

Leaf litter decomposition and utilisation by macroinvertebrates in a central Victorian river in Australia

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Abstract

This study suggested that long-term persistence of willow roots can provide a positive effect on aquatic communities until the new native vegetation cover establishes. Leaf type has no significant influence over taxa richness; however their availability and persistence in the system has a significant effect on macroinvertebrate abundance in these streams. A combination of *Phragmites* reeds with *Leptospermum* and *Callistemon* shrubs in revegetation programs will ensure a persistent supply of leaf litter to macroinvertebrate communities in these streams thus should be retained until native canopy cover eg. *Eucalyptus* spp. is re-established. (*The Victorian Naturalist* 127 (4) 2010, 104–114)

Keywords: Leaf litter, exotic, willow, *Phragmites*, *Eucalyptus*

Introduction

The landscapes of central Victoria are largely volcanic in origin and highly modified through clearing for agriculture. Exotic willows *Salix fragilis* have successfully colonised and become naturalised taxa in many riverbanks in these landscapes (Ladson *et al.* 1997). It is estimated that willows have spread across approximately 30 000 km of the 68 000 km river frontage in Victoria (Ladson *et al.* 1997). Willows are considered a Weed of National Significance in Australia and willow management strategies recommend their removal as the preferred and generally only management option (National Weeds Strategy Executive Committee 2000). Revegetation is encouraged following removal. Therefore, the sequence of riparian changes is: willow lined streams → open streams → native vegetation lined streams. Decades will be required to achieve a canopy cover of native species equivalent to the preceding willow cover. *Phragmites australis* is one of the common native reeds of open streams and wetlands worldwide (Sainty and Jacobs 1981). There is increasing evidence to suggest that riparian disturbance, alteration of natural hydrologic regime, soil salinisation and increased sedimentation favour invasion and continued spread of *Phragmites* in lotic systems (McNabb and Batterson 1991; Saltonstall 2003). Invasion of *Phragmites* in open reaches with low riparian vegetation cover has been observed in many river catchments in Victoria (CALP 1997).

Redistribution of *Phragmites* in rivers managed by irrigation has been observed in south-eastern Australia (Roberts 2000). However, quantitative studies on the effects of this on river health and aquatic biodiversity are limited (Roberts 2000). In addition, *Phragmites* is sometimes used during revegetation, increasing the likelihood it will be a coloniser following willow removal. Native shrubs such as *Leptospermum* spp. and *Callistemon* spp. are common in many temperate Australian streams and are a significant component in the riparian zone of streams where willows are removed.

A key difference between willows and the native Australian riparian vegetation is the timing and quality of leaf fall (Pidgeon and Cairns 1981; Yeates 1994; Frankenberg 1995). It has been argued that a change in the timing or quality of litter fall resulting from a change in riparian vegetation phenology would affect stream energetics and be reflected in the composition of stream biota (Campbell 1993; Schulze and Walker 1997). These were attributed to the differences in breakdown rates, palatability and chemical composition of leaf types (Schulze and Walker 1997; Irons *et al.* 1988; Campbell and Fuchshuber 1995). A study by Yeates and Barmuta (1999) supported the idea that willow leaves were more palatable and preferred by macroinvertebrates than the leaves of Manna Gum *Eucalyptus vimi-*

nal. However, the availability of leaf litter was limited during some seasons in willow-lined streams because of the seasonality of litter-fall pattern of willows. It has been found that small streams that rely entirely on willows for their leaf inputs might run short of coarse particulate food matter during winter (Pidgeon and Cairns 1981; Cummins *et al.* 1989). Some authors suggest that the greater palatability of willow leaves compared to native leaves causes a short term boost of macroinvertebrates under willow lined channels during autumn when willows shed most of their leaves (Yeates and Barmuta 1999). *Phragmites australis* is lightly grazed in the living state, and the greatest part of the primary production ultimately enters detrital systems (Imhof 1973). Mathews and Kowalczewski (1969) and Thomas (1970) reported a faster decomposition rate for tree leaves than emergent macrophytes such as *Phragmites*. No information exists on decomposition and macroinvertebrate use of leaves of common shrubs such as *Leptospermum* and *Callistemon* spp. However, these leaves are sclerophyllous and frequently aromatic (Walsh and Entwisle 1996; Lis-Balchin *et al.* 2000), suggesting a high content of lignin and herbivore deterrents. These compounds may act as deterrents for macroinvertebrate and fungal activity leading to the slower decomposition of leaves.

Another important habitat structure remaining in streams from which willows have been removed are willow root mats, since stumps of willows are often left after removing the upper parts. Root decomposition is an often ignored, yet potentially important regulator of carbon and nutrient cycling in terrestrial systems (Ostertag and Hobbie 1999). It has been observed that willow roots remain in streams long after the trees have been cut down. This suggests that willow roots have slow decomposition rates but empirical evidence to support this observation is scant. It appears the effect of leaf litter input from such exotic and native vegetation successional processes may have important influences on the macroinvertebrate communities and energy transfer process of these streams. However, no comprehensive study has been carried out to investigate the effects of such vegetation changes on leaf litter availability and macroinvertebrate communities in Australia. Therefore, decomposition rates and macroinvertebrate colonisation of leaves and roots of exotic willow, *Salix fragilis*, leaves of native shrub species *Leptospermum lanigerum* and *Callistemon paludosus*, a native riparian woody tree the River Red Gum *Eucalyptus*

camaldulensis and native reed *Phragmites australis* were investigated. The outcome of this study will provide important information for management of exotic species and revegetation programs.

Study site

Moorabool River catchment covers approximately 148 000 ha. Over 75% of the catchment is used for agriculture, either grazing or broad-acre cropping (Department of Water Resources Victoria 1990). There are three areas of mixed-species forest in the middle reaches of the Moorabool River. Willows are commonly distributed along the riparian zone, particularly in the upper catchment. In the middle sections, willow removal programs have been undertaken. The study site was located near Morrisons on the Moorabool River (latitude 37° 6' S., longitude 144° 2'E., altitude 442 m) where willow removal has been carried out (Fig. 1). This section of the river is in moderate condition according to criteria of ISC classification (Index of Stream Condition) and has perennial flow (Department of Sustainability and Environment 2005). The experiment was conducted from early April (mid autumn) to the end of July (mid winter) 2005. The stream flow remained relatively constant throughout the experimental period, ranging from 0.01 to 0.15 m/sec. Channel depth and width ranged from 18 cm to 30 cm and 12 to 14 m. Dissolved oxygen concentration and pH ranged from 7.4 to 7.9 mg/L and 7.4 to 7.9 during the study period. Temperature and conductivity ranged from 6 to 14 °C and 287 to 245 µS/cm respectively.

Materials and Methods

For the experiment, fresh willow, *Eucalyptus*, *Phragmites*, *Leptospermum* and *Callistemon* leaves were collected from plants along with fresh willow roots. After collecting, leaves and willow roots were air dried for one week until a constant weight was attained. Roots were rinsed well to remove attached mineral particles before drying. Fifteen grams of dry leaves from each leaf type and roots were put into 5 mm mesh bags separately and tied to nylon lines in a random order. This mesh size was selected to allow macroinvertebrates to enter the mesh bags for feeding and also to reduce leaf loss through the net. Each nylon line was attached to six mesh bags containing five types of leaves and willow roots. The nylon lines were attached to bricks positioned one metre apart, in a homogeneous

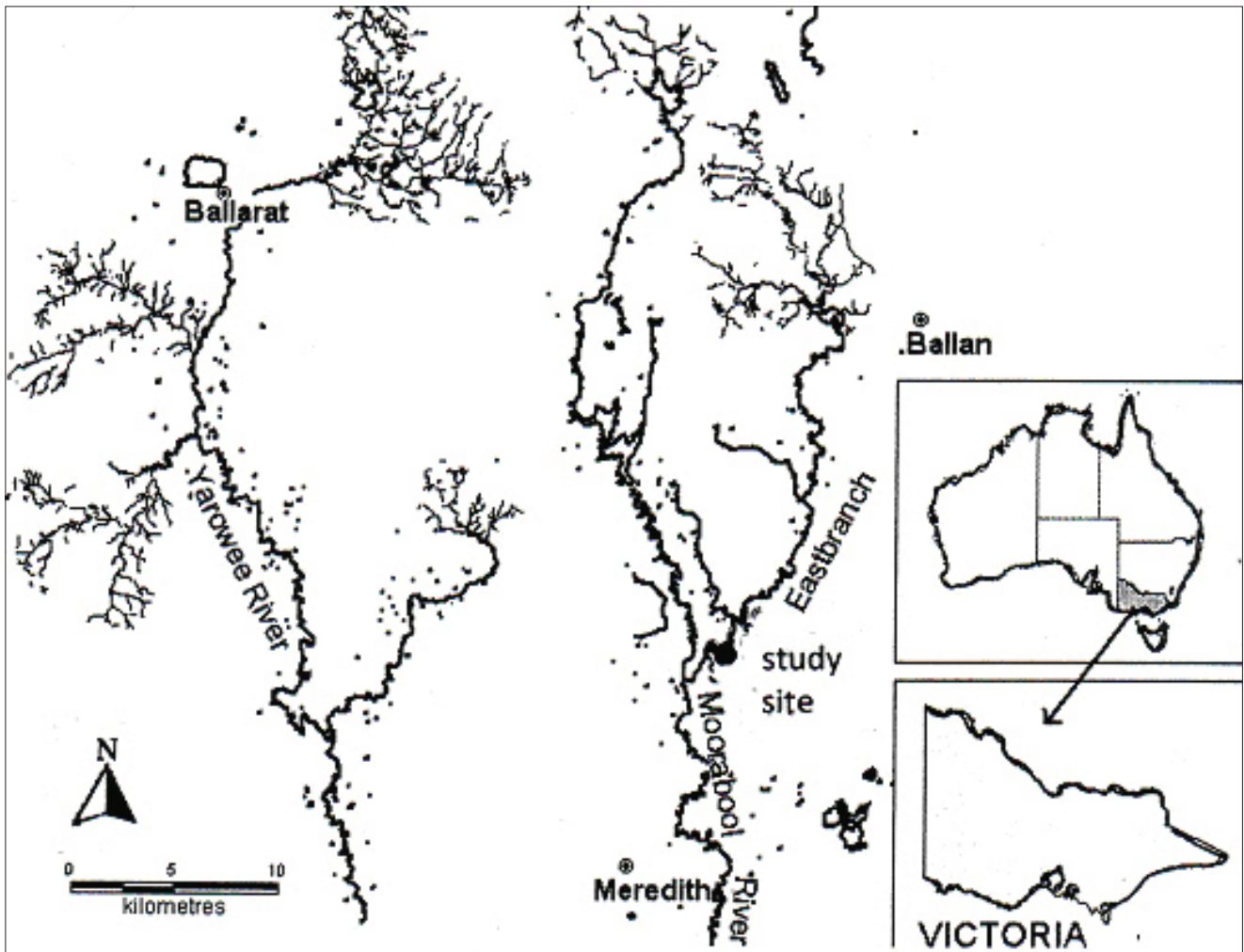


Fig. 1. Location of study sites.

section of the stream bed. Three replicate samples from each leaf type and root packs were randomly removed after 7, 14, 28, 42, 56, 70, 84, 98 and 112 days. Care was taken to avoid losing bag contents while removing them from the water. Water quality parameters were also recorded when removing leaves. Contents of the mesh bags were put in plastic trays and macroinvertebrates were separated and preserved in 70% alcohol for later identification. The macroinvertebrate taxa present in each sample were identified to the lowest possible taxonomic level (Pinder and Brinkhurst 1994; Cranston 1996; Dean and Suter 1996; Smith 1996; CSIRO 1999; Hawking and Theischinger 1999; Gooderham and Tsyrlin 2002). Information from a number of sources was used to assign the invertebrate fauna to major functional feeding groups, viz shredders, collectors, predators, grazers and filter feeders (Merritt *et al.* 1984; Hauer and Lamberti 1996; Gooderham and Tsyrlin 2002) (Appendix I). Remaining leaf matter without invertebrates

was dried for five days until constant weight was attained then dry weight was recorded.

Leaf/root weight loss with time

Decomposition rate of leaves and roots is based on 'mass loss of leaves/roots from initial mass' as defined by Hofsten and Edberg (1972). Leaf pack processing as measured by weight loss of packs through time was estimated with a simple exponential decay model (Petersen and Cummins 1974) as stated in Equation 1. Mean per cent of leaf weight remaining was used as the dependent variable.

Equation 1

$$W_t = W_0 e^{-kt}$$
 (i.e. $\text{Log}(W_t/W_0) = -kt$)
 W_t is the weight after t days,
 W_0 is the initial weight and
 k is the decay coefficient.

The decay coefficient, half-lives of decay of each leaf type and mean weight remaining also were calculated.

Macroinvertebrate taxa richness and abundance

A one way between group analysis of covariance (ANCOVA) was conducted to compare the effect of leaf type on total abundance, taxa richness and mean leaf weight remaining. The length of time packs remained in the stream was considered as a covariate in the analysis. Preliminary checks were conducted to ensure that there was no violation of the assumptions of normality, linearity, homogeneity of variance, homogeneity of regression slope and reliable measurement of the covariate. In situations when homogeneity of variance was not met, data were log transformed before analysis.

Macroinvertebrate community composition

Taxa community composition changes among leaf types were assessed using ANOSIM. Species responsible for assemblage differences were identified by SIMPER routine in PRIMER version 5 package (Plymouth Marine Laboratory, Plymouth, UK). This process allowed visualising overall percentage contribution of each taxon to the average Bray-Curtis dissimilarity between two groups of leaves. Data were log transformed ($\log(x+1)$) before analysis and Bray-Curtis dissimilarity measure and 999 permutations were conducted.

Results

Leaf decomposition

Decay coefficient values of *Eucalyptus*, *Phragmites* and willow roots were in the 'slow processing group' (<0.005) according to the criteria of Petersen and Cummins (1974) (Table 1). *Callistemon* ($-k = 0.007 \text{ day}^{-1}$) and willow leaves ($-k = 0.008 \text{ day}^{-1}$) could be categorised into 'medium processing group' (0.005-0.010). *Leptospermum* were in the 'fast processing group' (0.010-0.015). The percentage of leaf weight remaining at the end of the experimental period was higher for willow roots and *Eucalyptus* leaves (88.98% and 73.64%) (Fig.2). Percentage leaf weight remaining was lowest for *Leptospermum* (19.18%). *Phragmites*, willow leaves and *Callistemon* were intermediate (50.62%, 32.33% and 47.03% respectively). Pair wise comparisons of percentage weight remaining indicated the following order from highest to lowest; willow roots and *Eucalyptus* leaves $>$ *Phragmites* $>$ *Callistemon* $>$ willow leaves $>$ *Leptospermum* leaves (Table 2).

Macroinvertebrate colonisation, taxa richness and abundance

There is a consistent trend of increasing numbers of individuals and taxa in each pack type over the first two months (Fig. 3). In all pack types the number of taxa plateaus or declines over the subsequent two months. By contrast, the number of individuals trends upward over the two month time period in all pack types except willow leaves.

For all pack types, the number of taxa ranged from ten at seven days to approximately 25 at the peak in the experimental period. The variation between pack types in the number of individuals was greater. With the exception of willow leaves, most pack types had between 50 and 85 individuals per pack at day seven. The peak numbers in *Leptospermum*, *Eucalyptus* and *Phragmites* leaves were higher (approximately 380, 350 and 320 respectively) than other pack types; in decreasing order were *Callistemon*, willow leaves and willow roots (approximately 275, 225 and 200 respectively).

Results of ANCOVA showed no significant effect of leaf type on the taxa richness, $F(5,155)=1.27$, $p=0.28$ and a significant effect of leaf types on taxa abundance $F(5,155) = 4.88$, $P = 0.000$. There were significant differences ($p<0.05$) between the number of individuals in *Eucalyptus* leaves and willow leaves, *Leptospermum* leaves with willow roots, and willow leaves and *Callistemon* leaves.

Macroinvertebrate community composition

ANOSIM analysis indicated a significant difference in macroinvertebrate community composition between different substrate types (leaf/root) (Global $R = 0.3$, $p<001$). Main taxa responsible for discriminating different treatment groups are given in Table 3. In majority of comparisons, three taxa could be used to discriminate leaf/root pairs i.e. Amphipoda: Paramelitidae: *Antipodeus* sp., Ephemeroptera: Caenidae: sp. and Ephemeroptera: Leptophlebiidae: *Atalophlebia australasica*. One exception is in *Phragmites* and *Leptospermum* leaf packs where, Diptera: Chironomidae: Tanyptodinae predators are responsible for discriminating groups. There were few other taxa also responsible for community differences among leaf packs (Appendix 1).

Discussion

Decomposition of leaf litter

When comparing leaves, *Eucalyptus* and *Phragmites* could be categorised into slow processing categories according to the criteria of Petersen and Cummins (1974). It was previously speculated that *Phragmites* leaf decomposition is slower than terrestrial leaf litter. However, a comparison of half-lives of leaf decay between *Eucalyptus* (533.15 days) and *Phragmites* (169.05 days) showed a slower decomposition of *Eucalyptus* than *Phragmites* leaves. The decomposition rate recorded for *Eucalyptus* was consistent with that recorded for River Red Gum by Schulze and Walker (1997). Leaf decomposition rate recorded in the present experiment for *Phragmites* was within a similar range to that recorded for *Phragmites* by Menendez *et al.* (2001) in streams in Spain under a similar temperature range. Willow leaves were in the medium category (half life of decay = 88.86 days). This was consistent with the decomposition rate of willow leaves recorded by Essafi *et al.* (1994). In contrast, Gessner *et al.* (1991) and Schulze and Walker (1997) recorded faster decomposition rates for willow leaves. *Leptospermum* and *Callistemon* leaves were expected to be in the slow decomposing category because of their antiseptic characteristics (Williams *et al.* 1993). However, a faster decomposition rate for *Leptospermum* leaves and moderate rate for *Callistemon* leaves was recorded.

Breakdown and decomposition of leaf litter in aquatic ecosystems are complex processes, influenced by many factors. Factors such as temperature, pH, nutrient (e.g. N, P) supply, activity of fungi and bacteria and structure of

invertebrate communities influence the plant litter decomposition (Bärlocher 1990; Sridhar and Bärlocher 1993). This has also led to differences in leaf decomposition rates recorded for some species under different geographic or catchment conditions. Some of the inconsistencies in the decomposition rates of leaves in the present and previous studies may have resulted from such differences. Further, in many studies senescent leaves were used to compare decomposition rates, but in the present experiment green leaves and fresh roots were used. Among factors responsible for leaf decomposition rates, chemical composition of leaves is important. *Eucalyptus* leaves have high lignin (15-30% dry weight) (Cork and Pahl 1984), moderately high phenolic (16%) and condensed tannin contents (Campbell and Fuchshuber 1995). Willow leaves have less lignin and low levels of condensed tannin (Pasteels and Rowell-Rahier 1992) but high levels of other phenols (Binns *et al.* 1968). Willow leaves also have a lower C: N ratio than do *Eucalyptus* (*S. alba* C: N =25.4 [Chauvet *et al.* 1993]; *E. obliqua* 52.5 [Barmuta 1978]). This may affect the palatability of these leaves for macroinvertebrates and thus lead to differences in decomposition rates.

Leptospermum and *Callistemon* leaves lost most of their initial weight at the end of the incubation period. It is possible that leaves are more vulnerable to disintegration, rapid loss from the system or utilisation by biota. Therefore it can be expected that slower decomposing *Eucalyptus* and *Phragmites* contribute a persistent low level of nutrient input to the system compared to willow, *Leptospermum* and *Callistemon* leaves.

Decomposition of willow roots

As predicted, the decay coefficients calculated for roots and leaves in the present study indicated that roots have long processing rates. The predicted half-life of decay for willow root mats in the present study is 6931 days. However, it can be expected that the root breakdown may start after a conditioning period (which is well beyond the present experimental period) thus making a much shorter half-life. Therefore, it can be expected that extending the incubation period is necessary for the accurate prediction of root decomposition rates. Further studies on chemical composition of roots and leaves are desirable for accurate prediction of root decomposition mechanisms.

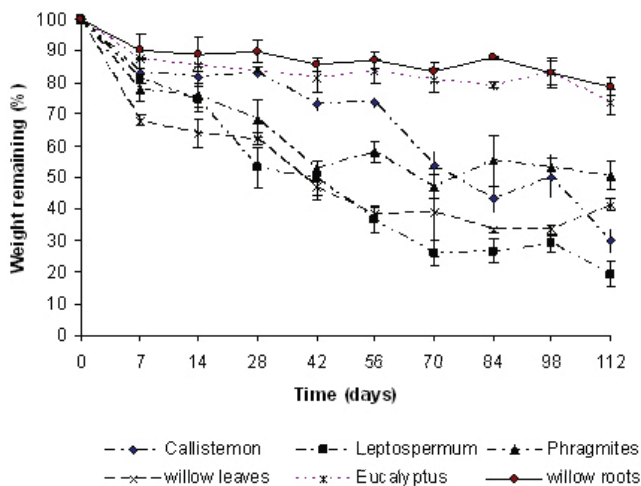


Fig. 2. Percent initial weight (mean \pm SE) remaining of leaves/roots with time.

Table 1. Rates of processing of leaf types and roots

Leaf type	R2	K (-day)	T50 (days)	P	category
Willow roots	0.08	0.0001	6931.00	Ns	Slow
<i>Eucalyptus</i>	0.86	0.001	533.15	0.005	Slow
Willow leaves	0.92	0.008	88.86	0.002	Medium
<i>Phragmites</i>	0.69	0.004	169.05	0.005	Slow
<i>Callistemon</i>	0.90	0.007	105.02	0.000	Medium
<i>Leptospermum</i>	0.94	0.013	54.15	0.001	Fast

Table 2. Estimated marginal means for: total number of individuals, taxa richness, leaf/root weight remaining (log) in leaf types and willow roots.

Treatment	Total no. of individuals	Taxa richness	Log leaf weight remaining
Willow roots	170.70 ± 13	11.53 ± 0.6	1.12 ± 0.03
<i>Eucalyptus</i>	201.07 ± 14	11.53 ± 0.7	1.09 ± 0.02
Willow leaves	141.44 ± 12	10.70 ± 0.5	0.83 ± 0.01
<i>Phragmites</i>	174.93 ± 13	11.78 ± 0.4	0.95 ± 0.03
<i>Callistemon</i>	140.96 ± 15	9.89 ± 0.6	0.93 ± 0.04
<i>Leptospermum</i>	209.19±17	10.00 ± 0.5	0.77 ± 0.02

Table 3. Main taxa responsible for discriminating leaf /root groups based on the SIMPER analysis.

Treatment groups	Main taxa responsible for discriminating treatment groups
Willow root & <i>Eucalyptus</i>	Paramelitidae, Caenidae
Willow roots & Willow leaves	Paramelitidae, Caenidae
<i>Eucalyptus</i> & Willow leaves	Paramelitidae, Caenidae
willow roots & <i>Phragmites</i>	Caenidae , Leptophlebiidae
<i>Eucalyptus</i> & <i>Phragmites</i>	Caenidae , Leptophlebiidae
Willow leaves & <i>Phragmites</i>	Caenidae, Leptophlebiidae
Willow roots & <i>Callistemon</i>	Paramelitidae, Caenidae
<i>Eucalyptus</i> & <i>Callistemon</i>	Caenidae, Tanypodinae
Willow leaves & <i>Callistemon</i>	Caenidae, Leptophlebiidae
<i>Phragmites</i> & <i>Callistemon</i>	Caenidae, Leptophlebiidae
Willow roots & <i>Leptospermum</i>	Paramelitidae, Caenidae
<i>Eucalyptus</i> & <i>Leptospermum</i>	Caenidae, Leptophlebiidae
Willow leaves & <i>Leptospermum</i>	Caenidae, Leptophlebiidae
<i>Phragmites</i> & <i>Leptospermum</i>	Leptophlebiidae, Tanypodinae, Caenidae
<i>Callistemon</i> & <i>Leptospermum</i>	Caenidae, Leptophlebiidae

Macroinvertebrate taxa richness and abundance

Macroinvertebrate feeding is an important component in leaf decomposition processes. In the present study, macroinvertebrate abundance and colonisation followed general trends reported in other studies (e.g. Collier and Winterbourn 1986; Schulze and Walker 1997). In all leaf types, macroinvertebrate taxa increased slowly through the first phase of colonisation and peaked after a rapid increase of taxa numbers. This trend seems to confirm a ‘conditioning period’ during which pack material is made palatable for macroinvertebrates by microbial activity (Cummins 1974; Petersen and Cummins

1974). Time of peak macroinvertebrate colonisation of willow leaves observed in the present study is consistent with the recorded values of Collier and Winterbourn (1986). Even though differences in taxa richness and total number of individuals were expected in different leaf types and roots, taxa richness among leaf types showed no significant differences. However, there was a significant increase in total number of individuals in *Eucalyptus* and *Leptospermum* leaves compared to other leaf types and willow roots. The highest number of individuals was recorded for *Leptospermum* leaf packs, followed by *Eucalyptus* leaves. Even though it was

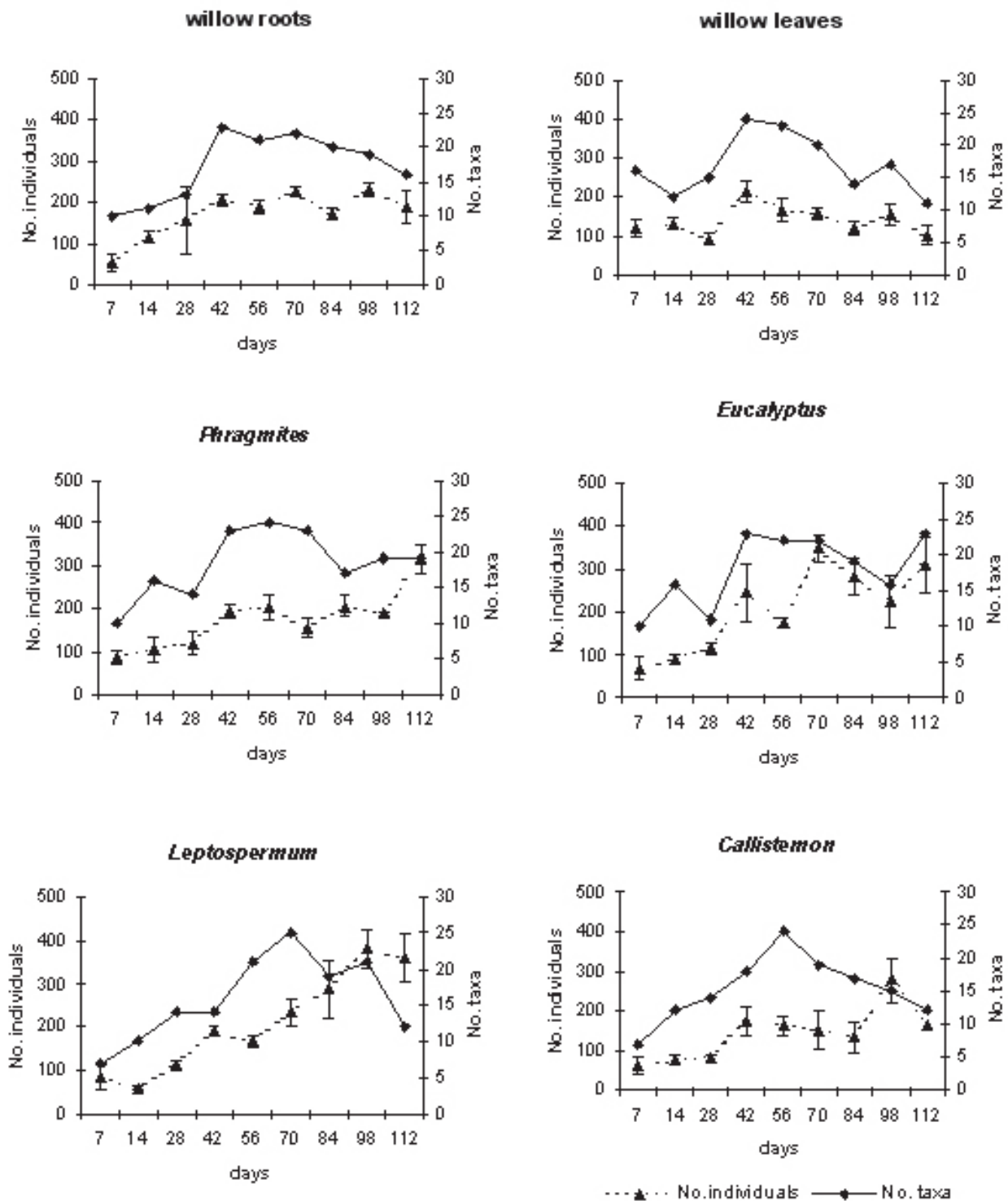


Fig. 3. Total number of individuals (mean \pm SE) and taxa richness associated with each leaf type/ roots with time.

expected that willow leaves would harbour a higher number of individuals, willow and *Callistemon* had a comparatively lower number of individuals. This was inconsistent with the findings of Schulze and Walker (1997) who found minor differences in diversity and composition of macroinvertebrates associated with willows and native *Eucalyptus* in the River Murray.

The comparison of macroinvertebrate coloni-

sation of natural and artificial leaves by Cortes *et al.* (1997) proved that use of leaf litter is principally determined by its food value rather than the microhabitat and substrate. Palatability of the leaves is determined by their chemical composition, particularly the secondary chemicals and the ratio of hard degradable components. Feeding choice of leaves by macroinvertebrates is related to lignin, tannin/phenol and fibre

content, the C:N ratio and the type of biofilm (Suberkropp *et al.* 1975; Arsuﬃ and Suberkropp 1984; Lester *et al.* 1994a). Tannin and other phenolic compounds have been shown to be negatively associated with invertebrate leaf consumption and growth (Irons *et al.* 1988). Higher lignin and moderately high phenolic and condensed tannin contents in *Eucalyptus* leaves may have a negative effect on leaf consumption by macroinvertebrates (Campbell and Fuchshuber 1995). Willow leaves have been found to be more palatable to macroinvertebrates due to less lignin and low levels of condensed tannin (Pasteels and Rowell-Rahnen 1992). Glova and Sagar (1994) and Lester *et al.* (1994a,b) reported an enhanced diversity of invertebrate taxa associated with willows due to contribution of readily processed litter or to stimulating production through nutrients from leaf leachate. Many authors have found a positive correlation between biofilm and invertebrate colonisation (Hax and Golladay 1993; Schulze and Walker 1997). A study by Schulze and Walker (1997) showed that increased weight of diatoms in eucalypt leaves compared to willow leaves after eight weeks' submersion attracted many invertebrates. It also showed that *Paratya australiensis* preferred *Eucalyptus* leaves, which are colonised by micro-organisms. Increased invertebrate numbers were observed on *Eucalyptus* leaves in the present experiment, possibly because of the growth of biofilm on those leaves. Similarly Hax and Golladay (1993) found that the density and richness of invertebrates were correlated with indices of biofilm biomass (ATP, ergosterol, Chlorophyll a) and concluded that microbial density was higher on wood than leaves because of its greater stability and surface complexity. It can be expected that a similar response of biofilm growth in willow roots may have attracted many invertebrates in the present study.

After about 70 days, most *Leptospermum* leaf packs lost their leaves and only fine branches remained. It was previously predicted that *Leptospermum* leaves would decompose more slowly due to their antiseptic qualities. However, no decline in total number of individual invertebrates was observed. A similar trend of taxa colonisation has been observed for willow leaves by Essafi *et al.* (1994) who indicated no decrease in invertebrate biomass once willow leaves were skeletonised and lost most of

their nutritive value. They concluded that invertebrates were then attracted to the packs as a refuge rather than for their palatability. The persistence of invertebrate numbers even after losing leaves of *Leptospermum* may also be attributed to the refuge provided by fine branches of *Leptospermum*.

Macroinvertebrate colonisation

Functional feeding group categories indicated that early colonisers of all leaf pack types were predominantly shredding detritivores, particularly *Antipodeus* sp. (Paramelitidae) and *Austrochiltonia* sp. (Hyalidae). Petersen and Cummins (1974) postulated the presence of a hierarchy of leaf species along a processing continuum in woodland streams. It follows that shredder species would take advantage of a leaf-processing continuum and probably depend upon the continuum for survival. In contrast to that, a study by Bunn (1986) reported that shredders did not respond to the input of leaf litter in northern Jarrah forest streams in Western Australia. Similarly Benfield *et al.* (1977) showed a lack of shredders in leaf processing in a pastureland stream in Virginia, USA. They speculated that the absence of shredders in those streams is related to the absence of a functional leaf-processing continuum. However, the present study indicated that, in this river, shredding detritivores are important in leaf processing, consistent with the postulation of Petersen and Cummins (1974). This suggests that, in this stream system, shredding detritivores are an important functional feeding group in the leaf decomposition process. Shredding detritivores gradually declined over time and collectors dominated the leaf packs. This can be related to increased fine particulate organic matter accumulation with leaf decomposition process over time. However, in willow roots, shredder numbers were relatively stable and continued to be so until the end of the study period. The number of shredders in willow roots was significantly higher than in leaf litter, and there was a significant reduction in collectors in willow root mats compared to the leaf litter. This suggests that shredders or detritivores may be using roots as refuge sites rather than food, or may be because of the long processing time of roots compared to leaves.

An interesting finding in this experiment is that even though 39 taxa were recorded at the sampling site, only three taxa were predominantly responsible for discriminating leaf/root types. They were Amphipoda: Paramelitidae: *Antipodeus* sp., Ephemeroptera: Caenidae: sp.

and Ephemeroptera: Leptophlebiidae: *Atalophlebia australasica*. One exception is in *Phragmites* and *Leptospermum* leaf packs, where Diptera: Chironomidae: Tanypodinae predators are responsible for discriminating groups. There were few other taxa also responsible for community differences among leaf packs. This suggests that despite the differences in composition of riparian and in-stream leaf litter input to these streams, relatively fewer taxa of macroinvertebrates can successfully contribute to processing and energy dynamics of these streams.

Conclusion

These results suggest that leaf litter is an important food source for shredders in this river. Leaves of *Eucalyptus* followed by those of *Phragmites*, persisted longer in the river compared to willow, *Callistemon* and *Leptospermum*. These persistent leaves provide a continuous supply of food for communities in those streams. These results also indicate that leaf type does not affect taxa richness in this river, though it may affect the community composition of macroinvertebrates. Willow root mats may also be important because of the long processing life and the refuge provided for macroinvertebrates. Their long-term persistence was found to facilitate higher invertebrate numbers. This suggests that long-term persistence of willow roots in this system, until the new native vegetation cover establishes may have a positive effect on aquatic communities.

There are some limitations in this study that need to be addressed in any continuation of the study. The study was carried out in a single site of a selected stream because of time and practical constraints. It is desirable for this experiment to be replicated in several sites in several streams, to enable generalisation of the outcome on a broader scale. Root and leaf decomposition is complex, involving several processes such as leaching of soluble components, physical fragmentation, microbial catabolism and feeding by invertebrates (Boulton and Boon 1991). In the present experiment, leaf/root decomposition rates and macroinvertebrate colonisation have been investigated. For a better estimate of the mechanisms leading to decomposition process of these materials, it is also important to estimate chemical composition and microbial decomposition processes of these leaves.

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References

- Arsuffi TL and Suberkropp K (1984) Leaf processing capabilities of aquatic hyphomycetes, interspecific differences and influence on shredder feeding preference. *Oikos* **42**, 144-154.
- Bärlocher F (1990) Factors that delay colonization of fresh alder leaves by aquatic hyphomycetes. *Archiv für Hydrobiologie* **119**, 249-255.
- Barmuta LA (1978) The decomposition of *Eucalyptus obliqua* leaf packs in small stream ecosystems. (BSc (Hons.) Thesis, Department of Zoology, University of Adelaide, South Australia)
- Benfield EF, Jones DS and Patterson MF (1977) Leaf pack processing in a pastureland stream. *Oikos* **29**, 99-103.
- Binns WW, Blunden G and Woods DL (1968) Distribution of leucoanthocyanidins, phenolic glycosides and amino acids in leaves of *Salix* spp. *Phytochemistry* **7**, 1577-1581.
- Boulton AJ and Boon PI (1991) A review of methodology used to measure leaf litter decomposition in lotic environments: Time to turn over an old leaf? *Australian Journal of Marine and Freshwater Research* **42**, 1-43.
- Bunn SE (1986) Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: functional organisation. *Freshwater Biology* **16**, 621-632.
- CALP (1997) Corangamite Regional Catchment Strategy. Colac, Corangamite Catchment and Land Protection Board.
- Campbell IC (1993) Riparian stream linkages: an Australian perspective on in-stream issues. In *Ecology and Management of Riparian Zones in Australia*, pp. 21-30. Eds SE Bunn, BJ Pusey, and P Price. (LWRRDC: Canberra)
- Campbell IC and Fuchshuber L (1995) Polyphenols, condensed tannins and processing rates of tropical and temperate leaves in an Australian stream. *Journal of North American Benthological Society* **14**, 174-182.
- Chauvet E, Giani N and Gessner MO (1993) Breakdown and invertebrate colonisation of leaf litter in two contrasting streams: significance of oligochaetes in a large river. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 488-495.
- Collier KJ and Winterbourn MJ (1986) Processing of willow leaves in two suburban streams in Christchurch, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **20**, 575-582.
- Cork SJ and Pahl L (1984) The possible influence of nutritional factors on diet and habitat selection by the ringtail possum (*Pseudocheirus peregrinus*). In *Possums and Gliders*, pp. 269-276. Eds A Smith and L Hume (Surrey Beatty: Sydney)
- Cortes RM, Abelho M and Rebelo SB (1997) The macroinvertebrate colonization of leaf bags: is there a pattern? *Limnetica* **13**, 71-75.
- Cranston P (1996) *Identification Guide to the Chironomidae of New South Wales*. AWT Identification Guide No.1. (AWT Pty Ltd: NSW, Australia)
- CSIRO (1999) Interactive Guide to Australian Aquatic Invertebrates. CD ROM. 2 ed (CSIRO Publishing: Australia)
- Cummins KW (1974) Structure and function of stream ecosystems. *Bio Science* **24**, 631-41.
- Cummins KW, Wilzbach MA, Gates DM, Perry JB and Taliaferro WB (1989) Shredders and riparian vegetation. *Bio Science* **39**, 24-30.
- Dean JC and Suter PJ (1996) *Mayfly nymphs of Australia: A Guide to genera*. Identification Guide No.7. (Co-operative Research Centre for Freshwater Ecology, Albury, NSW)

- Department of Sustainability and Environment (2005) Index of Stream Condition: The Second Benchmark of Victorian River Condition, Melbourne, Victoria.
- Department of Water Resources Victoria (1990). *Water Victoria: an Environmental Handbook*. (Victorian Government Printing Office: North Melbourne, Victoria)
- Essafi K, Chergui H, Pattee E and Mathieu J (1994) The breakdown of dead leaves buried in the sediment of a permanent stream in Morocco. *Archiv für Hydrobiologie* **130**, 105-112.
- Frankenberg J (1995) Willows: the species, their biology and control. In. *Willows, Weeds and Fish*, pp 1-16. Ed R Hodges. (Proceedings of River Basin Management Society, Geelong, Victoria)
- Gessner MO, Meyer E and Schwoerbel J (1991) Rapid processing of fresh leaf litter in an upland stream. *Verhandlungen Internationaler Vereinigung für Theoretische und Angewandte Limnologie* **24**, 1846-1850.
- Glova GJ and Sagar PM (1994) Comparison of fish and macroinvertebrate standing stocks in relation to riparian willows (*Salix* sp.) in three New Zealand streams. *New Zealand Journal of Marine and Freshwater Research* **28**, 255-266.
- Gooderham J and Tsyrlin E (2002) The Waterbug Book: A Guide to the Freshwater Macroinvertebrates of Temperate Australia. (CSIRO Publishing: Australia)
- Hauer FR. and Lamberti GA (1996) *Methods in stream ecology*. (Academic Press: San Diego, California)
- Hawking JH and Theischinger G (1999) *Dragonfly Larvae (Odonata): A guide to the Identification of Larvae of Australian Families and to the Identification and Ecology of Larvae from New South Wales*. AWT Identification Guide No.3 and CRCFE Identification Guide No. 24. (CRCFE: Albury and AWT Pty Ltd: West Ryde, Australia)
- Hax CL and Golladay SW (1993) Macroinvertebrate colonisation and biofilm development on leaves and wood in a boreal river. *Freshwater Biology* **29**, 79-87.
- Hofsten BV and Edberg N (1972) Estimating the rate of degradation of cellulose fibres in water. *Oikos* **23**, 29-34.
- Imhof G (1973) Aspects of energy flow by different food chains in a reed bed. A review. *Polshie Archives für Hydrobiologie* **20**, 165-168.
- Irons JG, Oswood MW and Bryant JP (1988) Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. *Hydrobiologia* **160**, 53-61.
- Ladson A, Gerrish G, Garr G and Thexton E (1997) Willows along Victorian Waterways. Towards a management strategy. Waterways Unit. Department of Natural Resources and Environment.
- Lester PJ, Mitchell SF and Scott D (1994a) Effects of riparian willow trees (*Salix fragilis*) on macroinvertebrate densities in two small Central Otago, New Zealand, streams. *New Zealand Journal of Marine and Freshwater Research* **28**, 267-276.
- Lester PJ, Mitchell SF and Scott D (1994b) Willow leaf and periphyton chemical composition, and feeding preference of *Olinga feredayi* (Trichoptera, Conoesucidae). *New Zealand Journal of Marine and Freshwater Research* **28**, 13-18.
- Lis-Balchin MS, Hart L and Deans SG (2000) Pharmacological and antimicrobial studies on different tea-tree oils (*Melaleuca alternifolia*, *Leptospermum scoparium* or Manuka and *Kunzea ericoides* or Kanuka), originating in Australia and New Zealand. *Phytotherapy Research* **14**, 623-629.
- Mathews CP and Kowalczewski A (1969) The disappearance of leaf litter and its contribution to production in River Thames. *Journal of Ecology* **57**, 543-552.
- Mc Nabb CD and Batterson TR (1991) Occurrence of the common reed *Phragmites australis* along road side in Lower Michigan. *Michigan Academician* **23**, 211-220.
- Menendez M, Martinez M, Hernandez O and Comin FA (2001) Comparison of leaf decomposition in two Mediterranean rivers: a large eutrophic river and an oligotrophic stream. *International Review of Hydrobiology* **86**, 475-486.
- Merritt RW, Cummins KW and Burton TM (1984) The role of aquatic insects in the processing and cycling of nutrients. In *The Ecology of Aquatic Insects* pp 134-163. Eds VH Resh and DM Rosenberg. (Praeger Scientific, New York)
- National Weeds Strategy Executive Committee (2000) National Weeds Strategy Web Page. [WWW web page] URL <http://www.weeds.org.au>.
- Ostertag R and Hobbie SE (1999) Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia* **121**, 564-573.
- Pasteels JM and Rowell-Rahier M (1992) The chemical ecology of herbivory on Willows. *Proceedings of Royal Society of Edinburgh* **98B**, 63-73.
- Petersen RC and Cummins KW (1974) Leaf processing in a woodland stream. *Freshwater Biology* **4**, 343-368.
- Pidgeon RWJ and Cairns SC (1981) Decomposition and colonisation by invertebrates of native and exotic leaf material in a small stream in New England (Australia). *Hydrobiologia* **77**, 113-127.
- Pinder AM and Brinkhurst RO (1994) *A Preliminary Guide to the Identification of the Microdrile Ologochaeta of Australian Inland Waters. Identification Guide No.1*. (CRCFE: Albury, NSW)
- Read MG and Barmuta LA (1999) Comparison of benthic communities adjacent to riparian native eucalypt and introduced willow vegetation. *Freshwater Biology* **42**, 359-374.
- Roberts J (2000) Changes in *Phragmites australis* in south eastern Australia: A habitat assessment. *Folia Geobotanica and Phytotaxonomica* **35**, 353-362.
- Sainty GR and Jacobs SWL (1981) Waterplants of New South Wales. Water Resource Commission New South Wales, Sydney.
- Saltonstall K (2003) Recent Research on *Phragmites australis* in North America: Implications for management, University of Maryland Center for Environmental Science. Proceedings of the Aquatic Invaders of the Delaware Estuary Symposium, Malvern, Pennsylvania, May 20, 2003 pp. 12-15.
- Schulze DJ and Walker KF (1997) Riparian willow and eucalypt trees and their interactions with littoral invertebrates in the River Murray, South Australia. *Regulated Rivers: Research and Management* **13**, 557-77.
- Smith BJ (1996) *Identification Keys to the Families and Genera of Bivalve and Gastropod Molluscs found in Australian Inland Waters. Identification Guide No. 6*. (CRCFE: Albury, Australia)
- Sridhar KR and Bärlocher F (1993) Seasonal changes in microbial colonization of fresh and dried leaves. *Archiv für Hydrobiologie* **128**, 1-12.
- Suberkropp K, Klug MJ and Cummins KW (1975) Community processing of leaf litter in a woodland stream. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* **19**, 1653-1658.
- Thomas WA (1970) Weight and calcium losses from decomposing tree leaves on land and water. *Journal of Applied Ecology* **7**, 237-241.
- Walsh NG and Entwisle TJ (1996) *Flora of Victoria* (vol. 3). (Inkata Press: Melbourne)
- Williams LR, Home VN and Lusanzi I (1993) An evaluation of the contribution of 1,8-cineole and terpinen-4-ol to the overall antimicrobial activity of tea tree oil. *Cosmetics, Aerosols and Toiletries in Australia* **7**, 25-28.
- Yeates LV (1994) The role of invertebrates and microorganisms in the breakdown of willow and eucalypt leaves in a Tasmanian stream. (B Sc (Hons) Thesis, University of Tasmania)
- Yeates LV, and Barmuta L (1999) The effects of willow and *Eucalyptus* leaves on feeding preference and growth of some Australian aquatic macroinvertebrates. *Australian Journal of Ecology* **24**, 593-598.

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Appendix 1. Macroinvertebrate Functional Feeding Group assignment

Class/ Order	Family	Species	Assigned FFG	
Amphipoda	Hyalidae	<i>Austrochiltonia</i> sp.	shredder	
	Paramelitidae	<i>Antipodeus</i> sp.	shredder	
Isopoda	Janiridae	<i>Heterias</i> sp.	shredder	
Decapada	Atyidae	<i>Paratya australiensis</i>	shredder	
Plecoptera	Gripopterygidae	<i>Leptoperla</i> sp.	shredder/grazer	
Trichoptera	Atriplectididae	<i>Atriplectides dubios</i>	collector	
	Calamoceratidae	<i>Anisocentropus</i> sp.	shredder	
	Ecnomidae	<i>Ecnomus</i> sp.	predator	
	Hydropsychidae	<i>Cheumatopsyche</i> sp.	collector	
	Leptoceridae	<i>Oecetis</i> sp.	predator	
	Leptoceridae	<i>Triplectides</i> sp.	shredder	
	Leptoceridae	<i>Triplectides volda</i>	shredder	
	Limnephilidae	<i>Archaeophylax</i> sp.	shredder	
	Odontoceridae	<i>Marilia</i> sp.	collector	
	Coleoptera	Elmidae	<i>Austrolimnius</i> sp.	collector
		Hydrophilidae	<i>Berosus</i> sp.	predator
		Psephenidae	<i>Sclerocyphon</i> sp.	grazer
	Hemiptera	Corixidae	<i>Micronecta</i> sp.	predator
		Diptera	Ceratopogonidae	sp.
Chironominae	sp.		collector	
Orthoclaadiinae	sp.		grazer/collector	
Tanypodinae	sp.		predator	
Odonata	Coenagrionidae	<i>Ischnura</i> sp.	predator	
	Corduliidae	sp.	predator	
	Isostictidae	sp.	predator	
	Isostictidae	<i>Austrosticta</i> sp.	predator	
Ephemeroptera	Caenidae	sp.	collector	
	Caenidae	<i>Tasmanocoenis</i> sp.	collector	
	Leptophlebiidae	<i>Atalophlebia australis</i>	collector	
Gastropoda	Leptophlebiidae	<i>Atalophlebia australasica</i>	collector	
	Ancylidae	<i>Ferrissia</i> sp.	grazer	
	Hydrobiidae	<i>Potamopyrgus antipodarum</i>	grazer	
	Planorbidae	<i>Glyptophysa</i> sp.	grazer	
	Physidae	<i>Physa acuta</i>	grazer	
	Planorbidae	<i>Gyraulus</i> sp.	grazer	
	Bivalvia	Corbiculidae	<i>Corbicula</i> sp.	filter feeder
Hirudinea	Glossiphoniidae	sp.	predator	
Oligochaeta	Lumbriculidae	<i>Lumbriculus variegatus</i>	collector	
	Phreodrilidae	<i>Antarctodrilus proboscidea</i>	collector	



Beetles (including weevils) on footpath. Photos by Virgil Hubregtse. See article on page 155.