Hyporheic macroinvertebrates in riffle and pool areas of temporary streams in south eastern Australia

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Abstract

The hyporheic zone is an important refuge for invertebrates as surface water recedes in temporary streams. In this study, the structure and functional organisation of hyporheic macroinvertebrate assemblages in pool and dry riffle bed habitats of two episodic streams were compared over summer and winter. Multivariate analyses revealed macroinvertebrate assemblages differed significantly between streams, habitats and seasons. While some seasonal differences were expected, the differences between streams were not, given the similarity and proximity of the catchments, and were due to shifts in the abundance of common taxa. Distinct differences between riffle and pool habitats were evident in both the taxonomic and functional feeding group composition of the assemblages. In particular, riffle habitats contained greater numbers of taxa and individuals and a greater proportion of filter-feeding animals compared to pool habitats. Summer samples also had greater numbers of taxa and individuals and greater proportions of collector-scrapers than winter samples. The relative abundance of functional groups was similar between streams in summer but was more variable in winter. Patterns observed in the taxonomic and functional feeding group structure of the macroinvertebrate assemblages were more characteristic of perennial than episodic streams, despite the absence of regular surface flows. This could be attributed to the relatively constant hyporheic flow in these streams. We suggest that classifications of stream flow should consider hyporheic discharge (not just surface flow) as this clearly influences the stream biota.

Introduction

Temporary streams are dry or have no surface flow for large parts of the year. In these streams, flow occurs either seasonally (intermittent streams) or in response to irregular rain (episodic streams) (Bayly & Williams, 1973).

Intermittent and episodic streams in arid and semi-arid areas have been relatively well studied as researchers attempt to understand the response and recovery of biota to drought (e.g. Boulton & Suter, 1986; Davis et al., 1993; Stanley et al., 1994; Wood & Petts, 1994; see review by Boulton, 2003). However, episodic streams in higher rainfall areas, such as those in small, steep catchments, have received little attention. The small catchments of these streams are insufficient to sustain prolonged surface discharge. As a result, surface flows are limited to the period during and for a short time after rain events. As surface flow disappears, streams are often reduced to a series of isolated pools (Boulton, 2003). However, in streams with a porous substratum, pools may remain connected by subsurface flow through the hyporheic zone

(Boulton, 2003). The hyporheic zone thus becomes an important refuge (Boulton & Lake, 1988), although it may not be used by all taxa (del Rosario & Resh, 2000).

Episodic and intermittent stream environments are harsh and unpredictable. The ability to survive the cessation of flow, loss of habitat, desiccation and/or extreme physico-chemical conditions, either by behavioral or physiological adaptation, is crucial to residents of temporary streams (Boulton & Lake, 1988). These conditions therefore, shape the structure and function of communities in temporary streams.

In this study, the macroinvertebrate fauna of two episodic streams is investigated. Because these streams have little or no surface flow for most of the time, we investigated the macroinvertebrate fauna that inhabit the subsurface (hyporheic) zone below pools (containing some water) and dry riffle beds. Our predictions for this study were (1) that seasonal climatic variation would lead to changes in the hyporheic fauna, (2) differences in riffle and pool assemblages in perennial streams (e.g. Logan and Brooker, 1983) would also occur in the hyporheos, and (3) that differences between streams would be small because of the similarity and proximity of the catchments. We expected these patterns to be evident in both the taxonomic and functional feeding group structure of the macroinvertebrate assemblages.

Methods

Experimental design and sampling sites

Sassafras Creek (32° 09′ S, 151° 43′ E) and Coachwood Creek (32° 10′ S, 151° 43′ E), are located in the Karuah Hydrology Research Area (Fig. 1) in the Chichester State Forest near Dungog, New South Wales, Australia. Both streams are tributaries of the Telegherry River, which drains into the Karuah River and Pacific Ocean. The streams share similar catchment characteristics (Table 1) and have similar patterns of discharge (Fig. 2). The channels of both creeks are 2–3 m wide and both have a similar substrate dominated by gravel (2–10 mm). Under base flow conditions, there is little or no surface flow in the streams. At such times, the streams are reduced to
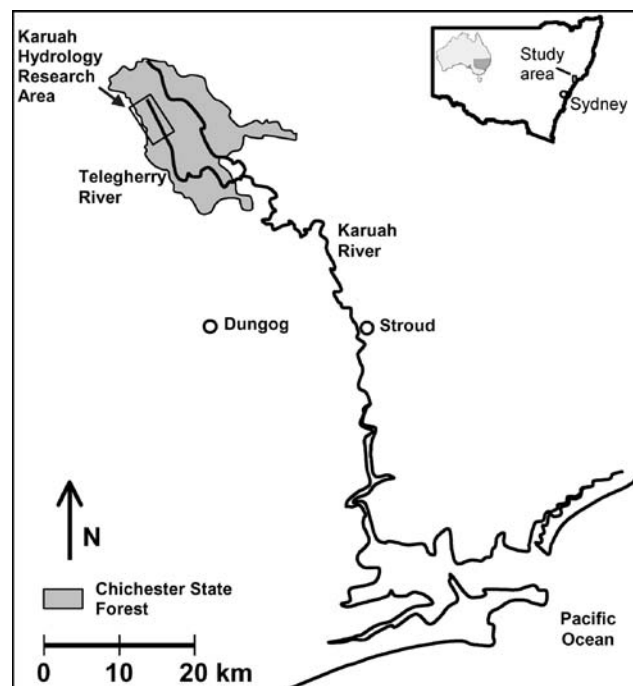

Figure 1. Location of the Karuah Hydrology Research Area.

Table 1. Characteristics of the Sassafras and Coachwood Creek catchments

	Sassafras	Coachwood
Catchment area (ha)	25.2	37.5
Stream length (m)	1100	1240
Mean Slope (°)	17.7	13.1
Max elevation (m)	773	687
Rainfall (mm)*	1114	1207
Median discharge (ML/day)*	0.02	0.07

* Data provided by NSW Forests for the period July 1990 to June 1991.

a series of pools (≤30 cm deep), connected by subterranean discharge.

The catchments were completely forested at the time of the study. The vegetation is dominated by Sydney blue gum (*Eucalyptus saligna* Smith) with some silvertop stringybark (*E. laevopinea* R. Baker) and a rainforest understorey (Cornish, 2001). The Coachwood Creek catchment was partly logged and replanted with eucalypts in 1982. Riparian buffer strips retained around Coachwood Creek during logging were sufficient to protect stream habitats (Davies & Nelson, 1994). No significant difference in water quality or quantity was detected between Coachwood and Sassafras Creeks following logging (Cornish, 2001; Cornish & Vertessy, 2001).

Sampling sites on each stream were at the bottom end of the catchment, approximately 200 m upstream of the confluence with the Telegherry

River. Each site consisted of a 100 m stream reach. Samples of hyporheic fauna were collected from pools containing water and dry riffle beds. These samples will hereafter be referred to as pool and riffle samples, respectively. Pool and dry riffle bed habitats will simply be referred to as pool and riffle habitats respectively. Both streams were sampled in summer (January 1991) and winter (June 1991) and on each occasion it had been at least 2 weeks since rain sufficient to generate surface flow had fallen. Six replicate samples were collected from each habitat at each site on each occasion.

The pool areas were sampled by haphazardly placing a quadrat (0.25 m²) in the pool. Leaf litter and other debris within the quadrat was removed by hand from the streambed surface and discarded. Thirty litres of substrate was then dug from within the quadrat to a depth of approximately 30 cm and placed in buckets. The sediments were processed in the field by washing and agitating small portions of sediment in water and collecting displaced animals and organic matter in a 1 mm mesh net. Each portion of sediment was washed three times. Organic matter and animals collected for each portion were pooled and preserved in 4% formalin.

The hyporheic fauna in the dry riffle areas was collected and processed as described above for the pool habitat. The only difference was that we first dug down 10–20 cm to the water table before 30 l of sediment was removed and processed.

In the laboratory, samples were sieved into two fractions, 200–1000 μm (fine) and >1000 μm
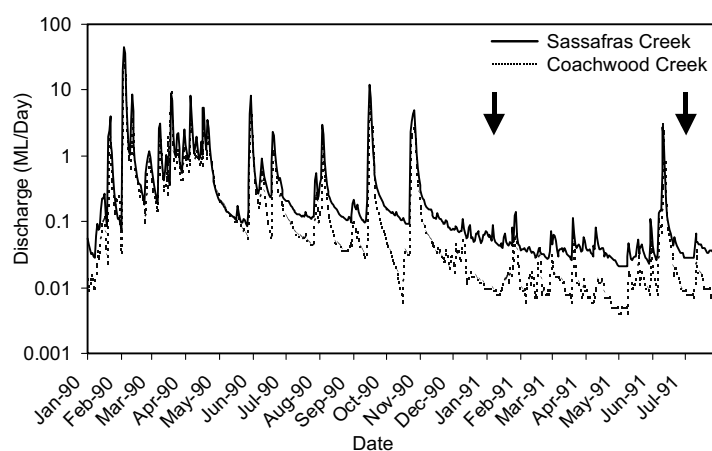

Figure 2. Daily discharge for Sassafras and Coachwood Creeks from July 1990 to July 1991. Arrows indicate sampling periods.

(coarse). The coarse fraction was completely sorted. The fine fraction was often subsampled by weight (Sebastien et al., 1988) due to the large volume of organic debris and number of organisms. The 0.2 mm mesh sieve was used so that any animals smaller than 1 mm that were retained in the sampling net were not lost during sample processing. Animals were picked from the samples with the aid of a magnifying lamp. All macroinvertebrates were identified to family or genus except for Chironomidae and Ceratopogonidae (subfamily), and Nematoda, Temnocephalidea and Oligochaeta (class).

Macroinvertebrate taxa were assigned to a functional feeding group based on the literature (Merritt & Cummins, 1984; Bunn, 1986; Chessman, 1986; Boulton & Lake, 1992a). Animals using more than one mode of food collection were treated as separate functional groups (Boulton & Lake, 1992a).

Data analysis

Macroinvertebrate assemblage data (both taxonomic structure and functional feeding group data) were analysed using non-metric multidimensional scaling (nMDS) in PRIMER (version 5.2.4, Plymouth Marine Laboratories, UK). Taxonomic structure data were square root transformed and analysed using the Bray–Curtis similarity coefficient (Clarke & Green, 1988). Functional feeding group data were not transformed and were analysed using euclidean distance. Euclidean distance was chosen for these data so as to include joint absences (which are excluded by the Bray–Curtis coefficient) in the analysis. Joint absences of particular functional feeding groups were considered important given the small and finite number of feeding groups being compared. SIMPER analysis (Clarke, 1993) was used to determine the taxa that contributed most to the differences in the macroinvertebrate assemblages between habitats, seasons and streams. RELATE analysis (Clarke et al., 1993) was used to correlate the similarity matrices from the assemblage structure and functional feeding group data. An index of multivariate dispersion (IMD) was used to compare the variability among samples collected from each season and habitat (Clarke & Warwick, 1994).

Differences in the macroinvertebrate assemblages between habitats, streams and seasons were compared using non-parametric multivariate analysis of variance (NPMANOVA) (Anderson, 2001) using the DISTLM software (Anderson, 2003). We permuted residuals under the full model because the residual mean square was the denominator for each term in the analysis. The Bray–Curtis similarity coefficient and square-root transformation were used for these analyses. Both multivariate and univariate analyses of variance had a full factorial (crossed) design with season, habitat and stream all as fixed factors. For all analyses, the significance level (α) was 0.05.

Univariate data (e.g. taxon richness) were compared using a three-way analysis of variance (ANOVA). All data were tested for homogeneity of variance using Cochran's test (Winer, 1971) and if required, data were $\ln(x + 1)$ transformed, except for proportion data which were arcsine-square root transformed *a priori*. Student–Newman–Keuls (SNK) comparisons were used to clarify any significant effects.

Results

Assemblage structure analyses

Eighty taxa were recorded across the streams, seasons and habitats. Diptera were numerically the most abundant and taxon-rich group. Ceratopogoninae, Chironominae and Tipulidae were the most abundant dipteran taxa, but the mayfly genera *Nousia* sp. and *Ulmerophlebia* sp. were similarly abundant. The total number of taxa was greatest in summer riffle samples and least in winter pool samples (Fig. 3a). The average number of taxa per sample was significantly ($p < 0.05$) greater in summer than in winter, and also significantly ($p < 0.05$) greater in riffle samples than in pool samples (Fig. 3a, Table 2). There was no significant difference ($p > 0.05$) in the number of taxa between streams (Table 2). Similarly, there was a significant difference ($p < 0.05$) in the number of individuals between seasons and habitats, but not between streams (Fig. 3b, Table 2).

The MDS ordination indicated strong differences in the macroinvertebrate assemblages in riffle and pool habitats and between times, but differ-
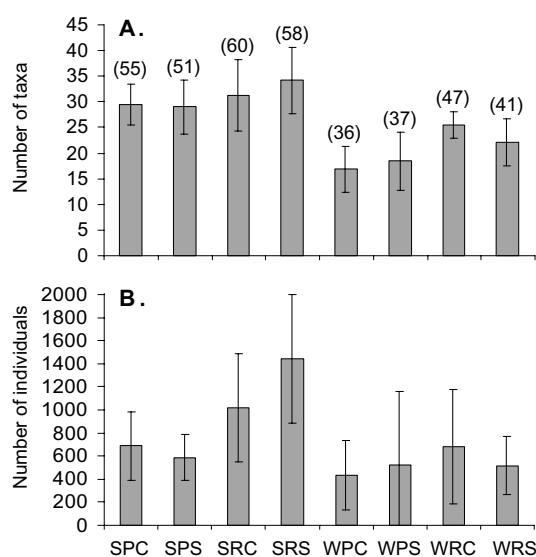
Figure 3. Average ($\pm$ SD) number of (A) Taxa and (B) Individuals in hyporheic samples from riffle and pool habitats in summer and winter. Numbers in parentheses indicate total taxa richness for that category. SPC = Summer Pool Coachwood, SPS = Summer Pool Sassafras, SRC = Summer Riffle Coachwood, SRS = Summer Riffle Sassafras, WPC = Winter Pool Coachwood, WPS = Winter Pool Sassafras, WRC = Winter Riffle Coachwood, WRS = Winter Riffle Sassafras ($n = 6$).

between riffles and pools differed in magnitude between seasons. Differences in the macroinvertebrate assemblages between streams were significant ($p < 0.05$) (Table 2).

The spatial spread of samples in Figure 4 suggests that the variability within summer samples was less than that within winter samples. This was confirmed by indices of multivariate
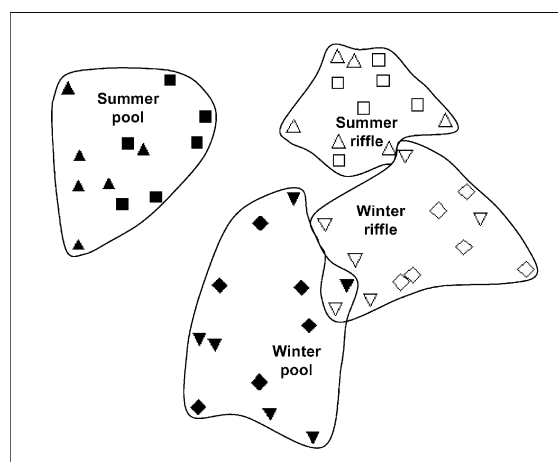

Figure 4. MDS ordination of hyporheic macroinvertebrate fauna composition. (▲) Summer Coachwood Ck, (▼) Winter Coachwood Ck, (■) Summer Sassafras Ck, (◆) Winter Sassafras Ck. Closed symbols: pool habitat, open symbols: riffle habitat. Stress: 0.15.

ences between streams were less marked (Fig. 3). A significant ($p < 0.05$) interaction between habitats and seasons (NPMANOVA, Table 2) suggests that differences in the macroinvertebrate assemblages

Table 2. F values and their associated levels of significance for three-way NPMANOVA and ANOVA

Variable	Source of Variation						
	Season (Se)	Habitat (Ha)	Stream (St)	Se*Ha	Se*St	Ha*St	Se*Ha*St
NPMANOVA							
Taxonomic structure	12.839**	14.201**	2.822**	4.859**	1.187ns	0.825ns	1.481ns
Functional feeding groups	16.648**	28.348**	5.766**	21.465**	5.689**	0.932ns	2.183ns
ANOVA							
No. of Individuals	10.309**	8.363**	0.249ns	3.620ns	0.650ns	0.294ns	2.417ns
No. of Taxa	47.204**	10.496**	0.012ns	0.799ns	0.449ns	0.078ns	1.950ns
Predators	37.748**	0.3ns	14.837**	26.312**	4.279*	1.969ns	2.063ns
Shredders	4.82*	0.003ns	0.889ns	14.214**	2.917ns	2.345ns	1.405ns
Collector-filterers	0.025ns	15.147**	5.488*	34.857**	21.247**	0.51ns	0.344ns
Collector-gatherers	0.389ns	25.317**	0.421ns	0.322ns	0.329ns	0.103ns	0.007ns
Unknown	4.875*	73.089**	3.041ns	0.462ns	0.204ns	0.781ns	0.014ns

**$p < 0.01$, ns, not significant ($p > 0.05$); degrees of freedom for all terms = 1.

Table 3. Global dispersion values for season and habitat combinations for hyporheic macroinvertebrate data

	Taxonomic structure	Functional feeding groups
Summer pool	0.917	0.766
Summer riffle	0.702	0.784
Winter pool	1.242	1.117
Winter riffle	1.139	1.333

dispersion (Table 3), which were smaller for summer samples compared to winter samples. These results also suggest that samples from riffle habitat were slightly less variable than the respective samples from the pool habitat (Table 3).

SIMPER analyses indicated that Ceratopogoninae, Tipulidae, *Nousia* sp. and Chironominae were important in determining differences between habitats (Table 4). In summer, Ceratopogoninae were more abundant in riffle habitats compared to pool habitats, but the opposite was true at the time of winter sampling (Table 4). In both seasons, Tipulidae and Chironominae were most abundant in riffle habitats, but the opposite was true for *Nousia* sp. (Table 4). In riffle habitats, Ceratopogoninae, Tipulidae, *Nousia* sp. and Chironominae were more abundant in summer than in winter (Table 4). In pool habitats, Calocidae, *Nousia* sp. and Chironominae were more abundant in summer, but Ceratopogoninae and Tipulidae were more abundant in winter (Table 4). Eusiridae and Calocidae were both more abundant in summer than winter and contributed strongly to the seasonal differences in the riffle and pool habitats respectively (Table 4).

Functional feeding group analyses

The MDS ordination of functional feeding group data revealed a similar pattern among samples as shown for the taxonomic structure data in Figure 4. In support, the similarity matrices for the taxonomic and functional feeding group structure were significantly correlated (RELATE, $\rho = 0.603$, $p = 0.001$). The functional feeding group structure of the hyporheic invertebrate assemblage varied significantly ($p < 0.05$) between habitats, seasons and streams (Table 2); there were also significant ($p < 0.05$) interactions between habitat and season, and season and stream (Table 2).

Table 4. Average abundance and contribution to between group dissimilarity of individual taxa in comparisons between riffle and pool habitats, and summer and winter (standard deviations are given in parentheses)

Taxa	Average abundance		Contribution to dissimilarity (%)
Summer	Pool	Riffle	
Tipulidae	8 (11)	166 (98)	7
Chironominae	34 (19)	269 (185)	7
Ceratopogoninae	11 (9)	180 (105)	7
Nousia sp.	278 (177)	100 (73)	5
Eusiridae	9 (15)	82 (102)	4
Winter	Pool	Riffle	
Tipulidae	19 (21)	104 (95)	8
Ceratopogoninae	180 (293)	132 (122)	7
Eusiridae	12 (25)	37 (35)	6
Ulmerophlebia sp.	35 (19)	28 (43)	5
Nousia sp.	78 (127)	36 (36)	4
Chironominae	27 (22)	31 (27)	3
Pool	Summer	Winter	
Nousia sp.	278 (177)	78 (127)	11
Ceratopogoninae	11 (9)	180 (293)	8
Calocidae	43 (54)	2 (2)	5
Tanyderidae	26 (20)	1 (3)	4
Eusiridae	9 (15)	12 (25)	3
Chironominae	34 (19)	27 (22)	2
Riffle	Summer	Winter	
Chironominae	269 (185)	31 (27)	8
Ceratopogoninae	180 (105)	132 (122)	5
Tipulidae	166 (98)	104 (95)	4
Eusiridae	82 (102)	37 (35)	4
Tanypodinae	44 (28)	6 (12)	4
Nousia sp.	100 (73)	36 (36)	4

As shown for the taxonomic structure data, the variability within habitats was much less in summer than in winter (Table 3). In contrast to the taxonomic structure data, samples from pool habitats were less variable than those from riffle habitats (Table 3).

Collector taxa (including collector-gatherers, collector-scrapers and collector-shredders) were the most numerically abundant functional group, but the predator group was the most taxon-rich.
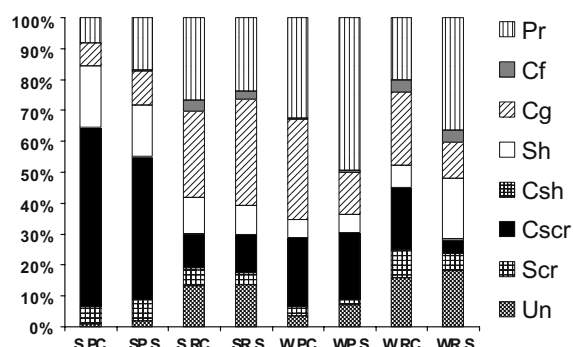
Figure 5. Average proportion of functional feeding groups in hyporheic macroinvertebrate communities based on number of individuals. Generalist and non-feeding taxa contributed < 0.6% (combined) to the total abundance and have been pooled with the Unknown group for clarity in this figure. SPC = Summer Pool Coachwood, SPS = Summer Pool Sassafras, SRC = Summer Riffle Coachwood, SRS = Summer Riffle Sassafras, WPC = Winter Pool Coachwood, WPS = Winter Pool Sassafras, WRC = Winter Riffle Coachwood, WRS = Winter Riffle Sassafras. Pr = Predator, Cf = Collector-filterer, Cg = Collector-gatherer, Sh = Shredder, Csh = Collector-shredder, Cscr = Collector-scraper, Scr = Scraper, Un-Unknown ($n = 6$).

The proportion of collector-filterer taxa in the riffle habitat was significantly greater ($p < 0.05$) than that in the pools, suggesting a distinct preference for riffle habitat (Fig. 5). The proportion of the 'unknown' taxon group was also significantly greater ($p < 0.05$) in the riffle than in the pool habitat, due largely to the abundance of Tipulidae. Non-feeding (Giordiidae) and generalist (Nematoda) groups combined contributed less than 0.6% to the total macroinvertebrate abundance and had no obvious preference for stream, habitat or season. Collector-scrapers were the dominant group in summer pool samples, largely due to the particularly high abundances of mayflies (*Nousia* sp. and *Ulmerophlebia* sp.) in these samples. The proportions of collector-gatherers and shredders were markedly different between habitats in summer; the difference was less marked in winter (Fig. 5) although differences in both seasons were significant ($p < 0.05$).

Discussion

The taxonomic and functional feeding group structure of the hyporheic macroinvertebrate assemblages varied within and between streams and over time. While some seasonal differences were expected, the differences between streams were not, particularly given the similarity and proximity of the catchments. Because of the relatively constant hyporheic flow, the streams showed characteristics of perennial streams, despite the absence of regular surface flows.

We consider the unexpected differences between streams were not due to logging as all evidence suggests the impacts of logging on Coachwood Creek were minimal. Following logging in 1982, there was no significant difference in the turbidity of Coachwood and Sassafras Creeks (Cornish, 2001), which suggests that sedimentation, a common impact associated with logging, was negligible. Up to the time of this study, there was no significant difference in the base flow or total runoff levels between the Coachwood and Sassafras Creek catchments (Cornish & Vertessy, 2001). This is further supported by the similar daily discharge during the study period (Fig. 2, Table 1).

Logging has been shown to reduce the richness and abundance of hyporheic invertebrates (Trayler & Davis, 1998) but in our study, there was no significant difference in either the richness or abundance of invertebrates between streams (Fig. 3, Table 2). SIMPER analyses (Table 4) indicated that the significant multivariate differences between streams (Table 2) were due more to differences in the abundance of common taxa than unique taxa in each stream. This suggests that the differences between streams are due to shifts in the relative abundance of some taxa rather than loss of taxa due to disturbance. It is possible that shifts in abundance are due to factors such as substrate composition or hydrological conditions (or other variables not considered in this study), which although expected to be similar, may vary subtly between catchments.

Both streams supported a rich hyporheic fauna dominated by insect taxa. This contrasts to true groundwater habitats and other hyporheic stream studies where crustaceans dominate (del Rosario & Resh, 2000; Boulton, 2001). The taxonomic richness of aquatic invertebrates in intermittent streams has been noted elsewhere in Australia (Boulton & Lake, 1988) and abroad (Williams, 1987). Boulton & Lake (1992a) attribute the

richness to the variety of habitats available in intermittent streams, and the adaptations of many species.

Significant differences between habitats (Table 2, Fig. 4) were evident in this study. Boulton & Lake (1992b) noted a considerable overlap in the surface-dwelling macroinvertebrate assemblage of riffle and pool habitats in temporary streams (using multivariate analyses), but found the overlap was less marked in the stream with more dependable flow. In our study, the riffle and pool habitats shared several common taxa, but the MDS analyses indicated a distinct separation of the habitats (Fig. 4). Thus, the streams in our study show traits more like those with more perennial than episodic flow, presumably because of the relatively constant hyporheic discharge.

Riffle habitats supported a greater abundance and richness of taxa than pool habitats. This trend is similar to that expected for perennial streams in which riffles generally support an equally (Logan & Brooker, 1983) or more diverse and abundant fauna than pools (Brown & Brussock, 1991) and contrasts to that expected for intermittent streams (Boulton & Lake, 1992a). Boulton & Lake (1992a) attributed greater abundance and richness of taxa in pools to habitat contraction and concentration of animals as water levels receded. Our study had a similar suite of taxa (at the family level) as found by Boulton & Lake (1992a), but animals were not concentrated in pool areas; presumably the hyporheic habitat provided an alternative refuge.

Ceratopogoninae, Tipulidae and Chironominae followed the general pattern of total invertebrate abundance, being more abundant in riffles than in pools. Worm-like taxa such as these are well suited to a hyporheic existence (Gibert et al., 1994). In contrast, Nousia sp. was more abundant in pools than riffles, and accounted for around 37–49% of the macroinvertebrate abundance in summer pool samples. Nousia sp. is well suited to life in intermittent streams as it has desiccation resistant eggs to help it survive stream drying (Boulton, 1989) and large gills which may be oscillated to enhance respiration in pools with low dissolved oxygen (Boulton & Lake, 1988).

The greater abundance of animals in the riffles compared to that of pools may be a consequence of the relatively harsher conditions in the surface water of the pool habitat. Pool environments are likely to have greater extremes of temperature and dissolved oxygen compared to hyporheic habitats (Boulton, 1989). The severity of extreme conditions in pools is likely to be greater in summer than in winter, and may be responsible for the greater differences in abundance between habitats in summer than in winter (Fig. 3; also evidenced by a near significant season ∗ habitat interaction for the number of individuals, $p = 0.06$). However, the severity of conditions appears not to be a significant factor in determining the abundance of all taxa because several taxa (e.g. Nousia sp., Calocidae and Chironominae) were more abundant in pools in summer than in winter. The habitat preferences and seasonal patterns of abundance are clearly taxon specific.

Summer samples contained a richer and more abundant fauna than winter samples in both streams and both habitats. This probably reflects general patterns of increased productivity in aquatic ecosystems during warmer seasons (Huryn & Wallace, 2000). It is also possible that the smaller number of animals collected in winter is a result of vertical migration deeper into the hyporheos. Marchant (1995) attributed this pattern, observed in the Acheron River (Victoria, Australia), to increased winter discharge. However, summer and winter flows were similar in Coachwood and Sassafras Creeks during our study (Fig. 2), suggesting that the vertical migration is unlikely to be contributing significantly to the seasonal difference.

The patterns in the functional feeding group structure of the macroinvertebrate assemblages were complex. Collector-gatherers and collector-scrapers dominated (numerically) the hyporheos of these streams, whereas predators were the most taxon-rich of the functional groups. Both of these patterns have been shown for intermittent (Boulton & Lake, 1992a) and perennial streams (Bunn, 1986), and temporary pools (Lake et al., 1989). The proportion of shredders in pools was greatest in summer, but the proportion of shredders in riffles was greatest in winter, which probably accounts for the significant habitat ∗ season interaction term of the ANOVA. The greater proportion of filterers in the hyporheos compared to the pool habitat is unlikely to be explained by the flow velocities at the time of sampling, but may reflect the distribution of filterers during periods of sur-

face flow. During such periods, flow velocities in the riffles are likely to be greater and better able to support filter-feeding organisms compared to velocities in the pool habitat.

The greater proportion of shredders in pools in summer may reflect the input of leaf litter, which in eucalypt forests, peaks in summer (Lake et al., 1986). However, evidence from previous studies suggests this is an unlikely causal link. In particular, Bunn (1986) found that the abundance of shredders was not synchronised with peak summer leaf fall. Furthermore, Barmuta (1988) found low correlations between surface organic matter and densities of shredders in Australian streams, and Towns (1985) noted that few taxa were utilising leaf litter in the pools of an intermittent stream. However, Smith & Lake (1993) showed that the grazing on buried leaves was greater than on leaves at the surface, suggesting that hyporheic shredders are more active than surface shredders. Eucalypt leaves require time to condition before they are palatable for macroinvertebrates (Bunn, 1996). In our study, the hyporheic shredders in winter may be capitalising on summer leaf fall (that has become conditioned and buried), but the high proportion of shredders in pools in summer remains unexplained.

The significance of the greater within-habitat variability between seasons is unknown. Increased variability in benthic communities is a symptom of stress (e.g. Warwick & Clarke, 1993; Stark et al., 2003); however, this response has not been studied in stream benthos. If the increased variability is a stress response, the observed patterns are contrary to what might be expected given greater physico-chemical stress in summer with higher water temperatures and lower dissolved oxygen expected. Hydrological conditions play a major role in explaining ecological variation in small ground-water-dominated streams (Wood et al., 2000) and it may be that low discharge prior to the winter sampling (Fig. 2) is responsible for the variability in the riffle assemblages. Clearly, further temporal and spatial sampling, and an experimental design that includes multiple sites per stream is needed to confirm these patterns and strengthen the conclusions drawn in this study.

The classifications for temporary streams by Bayly & Williams (1973) and Hansen (2001) are logically based on the degree of flow permanence but do not consider subsurface flows. It is evident from our study that such classifications should include the permanence of hyporheic flow as this may strongly influence the function, structure and dynamics of stream invertebrate communities.

Acknowledgements

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