second successive year of below average rainfall there was a record high discharge in February 1990 (Ruse, 1995) which could have been a dominant influence. In contrast, Hughes (1986) has predicted a log series distribution for unstressed communities without biological interactions. The larval assemblage did have a high degree of resource overlap (Ruse, 1994).

Models have been applied to describe and explain species abundance distributions obtained from other studies of river chironomid assemblages. Schmid (1992) found that the broken stick model best described larval species abundances in the River Danube above a dam while the log normal best described abundance patterns downstream. Disturbance by high flows below the dam was thought to be the single factor preventing the less equitable distribution that occurred upstream. Tokeshi (1990) found that an analogous model to the log normal described abundance data for an epiphytic chironomid assemblage, although only the most abundant species were tested. He believed that these chironomids belonged to a dynamic, unpredictable community. Boerger (1981) found the chironomid abundance distribution for a species rich, third order Canadian river did not fit the log normal model because there were too many rare species. A log series may have fitted the data but was not tested. Pielou (1975) believed that statistical models such as the log series and log normal explained nothing about species environmental tolerances or whether their abundances were limited by resources or competition. According to Tokeshi (1993) species abundance models are useful for interpreting patterns but should not be regarded as rigid descriptors of the mechanisms involved in community organisation. He also challenged whether statistical models had meaningful quantification and recommended that observed patterns be tested against confidence limits produced from replicated simulations of niche-orientated models. The availability of such tools would be an asset to understanding community organisation.

Conclusions

Although the use of species abundance models to explain community structure is controversial, they are an economical means of describing species abundance patterns without reference to species identity. Both pupal exuviae and larval data conformed with a log series model of species abundance distribution with a few dominant species and a large proportion of rare species. Pupal exuviae exhibited greater species richness and evenness than larvae. This was considered a consequence of the diversity of habitats represented by collections of pupal exuviae as compared with samples of larvae from gravel alone. This was also believed to result in proportional differences in species abundances between the two data sets, particularly species associated with macrophytes. Collections of pupal exuviae may have accurately reflected the relative proportions of larval species present, integrated over all the available habitats in the vicinity of the study area.

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