Spatial and temporal distribution patterns of drifting pupal exuviae of Chironomidae (Diptera) in streams of tropical northern Australia

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SUMMARY

1. Periodic collecting of floating cast pupal cuticles of chironomids (exuviae) in two tropical northern Australian streams demonstrates (i) spatial heterogeneity in species composition across a wide stream, (ii) temporal heterogeneity in the maximum abundance of each species, and that (iii) species accumulate as a function of sample size and duration of sampling.

2. Spatial heterogeneity is ascribed to variation in larval microhabitat across the wide stream, combined with short exuvial drift duration and restricted upstream mixing.

3. Temporal heterogeneity is ascribed to diel periodicity in adult emergence and, as with spatial heterogeneity, to the short floating life.

4. The consequences of spatial and temporal variation for the sampling of exuvial drift are discussed in relation to the objectives of particular programmes. Thus, if the objective is assessment of chironomid species composition for inventory purposes such as faunistics or conservation, the large sample sizes attained by 24-h sampling are necessary and appropriate. However, for rapid assessment that requires comparable samples at different sites, species numbers may be optimized by temporally and spatially restricted sampling of the maximal emergence period, which in this study is at dusk, or by subsampling from a 24-h sample.

Introduction

The development of biological monitoring procedures for assessing effects of mining operations on tropical freshwater ecosystems in the Alligator Rivers Region (ARR) of monsoonal northern Australia has depended upon recognition of species of predominantly immature benthic macroinvertebrates (Humphrey, Bishop & Brown, 1990; Faith, Humphrey & Dostine, 1991; Humphrey & Dostine, 1994). However, this is a labour-intensive, time-consuming task, compounded by taxonomic difficulties with larval Chironomidae, the insect family that typically dominates the macroinvertebrate community. These, and related problems, have stimulated study of a more streamlined approach ('rapid assessment') to biological monitoring of water quality in Australia (Bunn, 1995).

Sampling and identification difficulties might be alleviated by taking advantage of the floating cast chironomid pupal cuticle (exuviae). When the adult within the pupal cuticle is fully developed, the pupa rises rapidly to the water surface where the pupal

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cuticle splits dorsally, allowing the emergence of the winged adult. All individuals emerge at the water surface, irrespective of their submerged larval microhabitat, leaving the cast pupal case (an exuviae) floating on the water surface. The pupal exuviae, more than any other life stage, have species-distinctive morphological features that allow taxonomic description and their incorporation into identification guides (e.g. Langton, 1991; Cranston, 1992).

The potential value of the species composition of drifting exuviae collections for monitoring water quality was shown first by Wilson and his colleagues (Wilson & McGill, 1977; McGill, Wilson & Brake, 1979; Wilson, 1979, 1987, 1989). Benefits of using pupal exuviae, apart from their more rapid and accurate identification compared with larvae (Thienemann, 1910; Coffman, 1973; Martinbee, 1979), include ease of sampling and sorting, the revelation of the presence of species with cryptic or unknown larval biologies and, above all, the presentation of an integrated picture of chironomid communities, as sampling is unselective and collects material originating from all aquatic microhabitats. To these advantages may be added the ethical and non-destructive nature of the sampling of inanimate cast cuticles.

Several unaddressed questions concerning the use of pupal exuviae for water quality monitoring are addressed directly in this study: (i) does sampling location within a stream affect numbers or species of exuviae collected, and (ii) how does temporal variation
in emergence patterns of individual species influence sampling requirements? The evidence produced is used to address indirectly a third question, namely the duration of drift of pupal exuviae. These questions appear not to have been addressed previously in a tropical context and therefore we felt it appropriate to undertake the study in northern Australian tropical lotic systems.

**Materials and methods**

Fieldwork was undertaken in the Northern Territory in March–May, 1992, in seasonally flowing portions of Magela Creek (12°35'S 132°52'E) and Rockhole Mine Creek (RMC) (13°30'S 132°30'E) (Fig. 1). These softwater streams arise in the sandstone plateau (or outliers thereof, RMC) of western Arnhem Land. Detailed descriptions of the geography, climate and major characteristics of the streams of the ARR may be found in Humphrey et al. (1990). Sampling was conducted at the end of a generally poor wet season (1991–92) in which the total rainfall was 1017 mm at Jabiru East (in the catchment of Magela Creek, Fig. 1). This compares with an annual average of 1448 mm, and was the second lowest for the 21-year record kept at Jabiru.

Magela Creek was sampled at Gauging Station (GS) 8210009, located several kilometres downstream of Ranger Uranium Mine. At the time of sampling, the creek in these lowland sections was sandy, generally shallow (< 1 m) and slow-flowing though interspersed with short, deep (~ 2 m) pools. The cross-sectional profile of the creek at the study site comprised two channels, one of which, the western channel, was sampled. Submerged parts of riparian shrubs and trees, including Pandanus aquaticus F. Muell., Barringtonia acutangula (L.) Gaedner and Melaleuca and Syzygium spp., provided aquatic substrates in addition to the sand bed and macrophyte-covered, loamy banks. Habitat heterogeneity was greatest at the edges of the creek 'proper': macrophyte beds and riparian vegetation were more extensive, and shallow, weeded pools and backwaters were plentiful. During sampling (31 March–1 April, 1992) water temperature was 29–30 °C and the wind was a strong easterly. Discharge of the creek during the study period was < 5 m³ s⁻¹.

Rockhole Mine Creek, a small second-order tributary of the upper South Alligator River, is narrow with a substrate of mainly cobbles and boulders. Monsoon rainforest lines the banks and shades the stream for much of its length. Discharge of the creek during the study period was < 151 s⁻¹. The lower sections of RMC receive an inflow of acidic, heavy-metal-rich water, draining from an adjacent mine adit. An orange-brown ferruginous 'floc' was present on the stream bed (ARRRI, 1989).

Drift samplers consisting of 65-cm-long, 250-μm-mesh tapering net attached to a vertical 25-cm² steel frame hinged to a bent steel anchor bar surrounding a 25-cm² rectangular base, were placed in the stream flow, breaking the surface to intercept drifting exuviae. Plastic screwtop containers attached to tapered apices of the nets allowed rapid removal of samples and replacement of the nets. Samples were preserved in 70% ethanol and returned to the laboratory where undamaged exuviae were removed. Representative exuviae were dehydrated in 100% isopropanol and mounted in Euparal on a microscope slide. Identification to species level followed the keys and illustrations of Cranston (1992), to which readers are directed for taxonomic information.

In the tests of spatial (cross-sectional) variability, four drift samplers were placed 4 m apart across the width of the main (western) channel of Magela Creek. Net 1 was located 2 m from the creek edge on the western side of the channel and net 4, 2.6 m from the eastern edge of the channel. Nets 1 and 2 were located closest to the western bank of the creek, whereas nets 3 and 4 were located nearest the centre of the creek, actually a bank of a sand island dividing the western and eastern channels. Water flow (1 s⁻¹) passing through each drift sampler was estimated (Current meter, Hydrological Services model OSS PC1). Each drift sampler was emptied hourly between 12.00 h and 20.00 h on 1 April 1992. The number of species and the number of exuviae of each species were recorded for each sampling interval.

Temporal distribution patterns were investigated over a 24-h period at Magela Creek site GS8210009 on 31 March 1992, and subsequently, within the polluted section of RMC on 25 May 1992, by placing one drift sampler in the stream flow. Samples were removed every 4 h with the exception of a 04.00 h sampling occasion which was missed in RMC and consequently one sample represented the period 00.00–08.00 hours. Species and exuviae per species were enumerated for each sampling period.

Hierarchical classifications and two-way analysis
were performed using the PATN package (Belbin, 1991). All data were standardized to the maximum number of individuals of a species followed by transformation using log (x + 1). The Bray–Curtis similarity index was used to form the association matrix of the nets, and the two-step procedure was applied to form the association matrix of species. In the two-step procedure, first an asymmetric matrix is generated by application of the Bray–Curtis measure only when comparing species A with species B when A is present at a site. Conversely, species B is compared with species A only when B is present. The second step involves making the asymmetric matrix symmetrical by calculating the difference between rows, thereby permitting comparison of each species on the basis of how it responds to other species (Belbin, 1991). Hierarchical associations were formed using Flexible Unweighted Pair Group Method using Arithmetic Averages (UPGMA). All other statistical analyses were performed using Statview®.

Results

Spatial distribution

In Magela Creek 969 chironomid pupal exuviae from forty-one species, were collected over the 8-h sampling period. Whilst individual samplers varied significantly in the number of exuviae collected per hour (χ² = 175.8, d.f. = 18, P = 0.001), no single net consistently collected greater numbers of exuviae over the period sampled (Fig. 2a).

No net consistently showed higher species richness per hour than any other (χ² = 7.82, d.f. = 18, P = 0.98) (Fig. 2b). The number of species in common to any two nets ranged between 15 (nets 3 + 4) and 19 (nets 1 + 2), with creek edge nets sharing sixteen species and midstream nets sharing seventeen species.

Combining all sampling periods, the number of exuviae collected per net was higher in nets 1 and 2 than in nets 3 and 4 (Table 1). In a hierarchical classification of nets based on collected species and abundance, nets 1 and 2 always grouped together, separate from a second group containing nets 3 and 4. Exuvial numbers collected were not correlated with flow through the net. Thus net 3 had a comparable flow rate to net 2 and three times the flow rate through net 1, yet collected approximately half the number of exuviae of either nets 1 or 2 alone (Table 1).

Hierarchical classification allowed recognition of seven species groups if abundance of all forty-four species was included in the analysis. However, certain species groups comprised only taxa whose rarity per se appeared responsible for their restricted occurrence. Exclusion of rare species (defined as five or fewer individuals, Table 1), which reduced the number of species involved to seventeen, produced four species groups. Mapping these groups on to net location as

<table>
<thead>
<tr>
<th>Net</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exuviae collected</td>
<td>315</td>
<td>356</td>
<td>162</td>
<td>136</td>
</tr>
<tr>
<td>Flow rate per net (l s⁻¹)</td>
<td>4.3</td>
<td>18.3</td>
<td>13.8</td>
<td>4.5</td>
</tr>
<tr>
<td>Exuviae per l s⁻¹</td>
<td>73</td>
<td>20</td>
<td>12</td>
<td>30</td>
</tr>
<tr>
<td>Species collected</td>
<td>25</td>
<td>29</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>Rare species (&lt; 5 in total)</td>
<td>8</td>
<td>11</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Common species (&gt; 5 in total)</td>
<td>17</td>
<td>18</td>
<td>16</td>
<td>15</td>
</tr>
</tbody>
</table>

Table 1 Number of exuviae and species collected in the sampling nets and flow rate at each net.
indicated by the net groups (1 + 2 vs. 3 + 4) demonstrated a significant difference in species group collected as determined by net position ($\chi^2 = 9.053, \text{d.f.} = 3, P < 0.05$).

**Diel patterns**

The multinet study in Magela Creek described above revealed different rates of collection of exuviae over time, as shown by the hourly numbers of exuviae summed for all four positions (Fig. 3a). Combined exuvial numbers show one peak at 19.00–20.00 h period (the hour after dusk) when twice as many exuviae were collected as in the previous maximum hourly sample (16.00–17.00 h). Examination of the contribution of selected taxa (Fig. 3b) showed that *Nilotanytarsus* and *Rheotanytarsus* exuviae contributed substantially to the 19.00–20.00 h hours peak, whereas unknown genus K14 species 'a' dominated exuviae collected from 15.00 to 17.00 h. The number of species represented in the hourly exuvial collections increased marginally towards evening, with the 19.00–20.00 h period having the most species. From 12.00 to 16.00 h, exuviae of twenty-seven species were collected, yet in only 2 h between 18.00 and 20.00 h, exuviae of twenty-eight species were collected, six of which occurred in no other sample.

The type of diel variation in these temporal patterns over the dates of collection is revealed by the 24-h study in Magela Creek in which 231 exuviae represented thirty-three species. The period between 08.00 and 12.00 h produced the fewest exuviae, and 16.00–20.00 h gave maximum numbers (Fig. 4a). Species richness was greatest between 00.00 and 08.00 h (Fig. 4b). The 16.00–20.00 h sample, despite its high numerical richness, contained fewer species; indeed, this sample contained fewer species than any other
period, with the exception of the 08.00–12.00 h sample which contained least exuviae.

Four-hourly samples taken over 24 h from the polluted section of Rockhole Mine Creek resulted in the collection of 1191 exuviae belonging to forty-two species. Exuvial distribution varied markedly, with the greatest number of exuviae collected between 20.00 and 00.00 h (Fig. 5a) and the least between 08.00 and 12.00 h.

Species richness in RMC (Fig. 5b) increased with numbers of exuviae collected (total species = 0.039 total exuviae + 10.15, \( F_{[1.3]} = 27.48, P = 0.014 \)). Essentially the same relationship between species and exuviae collected was found for Magela Creek on 1 April 1992 (total species = 0.039 total exuviae + 11.54, \( F_{[1.6]} = 12.23, P = 0.013 \)). Such a relationship was not evident in Magela Creek on the previous day, however, as the highest number of exuviae (57) represented only ten species. Two species (Cryptochironomus K1

and unknown genus K14 species ‘a’) accounted for forty-three of the exuviae collected (75% of total) between 16.00 and 20.00 h, masking any relationship between species richness and exuvial abundance. Removing this time period from the analysis resulted in a significant relationship between exuvial abundance and numbers of species collected (total species = 0.038 total exuviae + 0.99, \( F_{[1.3]} = 12.51, P = 0.038 \)).

**Taxon-specific patterns**

The 24-h studies in Magela Creek and RMC revealed species-specific patterns in diel abundance of exuviae in drift, although few species were very abundant. Samples consisting of many exuviae but few species were derived from populations of abundant species with restricted temporal occurrence of exuviae.


Exuviae of *Larsia albiceps* collected in both Magela Creek and RMC (Fig. 6a) reflected near-identical patterns of nocturnal abundance. In both streams, numbers of exuviae of *L. albiceps* peaked between 20.00 and 24.00 h. A similar pattern of collection was observed for *Tanytarsus ‘K2’* in Rockhole Mine Creek (Fig. 6b) with exuviae scarcely present between 08.00 and 16.00 h, but occurring in substantial numbers between 16.00 and 08.00 h, with an evident peak in the 4 h preceding 00.00 h. In nearly all periods in RMC, *Tanytarsus ‘K2’* accounted for at least 50% of the collected exuviae.

The undescribed species ‘unknown genus K14 species ‘a’* collected in Magela Creek during the 24-h study (Fig. 6c) displayed maximum numbers of exuviae in the afternoon and early evening. In the period 1600–2000 h, which contained the highest total number of all exuviae, ‘unknown genus K14 species ‘a’* represented 40% of the sample.

The numbers of exuviae of *Nilotanytarsus* sp. nov. collected in Magela Creek (Fig. 6d) were quite uniformly distributed over the 24-h period.

**Discussion**

The constant recurrence of species-specific patterns of diel periodicity of exuviae collected in samplers (e.g. Coffman, 1974; Wartinbee, 1979; Lehmann, 1979; Singh & Harrison, 1982; Boothroyd, 1988) suggests that there
indicated by the net groups (1 + 2 vs. 3 + 4) demonstrated a significant difference in species group collected as determined by net position ($\chi^2 = 9.053$, d.f. = 3, $P < 0.05$).

**Diurnal patterns**

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Fig. 6 Distributions over 24-h period. (a) *Larsia albiceps* (Johannsen) in Magela Creek and Rockhole Mine Creek (b) *Tanytarsus* ‘K2’: distribution over 24-h in Rockhole Mine Creek (c) ‘Unknown genus K14 species ‘a’’ in Magela Creek (d) *Nilotanytarsus* sp. nov. in Magela Creek.

is a relatively short period of water surface transport of exuviae. In this study, *Larsia albiceps* exuviae were nocturnal in occurrence and showed a distinctive pattern that was replicated in two very different, geographically distinct streams (Fig. 6a). This implies a fixed period of adult emergence with subsequent exuvial drift undisturbed by the vagaries of long-distance drift.

The replication in two sites of specific diel patterns such as that of *Larsia albiceps* validates our temporally unreplicated sampling. Therefore, we can discuss the spatial and diel patterns of chironomid emergence indicated by this study.

**Spatial heterogeneity**

The spatial studies undertaken in Magela Creek demonstrated that collection of most abundant species was influenced by the location of drift samplers across the stream (Table 1). This is contrary to the finding of Wilson & Bright (1973) who observed that although numbers varied, the percentage species composition of exuviae collected remained consistent between adjacent nets in the River Chew, England. They argued that this supported the use of drift samplers to collect representative samples of chironomid pupal exuviae in community studies. Our work does not support this conclusion, as net position significantly affects the probability that a species will be collected.

Differences between performances of nets (more in 1 and 2 compared with 3 and 4) was unrelated to flow rate, as adjacent nets (2 and 3) filtering similar amounts of water differed in the numbers of exuviae collected. Two explanations for this are possible. The first of these relates to the braided nature of Magela Creek in its sandy lowland sections. The creek edge ‘proper’ sites (the location of nets 1 and 2) exhibited greater microhabitat heterogeneity (see earlier site description).
that may have encouraged a greater density and diversity of chironomid larvae here, which was reflected in the exuvial composition immediately downstream. The second factor that undoubtedly contributed to the pattern was the strong wind which may have driven exuviae towards the western edge of the creek.

Variations in the numbers of chironomid exuviae collected in individual nets at sites across a stream have been observed previously (e.g. Mundie, 1971; Wilson & Bright, 1973). Our results also showed that net position definitely affected species collection. Coffman (1973) suggested that in order to measure accurately the abundance of emergence from a known area there was a demonstrated need for quantitative sampling to be carried out across the entire width of a stream. However, as Coffman suggests (personal communication), leaving a single net to collect drifting exuviae for a sufficient period of time may still provide a qualitative indication of species composition and the relative abundance of species. It would not necessarily provide an accurate indication of the variation in numbers and species which may be present: our results imply this is true even if rare species are ignored.

The rate of collection of exuviae per net per hour (Fig. 2a) showed short-term, spatially related fluctuations in exuvial numbers. In any one hour of sampling, exuviae collected by one net could dominate that hour’s total catch. For example, in Magela Creek between 16.00 and 17.00 h, net 1 collected more than twice the number of exuviae collected by the other three nets together. Such narrow spatial variations influence the species richness of samples because it is a function of sample size (i.e. the larger the sample, the greater the probability that rarer species will be collected). In monitoring applications, the effects of this variation might be overcome either by collecting exuviae from a single net, or from multiple nets placed across the stream, for a length of time necessary to optimize the numbers of species collected (e.g. until a satisfactory percentage of the total species composition was represented). For the single net placement, the sampling period would need to be, in the first instance, of sufficient duration that the collected fauna was representative of the stream cross-section. The spatial and temporal data of the present study are of the type that are required to determine such a sampling regime. However, whilst these data suffice for the seasonal conditions prevailing in the present study (low flow, late wet season), further intensive sampling would be required under different seasonal conditions (e.g. high flow, mid wet season) to determine appropriate sampling regimes.

Species accumulation

Hourly sampling revealed temporal variations in the rate of addition of further species; for example between 19.00 and 20.00 h the number of species collected in Magela Creek rose (Fig. 3b). Exuviae of some chironomid species are restricted to this period (within the 8-h period sampled) and undoubtedly exuviae of more species would have been collected over a further sampling period from 20.00 h until the morning. Species with emergence restricted to late night, dawn and early morning were not sampled. However, from these results, and in this system at this season, if one was limited to a single sampling period, then optimally this would be late afternoon, as a greater species richness would be demonstrated within a short period of time.

Water temperature, velocity and depth influence emergence (Coffman, 1973), yet there is considerable species-specific stability in diel patterns over both time and space that reflects phylogeny (Learner, Wiles & Pickering, 1990). Our observations on _Larsia albiceps_ indicated that endogenous factors were dominant over exogenous factors because exuviae peaked simultaneously at two physically different sites. From the temporal investigations into drift of exuviae in the two ARR streams, an emergence peak within the 24-h period was demonstrated (Figs 4a and 5a), as in many temperate, northern hemisphere studies (e.g. Palmén, 1955; Mundie, 1971; Coffman, 1973; Hayes & Murray, 1987).

The periodic diel patterns of exuvial collection clearly relates to the well-known periodicity of adult emergence (reviewed by Armitage, 1994). The temporal changes in species composition represented by exuvial presence therefore result from differences in the periods of emergence of the species involved. Thus, the nocturnal peak in exuvial numbers of _Larsia albiceps_ (Fig. 6a) and _Tanytarsus 'K2'_ (Fig. 6b) reflect emergence during the night. On a finer time scale, the spatial study revealed that the abundance of exuviae of some species changed within a few hours. Several different patterns of emergence can be seen amongst

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is a relatively short period of water surface transport of exuviae. In this study, _Larsia albiceps_ exuviae were nocturnal in occurrence and showed a distinctive pattern that was replicated in two very different, geographically distinct streams (Fig. 6a). This implies a fixed period of adult emergence with subsequent exuvial drift undisturbed by the vagaries of long-distance drift.

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the species recorded in this work as found in previous studies of diel periodicity of chironomids (e.g. Palmén, 1955; Danks & Oliver, 1972; Wartinbee, 1979; Lehmann, 1979; Boerger, 1981; Singh & Harrison, 1984; Vilchez-Quero & Lavandier, 1986; Hayes & Murray, 1987; & many others reviewed by Learner et al., 1990).

Diel variation in the abundance of exuviae of different species implies that high species richness need not necessarily be related to high abundances, e.g. Megela Creek in March. Temporal variations in emergence patterns result in changes in the species composition and diversity of exuviae collected over a 24-h period. Temporal variations in the species composition reflected by the exuviae must be considered when attempting to make an inventory of an entire chironomid community.

A further consideration in recommending that sampling should be carried out over a 24-h period is the evidence from other studies that there may be a seasonal shift in the peak emergence time. Coffman's (1973) observations on the influences of seasonal factors on emergence patterns over time have applicability in this context. Generally, species with a nocturnal period of emergence in summer have an earlier, often afternoon, peak of emergence in winter (e.g. Coffman, 1974; Cobo & Gonzales, 1990, 1991). Such a change has not been investigated in northern Australia, but in the River Murray in south-eastern temperate Australia, a seasonal shift has been observed (P.S. Cranston & T. Hillman, unpublished data).

For comprehensive species inventory, 24-h sampling provides substantial samples obtained with little or no habitat disturbance of a life-history stage easier to identify than any other (Cranston & Hillman, 1992). However, in practice, long periods of collection may generate excessive numbers of exuviae for survey studies with logistical and financial constraints. Alternative options that reduce the problem of sample size, yet still address the problem of temporal variability, include use of multiple sampling intervals of shorter duration, or sub-sampling from a 24-h collection.

Outstanding questions concerning the exuvial technique include the need to demonstrate the concordance of the composition of exuvial collections made simultaneously at different sites in a stream [for use in upstream 'control', downstream 'to be disturbed' BACIP-type studies (Stewart-Oaten, Murdoch & Parker, 1986)]. Furthermore, 'rare' species that may form < 1% of the exuvial catch actually may represent larval densities of up to 100 larvae m⁻², perhaps characteristic of unusual microhabitats. Thus, it remains vital to establish the degree of concordance between community structure determined by conventional sampling of larvae (e.g. Smith & Cranston, 1995), and that derived from floating pupal exuviae.

Acknowledgments

This project fulfilled part of the requirements of an Honours degree by the senior author, undertaken in the Division of Zoology and Botany, Australian National University. The facilities and assistance provided there and the stipend and facilities provided by the Office of the Supervising Scientist (now ERISS) are gratefully acknowledged.

We are particularly grateful to Drs Vince Brown, Bill Coffman, Geoff Clarke, Penny Gullan, Max Finlayson, Ron Wilson and Mike Winterbourne for suggestions and improvements on earlier drafts.

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(Manuscrit accepted 21 June 1995)