Flow permanence affects aquatic macroinvertebrate diversity and community structure in three headwater streams in a forested catchment

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Abstract: Drying can be a common disturbance affecting macroinvertebrate communities in headwater streams. Whether intermittent and ephemeral streams have a lower diversity and (or) unique assemblage structure relative to physically similar and nearby perennial streams is still debated. We investigated changes in the diversity and assemblage composition of aquatic macroinvertebrates occupying debris dams in three headwater streams with a gradient of flow permanence (perennial, intermittent, and ephemeral) during a dry period in the austral summer of 2007 and a wet period in the spring of 2008. In the dry period, mean taxon richness and abundance in debris dams were lower in the intermittent and ephemeral streams than in the perennial stream, and the length of time without connected surface flow appeared to produce different patterns in community composition. However, during the wet period, mean taxon richness, abundance, and community composition of macroinvertebrates were very similar among the three streams. Hierarchical Bayesian modeling showed evidence for a strong effect of permanence on taxon richness, abundance, and evenness within debris dams. Taxa from the perennial stream were extremely efficient at colonizing seasonally dry nearby streams. Differences in assemblage structure between these temporary and permanent headwater streams may only arise seasonally and also appear related to flow permanence.

Résumé : La sécheresse peut être une perturbation qui affecte fréquemment les communautés de macroinvertébrés dans les cours d'eau d'amont. Il existe encore un débat à savoir si les cours d'eau temporaires et éphémères possèdent une diversité réduite et (ou) une structure de peuplement particulière par rapport aux cours d'eau permanents physiquement semblables et situés à proximité. Nous avons étudié les changements de diversité et de composition des peuplements de macroinvertébrés aquatiques dans les barrages de débris dans trois cours d'eau d'amont présentant un gradient de permanence du débit (permanent, intermittent et éphémère) durant une période de sécheresse pendant l'été austral en 2007 et une période de précipitations au printemps 2008. Durant la période sèche, la richesse moyenne en taxons et l'abondance dans les barrages de débris étaient plus basses dans les cours d'eau intermittent et éphémère que dans le permanent et la durée de la période sans écoulement continu en surface semble déterminer des patrons différents de composition de la communauté. Cependant, durant la période humide, la richesse moyenne en taxons, ainsi que l'abondance et la composition de la communauté de macroinvertébrés, sont très semblables dans les trois cours d'eau. Une modélisation hiérarchique bayésienne donne des indications d'un effet important de la permanence sur la richesse taxonomique, l'abondance et l'équitabilité dans les barrages de débris. Les taxons provenant du ruisseau permanent sont extrêmement efficaces pour coloniser les ruisseaux à sécheresse saisonnière situés à proximité. Les différences de structure de peuplement entre les cours d'eau d'amont temporaires et permanents peuvent n'exister que saisonnièrement et semblent reliées à la persistance de l'écoulement.

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Introduction

Drying of stream ecosystems is a local and regional disturbance for stream biota (Lake 2003) and a major factor influencing macroinvertebrate assemblage structure (Williams 1996). The temporary absence of surface flow is particularly common in headwater streams (springs excluded), and these streams can be highly responsive to single precipitation

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events (Richardson and Danehy 2007). Temporary waters can be subdivided into those that are dry at times of the year that are more or less predictable (intermittent) and those that contain water on an unpredictable basis (ephemeral) (Williams 1996). High heterogeneity of the physical habitat in headwater streams (Gooderham et al. 2007) and highly variable local discharge (Gomi et al. 2002) mean that single catchments often contain headwater streams that are both permanent and temporary.

Poff and Ward (1989) argued that macroinvertebrate diversity should be low under conditions of intermittency, and Vinson and Hawkins (1998) found that most studies reported lower richness in temporary streams than in permanent streams and that richness generally increased with increasing flow duration. Conversely, some studies have found taxon richness in temporary streams to exceed that of perennial streams (Dieterich and Anderson 2000). Taxa inhabiting temporary streams require one or more strategies to cope with the onset of drying and may possess functional traits that allow them to persist under such conditions. These may include short or flexible life cycles, long-lived propagules, resistance to desiccation, good dispersal ability, or behavioral adaptations such as drifting or seeking refuge (Williams 1996; Humphries and Baldwin 2003; Bêche et al. 2006). Therefore, temporary streams may harbour unique or distinctive macroinvertebrate communities that differ from nearby perennial streams (Feminella 1996; Williams 1996). Taxa without these functional traits may not persist in temporary streams or may seek refuge on a seasonal basis and return during periods of increased hydrologic connectivity through aerial or overland dispersal or drift.

We investigated aquatic macroinvertebrate communities in three nearby and physically similar headwater streams that differed primarily in their level of flow permanence to determine (*i*) whether flow permanence affects diversity, (*ii*) whether flow permanence affects community composition, and (*iii*) which macroinvertebrate taxa (or groups of taxa) show the strongest response to flow permanence. We focused on seasonal drying (over one year), but the study was undertaken during a time of severe and prolonged drought affecting streams in southeastern Australia over the past decade (Rose et al. 2008; McGowan et al. 2009).

Materials and methods

Study area and design

The study was conducted in three unnamed first-order streams in the Wallaby Creek Designated Water Supply Catchment Area (37°4′S, 145°2′E). This 9965 ha closed catchment is located at the southern end of the Hume Plateau on top of the Great Dividing Range in Victoria, Australia (Ashton 2000), and is approximately 50 km northeast of the state capital, Melbourne. In the wider catchment, annual mean rainfall was 1207 mm over the period 1995–2006 (Martin et al. 2007), and elevation ranges from 600–800 m above sea level (asl). The vegetation is dominated by an ecologically mature, eucalypt forest that encompasses a mixture of Ecological Vegetation Classes (EVCs), including restricted pockets of Cool Temperate Rainforest, Wet Forest, Damp Forest, Shrubby Foothill Forest, and Riparian Forest (Frood et al. 2001). EVCs are the recognized units of the Victorian Government vegetation classification system and represent groupings of vegetation communities based on floristic, structural, and ecological features. The catchment area is closed to the general public and is primarily managed for protection of water quality and water supply (Parks Victoria 1998). At the time of this study, the area was largely undisturbed, but there are historic disturbances (mostly occurring in the mid- to late 1800s), including bushfire, aqueduct construction, logging, human settlement, and bullock grazing (Ashton 2000).

All studied streams are tributaries of Silver Creek and are within 2 km of each other. Streams are similar with respect to width (<0.5 m), gradient (very low, no riffles present in any of the study streams), drainage area (<1.4 km^2), EVC (Riparian Forest), geology (Chesney Vale granite), and soils (rich krasnozemic loam, which has a high organic matter content in the uppermost layers) but have a range of flow permanence from perennial to ephemeral. Permanency was calculated as the proportion of site visits in which a stream was flowing. Twelve site visits were made over a period of 26 months commencing three months before the first sampling period and concluding one week after the last sampling period. The perennial stream was flowing in 10 out of 12 visits (F (flow permanence) = 0.83), the intermittent stream was flowing in 7 out of 12 visits (F = 0.58), and the ephemeral stream was flowing on only one occasion (F = 0.08).

It was not possible to obtain replicates of each stream type, as there were no other streams in this catchment that displayed a high degree of permanency. Additionally, of the small number of headwater streams in the catchment (~10), several streams were inaccessible or had been artificially modified by the construction of small aqueducts. In light of this, we recognize that our findings cannot provide generalizations about patterns and processes in all temporary streams, but nonetheless, they can provide an insight into the patterns and processes occurring in this catchment, which is an important example of a mature and largely undisturbed forest with high biological integrity that would have been more widespread in the past.

Regional drying and drought history (1961–2008)

Ecological patterns and processes in streams (e.g., diversity patterns or life history strategies) may be correlated with long-term flow patterns (Lytle and Poff 2004) but also confounded by drying and drought events occurring at smaller temporal or spatial scales (Bêche and Resh 2007). To assess how representative flow conditions were during our study, we examined several decades (1961–2008) of daily stream flow data from a gauging station approximately 10 km northeast of the study site on King Parrot Creek at Flowerdale (station no. 405231) to determine whether the severity of the current drought was greater than in previous periods of drying or drought in the past half century. We calculated the cumulative streamflow deviation (in millimetres) for any run of consecutive wet or dry years. When there was a transition from an above-average or below-average streamflow year, we reset the deviation to zero.

Macroinvertebrate sampling

All study streams were located within the Riparian Forest

EVC. The structure of this EVC is generally open forest to tall woodland with a layered understory comprising a range of eucalypt species. The tall *Eucalyptus viminalis* is usually the dominant species and occurs with *Eucalyptus melliodora*, *Eucalyptus obliqua*, *Eucalyptus radiata* ssp. *radiata*, and *Eucalyptus ovata*. The dominance of eucalypt species beside these streams has considerable influence on in-stream habitat because, unlike many streams in North America and Europe, eucalypt species are not deciduous but have continuous leaf litter inputs throughout the year (with a peak in summer) and much slower rates of leaf breakdown (Pozo et al. 1997). This means that features such as leaf packs and debris dams are common habitats in temperate Australia streams and contribute significantly to the structural heterogeneity of low-gradient sand-bottom reaches. This is particularly true in small headwater streams where there is a high ratio of structural component size to stream width due to lack of stream competence to move material that has fallen onto the bed and banks (Gooderham et al. 2007).

Initial field observations of all headwater streams in the study area revealed only two dominant habitat types, sandy benthic areas and debris dams. We followed the definition of debris dams of Smock et al. (1989, p. 765) as "any wood > 5 cm in diameter in contact with sediment and spanning at least one-fourth of the channel. Also included were root masses from living riparian vegetation." The debris dams in the study streams generally were characterized by one larger piece of wood causing a partial obstruction of the channel and an accumulation of smaller pieces of wood, twigs, and leaves. Subsequent work for another study in the Silver Creek catchment quantified the previously observed dominance of the debris dam habitat type in the study area through records of the percentage of streambed in 30 m reaches occupied by debris dam habitats. The percentage of reach length occupied by debris dam habitats ranged from 33% to 53% in 2007 and from 13% to 73% in 2008 (A. Clarke, unpublished data). This study therefore focused on macroinvertebrate assemblages in debris dam habitats, and the findings will be relevant only to this particular habitat type. It is likely that the effects of flow permanence on macroinvertebrate assemblages in sandy benthic habitats will be greater than those in debris dams because these sections of the stream are the first to dry out when flow ceases and have little organic matter that can retain moisture. Debris dams also have long been considered to provide important habitat for macroinvertebrates and are the dominant source of energy in heavily forested streams (Bilby and Likens 1980; Smock et al. 1989).

Macroinvertebrates were sampled from debris dam habitats twice, once during the austral summer low-flow period (January 2007) and again during the spring high-flow period (November 2008). During the high-flow period, all sites had connected surface flow. During the dry period, the ephemeral stream had no surface water present and the streambed was dry although damp just below the surface. The intermittent stream had very little surface water present, although the streambed was slightly damp. The perennial stream had connected surface flow.

Ten debris dams were selected randomly from a 30 m reach in each stream and sampled by collecting one small handful of organic matter from the centre of the debris dam and preserving all material in 70% ethanol. Although these samples were not strictly quantitative, the use of this sampling technique in the catchment for other related investigations revealed no relationship between taxa richness and ash-free dry weight (AFDW, grams) of organic material collected in one handful (R^2 = 0.10 during 2007 and R^2 = 0.03 during 2008), despite some inevitable variation in the amount of organic material collected in one handful (4.71–32.47 g AFDW in 2007 and 3.82–31.98 g AFDW in 2008). Samples were washed over a 300 μm sieve in the laboratory, and insects were identified to the lowest possible taxonomic resolution (usually genus). Diptera were identified to family, except Chironomidae, which were identified to subfamily. Oligochaeta and Nematoda were not identified further. Terrestrial taxa found in the samples were not included in any of the analyses presented here.

Data analysis

We plotted mean taxon richness and mean abundance for the three streams during both dry and wet periods. The distribution of abundance (evenness) among taxa was graphically explored using rank-abundance plots in which one axis of the curve represents the taxon rank in a community and the other represents taxon abundance (Tokeshi 1990), which was plotted on a log scale.

Given that we had three reaches of differing permanence over two flow seasons, we used a regression approach to analyze the response variables. The model was

$$(1) \qquad L(\mu_{ik(j)}) = \alpha_1 + \alpha_2\delta_i + (\alpha_3 + \alpha_4\delta_i)P_j + b_j$$

where δ_i equals 0 for dry and 1 for wet. $L(\,)$ is a link function appropriate for measured values, $Y_{ik(j)}$, where the subscript i denotes season (0 = dry, 1 = wet), j is reach (1, …, 3), and k is "replicate" debris dam within reach (N = 10). Note that the k subscripts are nested within the corresponding reaches j (hence $k(j)$). α_1 is the general intercept; α_2 is the effect of season, which is measured as a deviation from the dry season occurring in the wet season (hence the δ); α_3 is the regression parameter relating the response variable to the measure of permanence (F_j) in the dry season; and α_4 is an interaction that modifies the response–permanence relationship for the wet season. F_j is a continuous variable and was not selected a priori as a "factor." The bs are reach-specific random effects having zero mean and common variance σ_b^2 (these are used because of the "repeated measures" for each reach).

Different generalized linear models were developed to analyze patterns of richness (L = Poisson, deemed appropriate for nonnegative counts data), total abundance (L = lognormal scale), and evenness (L = Beta distribution) in the three reaches. Evenness was calculated using the preferred (Jost 2007) Shannon's equitability ($E(H)$), where $E(H)$ has a value between 0 and 1, with 1 indicating complete evenness (i.e., all taxa having equal abundances). Adequacy of model fit was assessed using Bayesian posterior predictive assessment (Gelman et al. 1996), which has been regarded as "Bayesian P values." "Importance" of the parameters (i.e., do these differ substantially from zero?) was assessed using posterior probability distributions and odds ratios (ORs). ORs are ratios of posterior to prior odds and measure how much the data change our initial expectations. ORs > 10 are strong evidence supporting one hypothesis over another, and 3 < OR < 10 signals positive evidence (Kass and Raftery 1995). For negative parameters, inverse ORs hold (i.e., ORs < 1/10 are strong evidence). Inferences in Results use OR ≥ 10 (or ≤ 1/10) as the threshold.

WinBUGS Bayesian modeling software was used (Spiegelhalter et al. 2003). Model runs had "burns-in" of 10 000 and parameter samples of 10 000. Usual appraisals of model convergence were employed (Smith 2006). More complete specifications of the Bayesian modelling are presented in the online Supplementary materials.[2]

Multivariate analysis exploring changes in community composition was undertaken using nonmetric multidimensional scaling (NMDS) for untransformed taxon abundance data. The ordination solution was generated from 100 random starts and is displayed in two dimensions due to low stress for this dimensionality (<0.15). The use of multivariate analysis of variance (MANOVA) or analysis of similarity (ANOSIM) to assess differences between groups was not undertaken because of the lack of true replicates (i.e., samples were subsamples at the reach scale). Centroids and 90% confidence ellipses were plotted for each group of 10 subsamples (R, version 2.4.1, http://www.r-project.org/). Effects of permanence on community composition were determined by visual inspection of the ordination plot.

Results

Regional drying and drought history (1961–2008)

The current period of drying in the region (2001–2008) was the longest period of consecutive years that streamflow has been below average since 1961 (Fig. 1). Although the cumulative streamflow deviation was large (in a negative direction), the deviation from any single year in the period 2001–2008 was not substantially greater than other negative annual streamflow deviations that have occurred in the past half century. In particular, the annual streamflow deviation in 1982 was very large (i.e., far below average) and annual streamflow deviations in 1962, 1967, and 1980 were also large.

Aquatic macroinvertebrate diversity in temporary vs. permanent streams

Seventy-four aquatic taxa (21 557 individuals) were found in the three headwater streams over the two sampling periods. Diptera was the most diverse order, with 11 families (Athericidae, Empididae, Ceratopogonidae, Chironomidae, Culicidae, Dixidae, Tipulidae, Psychodidae, Stratiomyidae, Simuliidae, and the rare Tanyderidae). Ephemeroptera, Plecoptera, and Trichoptera (EPT) collectively made up 35% of the total number of taxa recorded: 10 of the 25 freshwater Trichoptera families known to occur in Australia (13 genera), all four Plecoptera families known to occur in Australia (eight genera), but only two of the seven Ephemeroptera families (five genera).

Taxonomic richness

Using the OR criterion, all parameters differed from 0 with high certainty (all ORs infinite) (Table 1). Mean random effects for reaches (b_j) differed little from 0 when compared with their standard deviations (SDs) of estimates (all <10%). Model results are consistent with the data presented in Fig. 2*a*. Dry-season richness increased substantially with degree of permanence (from a mean of 4.9 (F = 0.08) to 26.2 (F = 0.83)). Wet-season richness was little related to the stream's permanence (Fig. 2*a*), which is consistent with the interaction effect for wet season as a function of permanence, which essentially eliminated the permanence relationship ($\alpha_3 + \alpha_4 = 2.28 + -2.29 = -0.01$).

Pooling all samples for each stream over the two sampling times revealed increasing total richness with degree of stream permanence: 42 (F = 0.08), 54 (F = 0.58), and 63 (F = 0.83).

Total abundance of aquatic macroinvertebrates

All parameters differed substantially from 0 (all ORs > 16; Table 1). Stream permanence had a marked positive effect on numbers of individuals in the dry season, increasing on average from about 12 individuals (P = 0.08) to 454 (P = 0.83) (Fig. 2*b*). Permanence depressed numbers for the wet-season data given a net difference of $\alpha_3 + \alpha_4 = (4.8–5.9) = –1.1$ in the model parameters. Thus, the model supports the evident interaction in which the wet-season total abundance decreased with flow permanence from an average of about 663 individuals (P = 0.08) to 347 (P = 0.83) (Fig. 2*b*). Mean random effects for reaches again were small, differing little from 0 when compared with their SDs of estimate and also absolutely (<0.09).

Rank-abundance plots showed that during the dry period, evenness was not markedly different among the three streams, although the plots appear quite different because of the reduced abundance and taxon richness in the two more-temporary streams (Fig. 3*a*). During the wet period, the slope of the three plots was very similar, indicating that evenness, abundance, and taxon richness were all similar among the three streams (Fig. 3*b*).

Evenness of abundances among taxa

All parameters differed greatly from 0 (all ORs > 32, Table 1). The baseline dry-season average evenness exclusive of permanence effects was 0.90. When the latter were included, fitted means (actual means in parentheses) for the permanent, intermittent, and ephemeral streams were 0.71 (0.66), 0.78 (0.79), and 0.89 (0.80), respectively. Thus, evenness decreased slightly with permanence for the dry season. The wet-season effect (exclusive of the permanence effect) reduced the baseline value to 0.47. The interaction term changed the regression coefficient for the permanence effect from –1.6 to +1.4 for the wet season. The fitted (actual) means for perennial, intermittent, and ephemeral streams were 0.74 (0.74), 0.67 (0.60), and 0.50 (0.57), respectively. Hence, evenness increased with permanence for the wet season. Mean random effects for reaches differed little from 0 when compared with their SDs of estimate. These results are supported by the rank abundance curves for each stream during the wet and dry periods, which graphically display patterns of evenness (Fig. 3).

[2] Supplementary materials for this article are available on the journal Web site (http:/cjfas.nrc.ca).

Fig. 1. Regional drying and drought history in the region represented by cumulative annual streamflow deviation for the period 1961–2008.

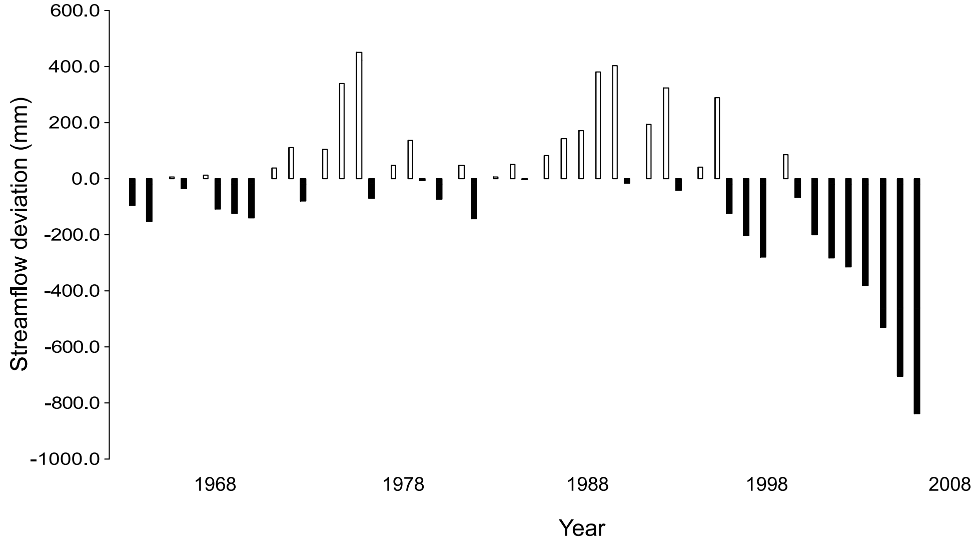


Table 1. Model parameter estimates (mean ± standard deviation, SD) for the analyses of species richness, abundance, and evenness.

Variable	Link (error)	α_1	α_2	α_3	α_4	PPP*
Richness	Log_e (Poisson)	1.4±0.3	1.8±0.2	2.4±0.6	–2.29±0.2	0.88
Abundance	Log_e (lognormal)	1.9±0.5	4.7±0.3	4.8±1.0	–5.9±0.5	0.78
Evenness	Logit (Beta)	2.2±0.5	–2.3±0.3	–1.6±1.0	3.0±0.4	0.69

*PPP, posterior predictive probability; values < 0.05 or > 0.95 suggest a poor model fit to the data.

Fig. 2. (*a*) Mean taxon richness and (*b*) mean abundance, with standard error bars in the three headwater streams during wet (solid diamonds) and dry (open diamonds) periods.

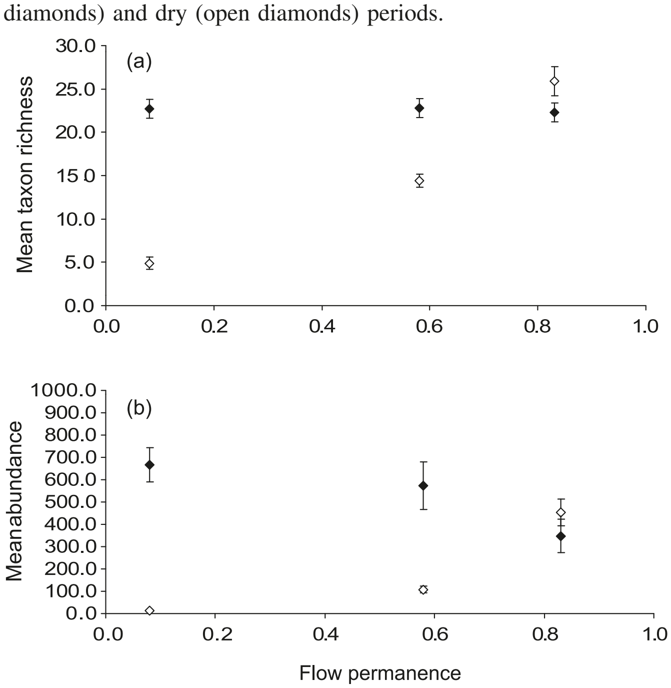
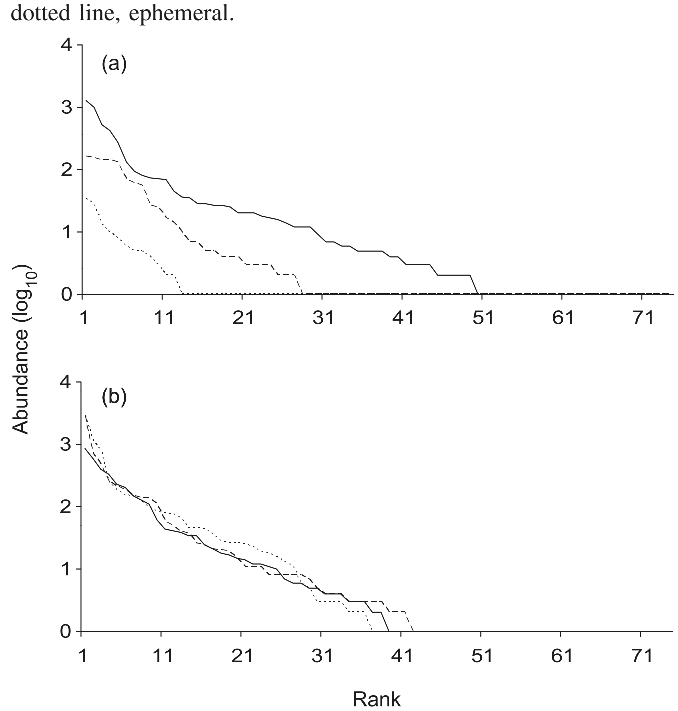


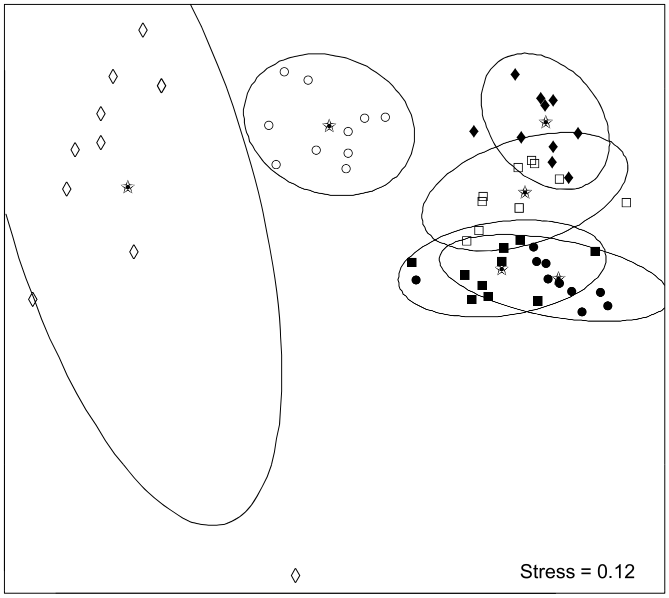
Fig. 3. Rank abundance curves (log-transformed) for (*a*) dry and (*b*) wet periods: solid line, perennial; broken line, intermittent; dotted line, ephemeral.



Aquatic macroinvertebrate assemblage structure in temporary vs. permanent streams

In the dry period, each stream had a distinct macroinvertebrate assemblage occupying debris dams with a clear grouping of samples separated by the difference in flow permanence for each stream (Fig. 4). The taxon list for each stream showed that during the dry period, the two temporary

Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination of 60 samples from the three headwater streams during wet (solid symbols) and the dry (open symbols) periods: squares, perennial; circles, intermittent; diamonds, ephemeral.



streams had 12 taxa that did not occur in the perennial stream. The other taxa present in the two temporary streams were a nested subset of the taxa present in the perennial stream at the same time.

However, during the wet period, macroinvertebrate assemblages from each stream were very similar. Therefore, there is limited evidence from this study to support the idea that temporary streams in our region permanently harbour unique or distinctive macroinvertebrate communities associated with debris dams. Ordination based on presence–absence data revealed similar patterns (not shown).

Taxonomic responses to flow permanence in headwater streams

The Orthocladiinae (Diptera) showed the weakest response to flow permanence because this taxon was the most widely distributed across all streams and both sampling periods, absent from only three samples in the ephemeral stream during the dry period. The EPT group showed a very strong negative response to drying stress because sampling during the dry period in the intermittent stream found no taxa from the Plecoptera or Ephemeroptera and only three genera from the Trichoptera. Sampling in the ephemeral stream during this period revealed the absence of any genera from the EPT group. However, subsequent sampling of these streams during the wet period showed that eight genera of Plecoptera, three genera of Ephemeroptera, and four other genera of Trichoptera had colonized the intermittent stream, although one Trichopteran genus (*Lectrides* sp.) that had been present during the dry period was not recorded during the wet period. In the ephemeral stream, sampling during the wet period revealed that one genus of Plecoptera, two genera of Ephemeroptera, and two genera of Trichoptera had colonized the previously dry stream.

Of the 12 taxa found exclusively in the two temporary streams during the dry period, five were coleopterans (*Notohydrus* sp. (Hydrophilidae), *Hydraena* sp. (Hydraenidae), *Sclerocyphon* sp. (Psephenidae), Hydrochidae, and Curculionidae). Two dipteran taxa that appeared to be exclusively associated with driest conditions were in the families Ceratopogonidae (Forcipomyiinae) and Stratiomyidae as these were only recorded in the temporary streams and only during the dry period.

Discussion

Regional drying and drought history (1961–2008)

The streamflow deviation data indicate that the current drought represents the longest period of consecutive years of below-average streamflow in the study region since at least 1961, which is consistent with the widely reported descriptions of the prolonged nature of the drought that is currently affecting southeastern Australia (Pezza et al. 2008; Rose et al. 2008; McGowan et al. 2009). However, the occurrence of large (negative) annual streamflow deviations in earlier parts of the record (e.g., 1962, 1967, 1980, and 1982) means that macroinvertebrate communities in the region have previously been exposed to the pressure of highly variable and well below average streamflow. We might infer that macroinvertebrates in these systems may have evolved and maintained adaptations (e.g., life history, morphological, and behavioral) to cope with this highly variable flow regime, which is punctuated by drying and drought. Thus, differences in patterns of macroinvertebrate diversity between permanent and more temporary streams are likely to reflect structuring of communities in response to long-term patterns in hydrologic variability rather than just short-term responses to the current supraseasonal drought. However, if the current period of drought continues, the cumulative streamflow deviation in the region may become so severe that the hydrologic regime of some headwater streams will shift so that previously perennial streams become ephemeral and so on with consequent effects on the biota.

Effect of flow permanence on aquatic macroinvertebrate diversity

Stream ecologists have predicted that macroinvertebrate diversity should be low under conditions of intermittency because loss of hydrologic connectivity constrains exchanges of matter, energy, and organisms between patches (Poff and Ward 1989; Ward et al. 1999). This prediction may be less applicable to regions with naturally high levels of stream intermittency because periods of seasonal drying occur with a high level of predictability, allowing for development of adaptations to cope with the seasonal reduction or absence of flow. Several studies of macroinvertebrate responses to predictable, seasonal drying in Mediterranean-climate streams in regions such as California and Spain have found that intermittent and ephemeral streams do not always harbour a lower macroinvertebrate diversity than their perennial counterparts (Bonada et al. 2006, 2007). A study in Oregon found that a temporary headwater contained 125 species compared with only 100 species in a nearby permanent headwater (Dieterich and Anderson 2000).

In this study, we investigated the effects of flow permanence on macroinvertebrate assemblages in debris dam habitats and found that summer taxon richness was lower in the two temporary streams than in the permanent stream, but taxon richness in the intermittent stream was much higher than in the ephemeral stream. Taxon richness was similar in all streams during the wet period, which suggests that although many taxa might be seasonally extirpated or move from the channel into nearby refugia, they are extremely effective at recolonizing temporary streams upon resumption of flow.

The permanent stream had higher total (pooling sampling periods) taxon richness than either of the temporary streams, indicating that during the dry period, taxa are lost from the temporary streams but very few "new" taxa more tolerant of the dry conditions arrive to take their place. The ephemeral stream, which experienced the longest period without connected surface flow, had much lower taxon richness than the intermittent stream, and so annual taxon richness appears to be positively correlated with flow permanence. Similarly, Dieterich and Anderson (2000) found that although temporary streams may harbour as many or more taxa than nearby permanent streams, species richness was lowest at the most ephemeral sites. Boulton and Lake (1992) compared macroinvertebrate assemblages between sites on two intermittent rivers in southern Australia and also found that species richness generally increased with longer flow duration.

Evenness was relatively high in all three streams, even during the dry period when the temporary streams contained few taxa. This pattern was driven by many taxa in the dry period occurring only as one or two individuals and no single taxon occurred in exceptionally high abundances. This result is consistent with a study of headwater streams by Heino et al. (2008), who found high evenness in small streams and inferred that this phenomenon might reflect so called "small stream effects" where abundances are more evenly divided among species because of inherent heterogeneity and variability in the conditions of small headwater streams.

Effect of flow permanence on macroinvertebrate assemblage structure

Towns (1985) suggested that fauna inhabiting temporary waters are highly specialized with unique life history adaptations to intermittent flow. However, several studies have reported only slight differences in the faunal composition of permanent and intermittent sites (Boulton and Lake 1992; Feminella 1996; Price et al. 2003). We found that although there were seasonal differences in assemblage structure, patterns were mostly driven by loss of taxa and there was a high degree of faunal overlap between the three sites once flow resumed. Only 12 taxa (16%) were found exclusively in the temporary streams. These findings suggest that the temporary streams in our study region do not contain a significant suite of specialist taxon adapted to intermittent flow and that for the many taxa that are seasonally extirpated from the temporary streams, recolonization from populations in the permanent stream is likely to occur in the wetter months.

Taxon responses to flow permanence in headwater streams

Orthocladiinae appeared to be the best adapted to a range of flow permanence, which is not surprising as they are known to occupy the widest range of habitats of all the Chironomidae (Oliver 1971). A substantial number of species from the Orthocladiinae are multivoltine with continuous recruitment for much of the year (Pinder 1986).

Of the EPT group, the Trichoptera appeared to have the greatest ability to withstand or recover from drying stress in our study, although their ability to survive in temporary streams during the dry period seemed limited to genera known to build a case or retreat of some type (*Caenota* sp., *Lectrides* sp. and genus Calocidae B). Larval case building by caddisfly taxa has previously been suggested as a form of resistance to drying or drought (Zamora-Munoz and Svensson 1996). Although eight genera of stoneflies colonized the intermittent stream once flow had resumed, only one genus was found to have colonized the ephemeral stream during the wet period, *Dinotoperla* sp. (see also Boulton and Lake (1992)).

Most aquatic Coleoptera and the Tipulidae (Diptera) pupate out of the stream channel in cells formed by damp soil and moss, a habitat that is prevalent when flow recedes or ceases (Cummins and Wilzbach 2005). This may explain the prevalence of coleopteran and dipteran taxon found in the temporary streams in our study (Boulton and Lake 1992). Price et al. (2003) found that intermittent and ephemeral streams tended to be richer in dipteran taxon, and Bêche et al. (2006) found that during the dry season, density of air-breathing macroinvertebrates with strong body armouring such as the Coleoptera increased. The success of dipteran taxa in colonizing temporary habitats is likely to be due to a suite of functional and life history traits that prove advantageous such as short life cycles, simple bodies, survival in a wide range of habitats, and high dispersal ability of adult stages (Oliver 1971; Pinder 1986).

Implications for management of intermittent headwater stream systems

Periods of drying and drought are an integral part of the Australian climate (Rose et al. 2008), and indigenous macroinvertebrate communities from such Mediterranean-type climates are likely to be adapted to naturally occurring low-flow or zero-flow conditions (Boulton 2003; Lake 2003; McMahon and Finlayson 2003) or have highly efficient mechanisms for recolonization when flow resumes, as suggested by the findings of our study. However, taxa may not be as resilient or resistant to the interactive effects of predictable seasonal drying and longer-term supraseasonal drought (Lake 2003) such as the current severe and prolonged drought occurring in southeastern Australia (Rose et al. 2008; McGowan et al. 2009). Analysis of long-term rainfall records in southeastern Australia (1910–2005) showed a decline in most rainfall indices, particularly since the 1950s when total autumnal rainfall began decreasing by approximately 11 mm per decade, contributing to a significant decrease in total annual rainfall of approximately 20 mm per decade (Gallant et al. 2007). Further intensifying the effects of natural intermittency of some headwater streams are increasing levels of water extraction from unregulated rivers and the future effects of climate change that are predicted to be substantial for upland streams (Durance and Ormerod 2007).

Managing freshwater systems in the face of growing demand for water resources and the predicted impacts of climate change will be challenging, but it is critical that actions to protect freshwater biodiversity be taken (Dudgeon et al. 2005). Although intermittent streams may harbour a lower diversity than their perennial counterparts during some parts of the year, it appears from our study that intermittent headwater streams may regain their full complement of taxa upon resumption of flow. However, these findings are limited to macroinvertebrate assemblages in debris dam habitats, and the effect of flow permanence on macroinvertebrate assemblages in sandy, benthic areas may be more pronounced due to the rapid onset of drying in these sections of stream once flow ceases. The permanent stream in our study may have provided a critical oversummering refuge for many taxa; Boulton (1989) highlighted the importance of such streams as sources of recolonization. In this system, taxa from the perennial stream appear extremely efficient at colonizing the seasonally dry, temporary streams. When planning for reserve design or disturbance mitigation, it may be important to ensure that intermittent headwater streams are not disconnected from nearby permanent streams by blocking or fragmenting aerial and upstream migration pathways. This study also highlighted the potential loss of diversity, at least seasonally, that may occur as the local and regional climates become drier and previously perennial and intermittent streams shift towards more ephemeral flow regimes.

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