DENSITY AND DISTRIBUTION OF EPIPHYTIC INVERTEBRATES ON EMERGENT MACROPHYTES IN A FLOODPLAIN BILLABONG

Balcombe^{1,2} S.R., Closs³ G.P. and Suter² P.J.

1. eWater Cooperative Research Centre, Australian Rivers Institute, Griffith University, Nathan, Qld, 4111.
2. Department of Environmental Management and Ecology, LaTrobe University, PO Box 821, Wodonga, Victoria, 3689.
3. Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Correspondence: Stephen R. Balcombe, Centre for Riverine Landscapes, Faculty of Environmental Sciences, Griffith University, Nathan, Qld, 4111. E-mail: s.balcombe@griffith.edu.au

ABSTRACT

The abundance of epiphytic invertebrates living on both submerged and emergent macrophytes in lentic systems are influenced by a range of environmental features at both spatial and temporal scales. Such features include water chemistry, habitat complexity, hydrology and external influences such as climatic cycles. Dugays 2 billabong is a floodplain lake on the highly regulated, mid-upper Murray River, in S.E Australia. Giant rush (*Juncus ingens* N.A. Wakefield) is the dominant habitat feature in this billabong. This plant is a simple, single-stemmed, densely packed emergent macrophyte that fringes the littoral margins. The macrophyte habitat available to epiphytic invertebrates in this billabong is highly variable through time largely due to the variable water levels imposed by the regulated river channel for downstream irrigation needs, particularly through summer. To investigate both spatial and temporal patterns in the epiphytic invertebrates of Dugays 2 billabong, invertebrates were sampled within giant rush stands on five occasions over one year. Spatial variability in epifaunal density was generally low, while temporal densities were highly variable through time. Spatial patterns of invertebrate abundance revealed few associations with

habitat structure or water quality, apart from those associated with water depth, particularly when sampling had been preceded by fluctuating water levels. High temporal variability in assemblage structure of the epifauna reflects the high background environmental variation that occurs in this system.

Keywords: epiphytic invertebrates, emergent macrophytes, billabong, habitat structure, temporal variation, water quality, hydrological variability, river regulation

Running Title: Epiphytic invertebrates in a floodplain billabong

INTRODUCTION

Epiphytic invertebrates (those associated with macrophytes) are an important component of riverine food webs, being significant consumers of algae, detritus and metazoans (Ward 1992; van de Meutter *et al.*, 2005) and are a significant food source for many fish (Schriver *et al.*, 1995; Balcombe and Humphries, 2006). The spatial distribution and abundance of epiphytic invertebrates are often influenced by habitat structure (Gregg and Rose, 1985; Taniguchi *et al.*, 2003), particularly most associated with complex macrophytes such as those with highly branched stems or with complex leaves (Cattaneo *et al.*, 1998; Taniguchi *et al.*, 2003). The abundance of epiphytic invertebrates may be strongly influenced by seasonal or annual climatic cycles through their influence on life-history attributes of such biota (Vannote and Sweeney. 1980; Ward, 1992). The influence of natural climatic regimes on riverine biota can, however, be modified to varying degrees through changes to the natural hydrological regime as a result of river regulation (Weisberg *et al.*, 1990; Humphries, 1996).

The River Murray in south eastern Australia is a highly regulated river with major dams and water diversions (Walker 1992). Billabongs (floodplain lakes) on the floodplain of the River Murray tend to be eutrophic and often contain a variety of submerged and aquatic plants and have a high abundance and diversity of invertebrate fauna (Boon *et al.*, 1990; Hillman and Shiel 1991). Dense stands of emergent macrophytes are also a characteristic features of these billabongs (Bunn and Boon, 1993) and their proliferation may be related to the effects of river regulation at the expense of submerged macrophytes (Chesterfield 1986). While emergent macrophytes are common in these billabongs, there is surprisingly little information on their invertebrate fauna given their potential subsidies to billabong and river food webs (Hillman, 1986; Hillman and Shiel 1991).

To increase our understanding of invertebrate assemblages in dense macrophytes we collected invertebrates in giant rush stands in Dugays 2 billabong, a floodplain billabong in the middle reaches of the River Murray. Giant rush is the major habitat feature available to epiphytic invertebrates. The dominant predators in the giant rush stands are native carp gudgeons, *Hypseleotris* spp. (Balcombe and Closs 2000, 2004; Balcombe and Humphries 2006). The regulated flows of the River Murray have altered the natural water level regimes within Dugays 2 billabong, and thus, directly influence the spatial and temporal availability of giant rush habitat (Balcombe and Closs 2004; Balcombe and Humphries 2006). Water levels in this billabong are highly variable

through summer and autumn, while they are lower and generally more stable through winter and spring. This pattern reflects the release of water from upstream dams in the summer months and then storage of water in winter months for the following summer – autumn irrigation needs for downstream users.

In this paper our primary aim was to investigate spatial and temporal patterns in the abundance of epiphytic invertebrates associated with giant rush. We predict that habitat structure will play an important role in the spatial distribution and abundance of the invertebrates. We also predict that the temporal patterns of invertebrate abundance will be highly variable given the unpredictable and unnatural hydrological regime in this billabong.

METHODS

Study location

Dugays 2 billabong (36°02'30"S 146°20'30"E), hereafter referred to as DB, is a 7.2 ha eutrophic billabong located on the floodplain of the River Murray (between Lake Hume and Lake Mulwala), near Rutherglen, Victoria, S.E. Australia (Fig. 1). Water level fluctuations in the billabong largely mirror that of the river channel (Balcombe, 2002; Balcombe and Closs, 2004), which are primarily controlled by water releases from Lake Hume. Giant rush grows in monospecific stands in DB, generally along the shore in water less than 1 m deep. It can occur in clumps as small as 2 m in diameter to long, continuous stands. The stems of this plant support an encrusting biofilm of varying thickness and complexity that can include diatoms, filamentous algae and inorganic matter (Balcombe 2002; Balcombe and Humphries 2006).

Invertebrate Sampling

Invertebrates were sampled in giant rush habitat along a 370 m stretch of shoreline. This area represented the most concentrated band of giant rush in DB and a habitat where stems were continually inundated even under the lowest billabong water levels recorded during the study.

Invertebrate samples were collected on five occasions between December 1995 and December 1996, with up to 28 samples collected on each sampling date. Samples were collected approximately bi-monthly, with the exception of August to December 1996. It was not possible to sample in this period due to very high water levels resulting from unusually prolonged water release from Lake Hume as a result of management actions to repair the dam wall. Sampling areas were haphazardly selected on each sampling date. Samples were always collected from the offshore edge of the stands, as the inshore margins were dry on occasions. This ensured that at least a portion of the sampled stems represented permanent wetted habitat. Sampling events and numbers of samples collected were as follows (Event 1: Dec 1995 (27); Event 2 Mar 1996 (28); Event 3 Apr 1996 (28); Event 4: Jun 1996 (27); Event 5: Dec 1996 (28))

A hybrid stovepipe (Cummins and Meritt, 1979) and bag sampler (Humphries, 1996) was used to collect the macroinvertebrate fauna. It consisted of a 1 m long, 30 cm diameter PVC pipe with a 250 µm mesh net attached. To sample invertebrates, stems were first cut at surface water level with a sharp hunting-knife, and the PVC pipe was quickly pushed over the stems to the substratum. Stems were cut at the sediment-

water interface, the net quickly drawn closed underneath and tied off, securing all stems within. The pipe was then lifted out of the water and its contents transferred to a 250 μ m holding net with a 500 mL sampling jar attached. Attached fauna were removed by rubbing off the biofilm from the stems by hand following the method of Aloï (1990) and were preserved in 10% V/V formaldehyde.

While the sampling pipe was in place, water depth, dissolved oxygen (YSI model 57 field probe), temperature and conductivity (Orion 156 conductivity meter) were measured next to the pipe at mid-water depth.

Laboratory Analysis

Invertebrate samples were identified and enumerated using a compound microscope. Most macroinvertebrates were identified to morpho-species level with the exception of microcrustacea, which were identified to family level. Identifications followed taxonomic keys (Williams, 1980; Pinder and Brinkhurst, 1994; Shiel, 1995; Dean and Suter, 1996; Cranston, 1996; Cartwright, 1997; Davis and Christidis, 1997; Hawking and Smith, 1997; Hawking and Theischinger, 1999). The freshwater shrimp, *Paratya australiensis*, was occasionally captured but was not included in the analysis as they were observed to avoid the sampler and could not be sampled efficiently.

Data Analysis

Temporal variation in physicochemical parameters and invertebrate abundance and richness were each investigated with one- way ANOVA using SPSS© 11.5 (SPSS inc, 1989-2002) with sampling occasion (Time) being the fixed factor. Data were screened to meet the assumptions of ANOVA, and $\log_e (x + 1)$ transformations were successfully used to meet assumptions where appropriate (Sokal and Rohlf, 1995).

Two measures of habitat structure were calculated for each sample collected: stem density and surface area. Stem density (STD) was chosen as a parameter expected to vary among sampling sites and potentially influence both invertebrate and predator (fish) abundance. Plant surface area (PSA) was also calculated as a likely parameter influencing aquatic invertebrate community structure (Brönmark, 1989; Beckett *et al.*, 1992). Stem density was calculated as $STD = N / SA$, where N = number of stems in sampling pipe, SA = benthic surface area enclosed by sampling pipe in m^2 . Plant surface area was calculated: $PSA = \pi D L N$ where Stem Diameter (D) = average diameter of 10 stems, Stem length (L) = average length of 10 randomly chosen stems. Invertebrate abundances were standardized to the total plant surface area within each individual

sampling patch. Hence invertebrate density (number of individuals m^{-2} plant) was the standard sampling unit.

All multivariate analyses were performed using Primer v5 (Clarke and Warwick, 2001) on invertebrate densities. Invertebrate species densities were analyzed using SIMPER to identify the main species representative of each sampling event (or groups of sampling events representing clear physical (water depth) or chemical (temperature and dissolved oxygen) based upon a cumulative contribution to >90% of the similarity. These grouped events were to be used if water quality attributes separated certain sampling events on the basis of environmental variables (see Results). Invertebrate assemblage patterns were subsequently analyzed using ordination based upon hybrid non-metric multi-dimensional scaling (MDS). MDS plots were generated from Bray-Curtis similarity matrices produced from $\log_{10}$ transformed densities. To examine patterns of temporal variation, one-way analyses of similarities (ANOSIM) based upon the same similarity matrices were used to identify assemblage differences among the five sampling events and pairwise comparisons identified differences between pairs of individual times or grouped events. SIMPER was used to describe the main species contributing to differences among each pairwise comparison.

BIO-ENV (Clarke and Warwick, 2001) was used to investigate potential relationships between invertebrate assemblage structure and both physical habitat and water chemistry for each of the individual sampling events. The similarity matrices used to differentiate invertebrate assemblage structure were the same as those used to generate the MDS plots. The environmental similarity matrices were based upon normalized Euclidean distance rather than Bray-Curtis as per Clarke and Warwick (2001).

Spatial patterns of individual species were investigated with Spearman rank correlations between species abundance and additionally total abundance and taxon richness for each sampling event. Only those species that accounted cumulatively, for >90% of the group similarity within a sampling event were used in this analysis. Given the high number of comparisons being made there was an increased chance of Type I error, hence, a more conservative α level (Keppel, 1991), was used with significant correlations only accepted at $\alpha < 0.005$.

RESULTS

Environmental Variables

Water levels varied throughout the study period (Fig. 2) with fluctuations of up to 50 cm in less than one week common during the irrigation season, from December 1995 to March 1996. However, water levels remained stable from April through to August, although they did increase by over 4m following prolonged flooding through to November because of an extended release of water from Lake Hume. In the 28 days prior to sampling, daily water level patterns were variable among the five sampling occasions (Table 1). April and June 1996 represented two relatively stable pre-sampling periods, in comparison to December 1995, March 1996 and December 1996, which represented fluctuating pre-sampling conditions. Water level variability dictated the available plant surface area with less change in the percentage of available habitat occurring for the two stable periods, compared with the larger changes in percentage available habitat in December 1995 and March 1996 (Table 1). By comparison, December 1996 constituted a pre-sampling, fluctuating water level period, yet the percentage of available habitat was less affected by water level change, particularly in the two weeks prior to sampling (Table 1).

Water depths sampled, were relatively consistent among samples collected on the same date (Fig. 3a). However, significant variation in sampling depth among dates ($F_{4,145} = 46.92$, $p < 0.001$) corresponded with changes in billabong levels (Fig. 2).

Significant temporal variation in water temperature was recorded ($F_{4,145} = 613.35$, $p < 0.001$), with mean temperature following a seasonal pattern; higher in summer, ($>20^{\circ}\text{C}$ in December to March) compared to winter ($<12^{\circ}\text{C}$ in June) (Fig. 3b). Dissolved oxygen (DO) was also significantly different among sampling dates ($F_{4,145} = 1221.1$, $p < 0.001$), with a tendency to a pattern opposite to that of temperature (Fig. 3 b,c). Conductivity showed no significant temporal variation with mean values between 95-100 μScm^{-1} ($F_{4,145} = 0.78$, $p > 0.05$, Fig. 3d).

Fauna

A total of 41330 invertebrates were collected during the study period. Chironomids were the dominant group, with 23049 individuals, accounting for 56 % of the total faunal abundance. Oligochaetes and zooplankton taxa accounted for 16% and 13% of the total fauna, while individual taxa such as Bryozoa, *Hydra* and *Ferrissia* sp. were also relatively abundant (Appendix I). Fifty-nine taxa were identified, the bulk of

which contributed little to the total abundance on any single date (Appendix I). On average, there were 39 taxa per sampling date, with 15 of these present across all sampling dates. The most abundant taxa across all dates were chironomids, *Kiefferulus martini*, *Kiefferulus intertinctus*, *Dicrotendipes jobetus*, *Polypedilum leei* and *P. convexum*; followed by oligochaetes: *Chaetogaster* sp. and *Nais* sp. and nematodes, *Nematoda* sp.

In general for any single sampling event, SIMPER identified up to eight species contributing to more than 5% of the similarity with chironomid species tending to have the highest contribution (Table 2). The most even spread of species dominance for any sampling event was in December 1995, with eight species contributing to at least 5% of the similarity, while in December 1996, the assemblage was dominated by only two taxa: the chironomid *K. martini* and the gastropod *Ferrissia* sp.

Temporal variation in the invertebrate fauna

Multivariate patterns in assemblage structure showed high variation across sampling events (Fig. 4A). ANOSIM revealed that time (sampling event) was a significant factor influencing assemblage structure (ANOSIM: $R = 0.72$, $p < 0.001$). Pairwise comparisons revealed all events to be significantly different to each other and these changes were largely driven by changes in abundance of chironomid species, particularly the most dominant ones: *P. convexum*, *P. leei* and *K. martini* (Table 3). To a lesser degree changes in abundance between sampling events of the oligochaetes: *Chaetogaster* and *Nais* spp. and the closely attached species such as *Ferrissia*, *Hydra* and Bryozoa also had some influence on differences between times (Table 3, Appendix I).

There were significant pairwise differences between sampling events grouped according to physicochemical status. Events 1 and 2 were characterized by their low DO₂ levels (Fig. 3) and these assemblages were significantly different to the other three events that were associated with high DO₂ levels (Table 3, Fig. 4B). Events 3 and 4 were characterized by low water temperatures combined with low water depths (Fig. 2 & 3) and these assemblages were significantly different to those associated with high water levels and water temperatures. The main species driving assemblage differences between the physicochemical groups were the two most abundant chironomids: *P. leei* and *K. martini* and the oligochaete: *Pristina* sp. (Table 3)

Spatial Variation in the invertebrate fauna

Across all sampling events the only variable that exhibited any association with invertebrate assemblage structure was DO₂, explaining approximately 25% of the variation in assemblage patterns (Table 4). Within any one sampling event the invertebrate assemblage did not appear to be strongly structured by either physical habitat or water chemistry based upon BIO-ENV analyses (Table 4). Any relationships were mostly weak and at most only accounted for <20% of the variation in assemblage structure.

There were few associations between individual species densities and habitat or water quality (Table 5). There were no positive associations between stem density and species density, although there were negative associations between *Nais* sp. and total density in event two and with *Bezzia* sp. 1 in event three. Significant associations between surface area and species densities were generally negative. The most consistent relationship found from the correlation analyses was between species densities (including taxon richness and total abundance) with water depth. These significant relationships were only found in the three sampling events with the highest mean sampling depths and preceded by fluctuating water levels (Events 1, 2 & 5).

DISCUSSION

The giant rush stands of DB support a diverse and abundant fauna despite their simple structure. The total numbers of individuals, taxa and the composition of the invertebrate fauna was similar to those of littoral habitats in other Australian lentic waterbodies. However, numbers of chironomids and oligochaetes were relatively higher than that recorded by other studies (Marchant, 1982; Maher, 1984; Outridge 1988; Boulton and Lloyd, 1991). Giant rush stands supported relatively fewer mobile invertebrates (e.g. coleopterans, ephemeropterans, hemipterans and odonates) than did littoral habitats in both Lachlan River wetlands (Maher, 1984) and Magela Creek billabongs (Marchant 1982). The lack of mobile invertebrates in the giant rush habitats corresponds with a fish diet study in DB with the dominant invertebrate consumers, carp gudgeons, eating few mobile invertebrates (Balcombe and Humphries 2006). The dominance of relatively immobile fauna indicates an assemblage with limited ability to respond to rapidly changing water levels.

Flow regulation and associated aseasonal flow patterns, including flow release and drawdown was expected to influence natural seasonal patterns of the invertebrate assemblage in DB (Balcombe and Humphries 2006). Our data show high variability in the abundance of invertebrate fauna across sampling dates consistent with patterns predicted under the influence of regulated flows with unnatural water level fluctuations driving down invertebrate densities. The high temporal variability in the abundance of most species was in the same direction, suggesting similar environmental influences are operating similarly across all species through time.

It was also notable that the invertebrate assemblages were differentiated when grouped according to dissolved oxygen levels. In effect this demonstrated that the invertebrate fauna was different during the irrigation period (Dec 1995 and March 1995) to the other three periods. This could imply that fluctuating water levels resulting from irrigation release patterns have a multiple level impact by not only reducing available invertebrate habitat, but also on water quality. It is conceivable that fluctuating water levels would result in significant dieback of littoral biofilms through dessication. Burns and Walker (2000) found lower algal biomass on wood blocks in fluctuating surface waters compared to the more stable sediment surface in the Lower Murray River. Thus, during the irrigation season there could be a greater turnover of organic matter via dead biofilm, hence increased respiration through decomposition of biofilms. These decomposition processes could presumably lead to reduced dissolved oxygen levels and consequently have a negative impact on the epiphytic invertebrates (Ward 1992).

Temperature has been demonstrated to be a strong driver of seasonal distribution and abundance of invertebrates (Hynes, 1970; Ward and Stanford, 1982). The climate, particularly temperature, within the study region is relatively predictable, and despite lack of seasonal replication (samples only taken over the course of one year), there is some evidence of seasonality. Reduced densities occurred in summer and early autumn after which numbers peaked in winter. Peak abundances of invertebrates in other regional River Murray billabongs have also been found in mid-winter (Hillman, 1986; Syariffuddin, 2000), suggesting that there is a predictable seasonal pattern for the invertebrate fauna of these systems. However, these billabongs no longer exist in their natural state due to modified flooding and drying regimes as a result of river regulation (Hillman, 1998). Invertebrate life-cycles in aquatic habitats in this region have been altered as a result of thermal disruption brought about by weir construction (Pardo *et al.*, 1998). Although temporal data were limited for testing seasonal variability, data could be compared for December 1995 and 1996. The taxonomic composition and abundance of many invertebrate groups were extremely different between the two years, suggesting that the assemblage may not cycle on a regular seasonal pattern.

The altered hydrological regime (fluctuating water levels through the irrigation season) might have directly influenced resource availability for macroinvertebrates, particularly for food and space. In the Lower River Murray, Burns and Walker (2000) found that biofilms growing on hardwood blocks had reached peak algal biomass and chlorophyll after 90 days of inundation. Furthermore, biofilms were in a succession phase, being dominated by cyanobacteria after 28 days of inundation, being gradually replaced by green algae from 56 through to 90 days, suggesting that biofilms may take months to recover from water level disturbance. Since water levels during the fluctuating periods were never stable for more than one week, biofilms would have been highly disturbed (either inundated and subsequently impacted by low light availability), or dessicated by exposure to air. Lower invertebrate abundance was observed in December 1995 and March 1996, when water level fluctuations across a large range were most frequent. In contrast, the highest numbers were observed in June 1996 when water level was the most stable. Stable water levels prior to April and continuing through June might have allowed invertebrate numbers to increase through reproduction and recruitment by taxa with flexible and relatively short life-cycles. Certainly chironomids are capable of rapid recovery after disturbance by producing multiple cohorts with non-synchronous emergence (Maher, 1984; Sweeney Jackson, and Funk, 1995). Another possible explanation for higher numbers during stable water levels is

that invertebrates were concentrated in the remaining available habitat as billabong water levels fell (Marchant 1982). This was certainly evident in June when only 5% of the total available plant surface area was submerged. Because most taxa were sedentary, it is unlikely that they could have relocated to find vacant and amenable habitat. This would be expected to impact on billabong food webs, as evidenced by negative impacts on fish assemblages at these times (Balcombe and Closs 2004; Balcombe and Humphries 2006).

It was surprising that invertebrate abundance was not strongly associated with habitat complexity given that such a pattern is often found because of increases in colonizeable area and/or predator refuge with greater plant complexity (Beckett *et al.*, 1992; Taniguchi *et al.*, 2003 Schriver *et al.*, 1995; Diehl, 1988). Carp gudgeons are the numerically dominant fish species and are significant macroinvertebrate predators in these stands (Balcombe and Humphries 2006). The lack of association between invertebrate numbers and stem density could suggest that carp gudgeons feeding is not constrained by plant stem density (Balcombe and Closs 2004). If so, there would be no advantage for the epifauna to select habitats within the giant rush based upon plant complexity.

Depth appeared to be the most important measured parameter influencing invertebrate distribution and abundance. This may suggest that depth provides something in addition to increased plant surface area. For example, increased water depth among giant rush stems could increase the number of potential microhabitats that would be provided by biofilm zonation (Mullen 1998). It was also interesting that the significant associations between water depth and abundance occurred following fluctuating water levels. Fluctuating water levels could lead to further biofilm zonation as different sections of stem would have been subject to varying periods of inundation. The biofilm composition and nutritional quality would be highly variable and dynamic during these periods of fluctuation (Burns and Walker 2000), providing invertebrates with a dynamic mosaic of habitat.

As habitat structure and invertebrate abundance relationships were not common, invertebrates may not have been responding to these measures of complexity *per se*, but rather to other variables associated with habitat structure, such as algal diversity within biofilms or biofilm density. Biofilm density and diversity are likely to be directly correlated with macrophyte surface area (Brönmark, 1989;) and invertebrate abundance will in turn be influenced by the nature of the biofilm (Hart, 1981; Dudley, 1986; Ward, 1992; Bergey, 1995; Lohleinn, 1996). The quantity and quality of

epiphytic food resources are known to influence the structure of invertebrate assemblages (Cummins and Merritt, 1984; Campeau, Murkin, and Titman, 1994; Russo, 1997). Within giant rush stands most invertebrates (either directly or indirectly) would gain at least some of their nutrition from the attached biofilms (Gregory, 1983; Lamberti and Moore, 1984). Filter feeders such as *K. martini*, probably feed upon material entering from the pelagic zone (Dvorak and Best, 1982), although some of this material may originate from sloughed biofilm or components dislodged by grazers (Lamberti *et al.*, 1989). Regardless of whether it is used as food by the epiphytic invertebrates, biofilms are likely to add habitat complexity to the simple structure of the giant rush stems. Close inspection of the stems revealed that most of the invertebrates were found within (such as chironomids and oligochaetes) or attached to the biofilm matrix (such as *Hydra* sp. and *Ferrissia* sp.).

In conclusion, the invertebrates associated with giant rush in DB show high variability in distribution and abundance that is largely driven by an unpredictable hydrological environment related to an altered hydrological regime in the adjacent River Murray. In DB, water level variation has an overriding influence upon invertebrate production amongst emergent macrophytes, a pattern that is likely to be widespread in floodplain waterbodies affected by managed river flows. Since dams and storages control the hydrological regime of the River Murray, knowledge of the how flow release patterns impact on both river and floodplain biota is important for the overall health of such systems. For example, our results suggest that to maximize aquatic invertebrate diversity in floodplain billabongs, rapid water level fluctuations during the irrigation season should be avoided and drawdown periods extended in associated rivers to allow the relatively immobile invertebrates opportunities to relocate rather than being stranded. The ramifications of continued poor management of these floodplain waterbodies is likely to result in reduced regional aquatic invertebrate diversity and productivity resulting in reduced energy transfer through riverine food webs (Balcombe and Humphries 2006). Such impacts are likely to flow through to higher organisms such as fish and waterbirds (Kingsford 2000; Balcombe and Closs 2004; Balcombe and Humphries 2006; Closs *et al.*, 2006), further reducing the integrity and diversity of these iconic ecosystems.

ACKNOWLEDGEMENTS

This study was supported by a LaTrobe University and CRC for Freshwater Ecology Postgraduate Stipends. The authors wish to thank Fran Sheldon, Wade Hadwen, Janet Hussein, Sarra Hinshaw and two anonymous referees for helpful comments on and earlier draft.

REFERENCES

- Aloi, J.E. (1990) A critical review of recent freshwater periphyton field methods. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 656-670.
- Balcombe, S.R. (2002). Resource use by *Hypseleotris* (Pisces: Gobiidae) in the littoral macrophytes of a floodplain billabong. Unpubl. PhD thesis. Department of Environmental Management and Ecology, LaTrobe University, Albury/Wodonga, Australia.
- Balcombe, S.R. and Closs, G.P. (2000) Variation in carp gudgeon (*Hypseleotris* spp.) catch rate in dense macrophytes. *Journal of Freshwater Ecology* **15**: 389-385.
- Balcombe S.R. and Humphries P. (2006) Diet of the western carp gudgeon (*Hypsleotris klunzingeri* Ogilby) in an Australian floodplain lake: the role of water level stability. *Journal of Fish Biology* **68**: 1484-1493.
- Closs, G.P., Balcombe, S.R., Driver, P., McNeil, D.G. & Shirley, M.J. (2006) "The importance of floodplain wetlands to Murray-Darling fish: What's there? What do we know? What do we need to know?" pp. 14-28. In "*Native fish and wetlands in the Murray Darling Basin: Action Plan, knowledge gaps and supporting papers.*" Proceedings of a workshop held in Canberra ACT, 7-8 June 2005. Murray-Darling Basin Commission, Canberra.
- Beckett, D.C., Aartila, T.P. and Miller, A.C. (1992) Invertebrate abundance on *Potamogeton nodosus*: effects of plant surface area and condition. *Canadian Journal of Zoology* **70**: 300-306.
- Bergey, E.A. (1995) Local effects of a sedentary grazer on stream algae. *Freshwater Biology* **33**: 401-409.
- Boon, P.I., Frankenberg, J., Hillman, T.J., Oliver, R.L., and Shiel R.J. (1990) Billabongs. In *The Murray* (Eds. N. Mackay and D. Eastburn). pp. 182-198. Murray Darling Basin Commission: Canberra.
- Boulton, A. J. and Lloyd, L. N. (1991). Macroinvertebrate assemblages in floodplain habitats of the lower River Murray, South Australia. *Regulated Rivers: Research and Management* **6**: 183-201.
- Bunn, S.E. and Boon, P.I. (1993) What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia* **96**: 85-94.
- Burns, A. and Walker, K.F. (2000) Effects of water level regulation on algal biofilms in the River Murray, South Australia. *Regulated Rivers: Research and Management* **16**: 433-444.
- Cartright, D.I. (1997) *Preliminary Guide to the Identification of Late Instar Larvae of*

- Australian Ecnomidae, Philopotamidae and Tasimiidae* Co-operative Research Centre for Freshwater Ecology, Albury.
- Campeau, S., Murkin, H.R. and Titman, R.D. (1994) Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 681-692.
- Chesterfield, E.A. (1986) Changes in the vegetation of the river red gum forest at Barmah, Victoria. *Australian Forestry* **49**: 4-15.
- Cranston, P.S. (1996) Identification Guide to the *Chironomidae* of New South Wales. Australian Water Technologies, EnSight, West Ryde, NSW.
- Cummins, R.W. and Merritt, R.W. (1984) Ecology and distribution of aquatic insects. In *An Introduction to the aquatic insects of North America*, 2nd edn. (Eds. R. W. Merritt and K.W. Cummins) pp 59-65. Kendall/Hunt, Iowa.
- Davis, J. and Christidis, F. (1997) *A Guide to Wetland Invertebrates of Southwestern Australia* Western Australian Museum, Perth.
- Dean, J.C. and Suter, P.J. (1996) *Mayfly Nymphs of Australia: A guide to Genera*. Co-operative Research Centre for Freshwater Ecology, Albury.
- Diehl, S. (1988) Foraging efficiency of three freshwater fish: effects of structural complexity and light. *Oikos* **53**: 207-214.
- Dudley, T. (1986) Beneficial effects of grazers on algal growth. *Bulletin of the North American Benthological Society* **3**: 87.
- Dvorak, J. and Best, E.P.H. (1982) Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. *Hydrobiologia* **95**: 115-126.
- Gregg, W.W. and Rose, F.L. (1985) Influence of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia* **128**: 45-56.
- Gregory, S.V. (1983) Plant-herbivore interactions in stream systems. In *Stream Ecology* (Eds. J.R. Barnes and G.W. Minshall) pp. 157-189. Plenum, New York.
- Hart, D.D. (1981) Foraging and resource patchiness: field experiments with a grazing stream insect. *Oikos* **37**: 46-52.
- Hawking, J.H. and Smith, F.J. (1997) *Colour Guide to Invertebrates of Australian Inland Waters*. Co-operative Research Centre for Freshwater Ecology, Albury.
- Hawking, J.H. 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*. Co-operative Research Centre For

Freshwater Ecology, Albury.

- Hillman, T.J. (1986) Billabongs. In *Limnology in Australia* (Eds. P. De Deckker and W.D. Williams) pp. 457-470. CSIRO/Dr W. Junk, Melbourne and Dordrecht.
- Hillman, T.J. (1998) Billabongs: management issues for floodplain wetlands. In *Wetlands in a Dry Land: Understanding for Management*. (Ed. W.D. Williams). pp. 41-47. Environment Australia, Biodiversity Group, Canberra.
- Hillman, T.J. and Shiel, R.J. (1991) Macro- and microinvertebrates in Australian billabongs. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* **24**: 1581-1587.
- Humphries, P. (1996) Aquatic macrophytes, macroinvertebrate associations and water levels in a lowland Tasmanian river. *Hydrobiologia* **321**: 219-233.
- Hynes, H.B.N. (1970) The ecology of stream insects. *Annual Review of Entomology* **15**: 25-42.
- Keppel, G. (1991) *Design and Analysis: A researcher's handbook*, 4th edn. Prentice-Hall, New Jersey.
- Kingsford, R.T. (2000) Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology* **25**: 109-127.
- Lamberti, G.A., Gregory, S.V., Ashkenas, L.R., Wildman, R.C. and Moore, K.M.S. (1989) Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. *Ecology* **70**: 1840-1856.
- Lamberti, G. A. and J. W. Moore (1984). Aquatic insects as primary consumers. In *The ecology of aquatic insects*. (Eds. V. H. Resh and D. M. Rosenberg) pp. 164-195. Praeger, New York.
- Lohlein, B (1996) Seasonal dynamics of aufwuchs Naididae (Oligochaeta) on *Phragmites australis* in a eutrophic lake. *Hydrobiologia* **334**: 115-123.
- Maher, M. (1984) Benthic studies of waterfowl breeding habitat in south-western New South Wales, I. The Fauna. *Australian Journal of Marine and Freshwater Research* **35**: 85-96.
- Marchant R. (1982) Seasonal variation in the macroinvertebrate fauna of billabongs along Magela Creek, Northern Territory. *Australian Journal of Marine and Freshwater Research*, **33**, 329-342.
- Mullen, C. (1998) Comparisons of biofilm growth on artificial substrata in static and fluctuating water levels in a weir pool in the Murray River. Unpublished Honours thesis. Department of Environmental Management and Ecology, LaTrobe University, Wodonga, Victoria, Australia

- Outridge, P.M. (1988) Seasonal and spatial variations in benthic macroinvertebrate communities of Magela Creek, Northern Territory. *Australian Journal of Marine and Freshwater Research* **39**: 211-223.
- Pardo, I., Campbell, I.C. and Brittain, J.E. (1998) Influence of dam operation on mayfly assemblage structure and life histories in two south-eastern Australian streams. *Regulated Rivers: Research and Management* **14**: 285-295.
- Pinder, A.M. and Brinkhurst, R.O. (1994) *A Preliminary Guide to the Identification of the Microdril Oligochaetes Of Australian Freshwaters*. Co-operative Research Centre for Freshwater Ecology, Albury.
- Russo, A.R. (1997) Epifauna living on sublittoral seaweeds around Cyprus. *Hydrobiologia* **344**: 169-179.
- Schriver, P., Bogestrand, J., Jeppesen, E. and Sondergaard, M. (1995) Impacts of submerged macrophytes on fish-zooplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology* **33**: 255-270.
- Shiel, R.J. (1980) Billabongs of the Murray-Darling system. In *An ecological basis for water resource management* (Ed. W.D. Williams) pp. 378-390. ANU Press, Canberra, Australia.
- Shiel, R.J. (1995) *A Guide to the Identification of Rotifers, Cladocerans and Copepods from Australian Inland Waters*. Co-operative Research Centre for Freshwater Ecology, Albury.
- Sokal, R.R. and Rohlf, F.J. (1995) Biometry. *The Principles and Practice of Statistics in Biological Research*. 3rd edn. Freeman, New York.
- Sweeney B.W., Jackson J.K. and Funk D.H. (1995) Semivoltinism, seasonal emergence, and adult size variation in a tropical stream mayfly (*Euthyplocia hecuba*) . *Journal of the North American Benthological Society* **14**: 131-146.
- Taniguchi, H., Nakano, S. and Tokeshi, M. (2003) Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshwater Biology* **48**: 718-728.
- van de Meutter, F., Stoks, R. and De Mester, L. (2005) The effect of turbidity state and microhabitat on macroinvertebrate assemblages: a pilot study of six shallow lakes. *Hydrobiologia* **542**:379-390.
- Vannote, R.L. and Sweeney, B.W. (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* **115**: 667-695.
- Ward, J.V. (1992) *Aquatic Insect Ecology*. John Wiley and Sons Inc., New York.

- Ward, J.V. and Stanford, J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27**: 97-117.
- Williams, W.D. (1980) *Australian Freshwater Life* MacMillan, Melbourne.
- Wilkinson, L. (1996) Systat 6.0 for Windows. SPSS, Chicago Illinois, USA.

TABLES

Table 1 Available invertebrate habitat (wetted stem surfaces) as percentage of total plant surface area in the giant rush stands at 0,7,14,21 and 28 days before each sampling date and summary of daily water levels in the same 28 days period.

Sampling date	28d.	21d	14d	7d.	0d	General water level conditions and their source
14 Dec. 1995	75	15	10	55	40	Large fluctuations to 6 days prior to sampling, followed by stable conditions. Early irrigation season imposing aseasonal fluctuations from managed flow release.
13 Mar. 1996	40	65	32	31	65	Large fluctuations in the 28 days prior to sampling. Late irrigation season with aseasonal fluctuating water levels.
27 Apr. 1996	25	15	10	10	10	Minor fluctuations 28-16d prior to sampling, stable thereafter. Low water level variability from final flow release of irrigation season, then natural seasonal stability due to low autumn rainfall.
29 Jun. 1996	5	5	5	5	5	Very stable water levels for full 28d. Natural winter stability, low evaporation and no run-off.
5 Dec. 1996	100	100	20	15	25	Large decrease in water levels between 28-14 days followed by fluctuating levels in the last 14d. Aseasonal fluctuations as a result of flow management at the start of irrigation season.

Table 2 Summary of the dominant taxa from SIMPER analysis (individually accounting for > 5 % of the similarity among sampling sites) for each individual sampling event and groups of events based upon environmental conditions.

Sampling date/factor	Average similarity (%)	Significant taxa (% similarity)
Event 1	44	<i>Polypedilum convexum</i> (19), <i>Polypedilum leei</i> (12), <i>Cyclopoida</i> spp. (10), <i>Kiefferulus martini</i> (9), <i>Procladius paludicola</i> (7), <i>Hydra</i> sp. (7), <i>Chaetogaster</i> sp. (6)
Event 2	41	<i>P. leei</i> (31), <i>Ferrissia</i> sp. (13), <i>Hydra</i> sp. (12), <i>Pristina</i> sp. (10), <i>K. martini</i> (9), <i>P. convexum</i> (6)
Event 3	58	<i>P. leei</i> (28), <i>K. martini</i> (19), <i>Pristina</i> sp. (14), <i>Daphniidae</i> spp. (10) <i>Kiefferulus intertinctus</i> (6), <i>Dicrotendipes jobetus</i> (6)
Event 4	54	<i>K. martini</i> (37), <i>Calanoida</i> spp. (14), <i>Pristina</i> sp.(13), <i>P. leei</i> (7), <i>Chaetogaster</i> sp. (6), <i>Nematoda</i> sp. (6), <i>Pristinella</i> sp. (6)
Event 5	49	<i>K. martini</i> (63), <i>Ferrissia</i> sp. (21)
Low DO2	36	<i>P. leei</i> (23), <i>Hydra</i> sp. (11), <i>P. convexum</i> (10), <i>K. martini</i> (10), <i>Pristina</i> sp. (8), <i>Ferrissia</i> sp. (7), <i>Chaetogaster</i> sp. (5)
High DO2	37	<i>K. martini</i> (46), <i>P. leei</i> (11), <i>Pristina</i> sp. (9), <i>Ferrissia</i> sp. (6),
Low water depth & temperature	28	<i>K. martini</i> (27), <i>P. leei</i> (19), <i>Pristina</i> sp. (15), <i>Daphniidae</i> spp. (7), <i>Nematoda</i> sp. (5), <i>Chaetogaster</i> sp. (5), <i>Calanoida</i> spp.(5)
High water depth & temperature	45	<i>K. martini</i> (24), <i>P. leei</i> (14), <i>Ferrissia</i> sp. (13), <i>Hydra</i> sp. (11), <i>P. convexum</i> (6), <i>Pristina</i> sp. (6)

Table 3 Results of ANOSIM pairwise temporal comparisons (R statistic) between sampling events or environmental groups based upon log transformed abundance data, plus the taxa identified by SIMPER as making significant contributions to pairwise differences between sampling events (individually accounting for > 5 % of the similarity among sampling events). * indicates significant differences at $P < 0.001$.

Pairwise comparison	Average dissimilarity	Global R	Significant taxa (%)
Event 1 v Event 2	70.2	0.48*	<i>P. convexum</i> (16), Cyclopoida spp. (9), <i>P. leei</i> (6), <i>Hydra</i> sp. (6), <i>K. martini</i> (6), <i>P. paludicola</i> (6), <i>Chaetogaster</i> sp. (6), <i>Ferrissia</i> sp. (5) <i>Bezzia</i> sp. (5), <i>Pristina</i> sp. (5)
Event 1 v Event 3	74.2	0.74*	<i>P. leei</i> (19) <i>K. martini</i> (14), <i>Pristina</i> sp. (10), Daphniidae spp. (9), <i>P. convexum</i> (7), <i>K. intertinctus</i> (7), <i>D. jobetus</i> (5)
Event 1 v Event 4	87.6	0.93*	<i>K. martini</i> (34), Calanoida spp. (12), <i>Pristina</i> sp. (10), <i>P. leei</i> (6), <i>Chaetogaster</i> sp. (5), Bryozoa sp. (5), <i>Pristinella</i> sp. (5), Nematoda sp. (5)
Event 1 v Event 5	82.9	0.86*	<i>K. martini</i> (44), <i>Ferrissia</i> (10), <i>P. convexum</i> (8)
Event 2 v Event 3	82.3	0.72*	<i>P. leei</i> (22), <i>K. martini</i> (17), Daphniidae spp. (11), <i>Pristina</i> sp. (11), <i>K. intertinctus</i> (8), <i>D. jobetus</i> (6)
Event 2 v Event 4	93.2	0.86*	<i>K. martini</i> (35), Calanoida spp. (13), <i>Pristina</i> sp. (11), <i>P. leei</i> (6), <i>Chaetogaster</i> (6), Bryozoa sp. (5), Nematoda sp. (5), <i>Pristinella</i> sp. (5)
Event 2 v Event 5	84.6	0.74*	<i>K. martini</i> (56), <i>Ferrissia</i> sp. (14)
Event 3 v Event 4	66.9	0.86*	<i>K. martini</i> (33), Calanoidea (13), <i>Pristina</i> sp. (8), <i>P. leei</i> (7), <i>Chaetogaster</i> sp. (6), <i>Pristinella</i> sp. (5), Bryozoa sp. (5)
Event 3 v Event 5	73.8	0.79*	<i>K. martini</i> (30), <i>P. leei</i> (18), <i>Pristina</i> sp. (9), Daphniidae (8), <i>Ferrissia</i> sp. (6) <i>K. intertinctus</i> (6)
Event 4 v Event 5	74.0	0.84*	<i>K. martini</i> (30), Calanoida spp. (13), <i>Pristina</i> sp. (11), <i>P. leei</i> (7), <i>Chaetogaster</i> (6), <i>Pristinella</i> sp. (5), Nematoda sp. (5), Bryozoa (5)
Low DO2 v High DO2	84	0.53*	<i>K. martini</i> (34), <i>P. leei</i> (10), <i>Pristina</i> sp. (7), <i>Ferrissia</i> (5), Calanoida spp. (5)
Low WD/T v High WD/T	81	0.36*	<i>K. martini</i> (27), <i>P. leei</i> (13), <i>Pristina</i> sp. (10), Calanoida spp. (7), Daphniidae spp. (6)

Table 4 Summary of BIO-ENV results based on Spearman rank correlations (r_s) between invertebrate assemblage structure and habitat measures and water quality variables: DO2=dissolved oxygen, Psa=plant surface area, Std=Stem density, Dep=water depth, Tem=temperature, Con=conductivity. Note: Results only presented for best possible solution, for three, two and single combinations.

Sampling event	<i>Best variable combination</i>		
	1 variable	2 variables	3 variables
All events	DO2 (0.48)	Psa, Tem (0.53)	Tem, DO2, Dep (0.50)
1	Std (0.05)	Tem, Con (0.03)	Tem, Dep, Con (.01)
2	Dep (0.28)	Tem, Dep (0.32)	Std, Tem, Dep (0.38)
3	DO2 (0.20)	DO2, Con (0.18)	Std, DO2, Con (0.18)
4	Psa (0.13)	Psa, Tem (0.08)	Std, Psa, Tem (0.05)
5	Tem (0.24)	Psa, Tem (0.28)	Psa, Tem, DO2 (0.22)

Table 5 Summary of spearman rank correlations for invertebrate fauna abundance with habitat variables in giant rush patches * = p<0.005 ** = p< 0.0005

Sampling event	species	Std	Psa	Temp	DO2	Con	Depth
1	<i>Parachironomus</i>						0.64**
2	<i>Nais</i> sp.	-0.55*					0.58**
2	<i>Ferrissia</i> sp.				0.52*		
2	total abundance	-0.63**	0.57*				
2	taxon richness						0.70**
3	<i>Bezzia</i> sp. 1	-0.57*					
3	<i>K. intertinctus</i>					-0.52*	
3	Nematoda sp.		-0.56*				
4	<i>P. leei</i>		-0.64*				
4	<i>Hellyethira simplex</i>		-0.60*				
4	Calanoida spp.		-0.60*				
4	total abundance		0.52*				
5	<i>K. martini</i>			0.56*		0.59*	
5	<i>Ferrissia</i> sp.			-0.57*			
5	<i>Triplectides australis</i>						0.6*
5	<i>H. simplex</i>					0.59*	
5	<i>Chaetogaster</i> sp.					0.52*	
5	total abundance			0.52*		0.63**	
5	taxon richness						0.56*

Figure Legends

Figure 1. Location of Dugays billabong (D2) in relations to Lake Hume, Lake Mulwala and inset in relation to the Murray-Darling Basin, Australia.

Figure 2. Daily water levels in Dugays 2 billabong over 12 months. Note: Irrigation period as indicated. Arrows indicate dates when invertebrate samples were collected. Stem and leaf plots represent mean, standard deviation and range of daily water levels in the 28d prior to sampling.

Figure 3. Seasonal variation ($\pm$ 1S.E.) in sampling depth, temperature, dissolved oxygen and conductivity between December 1995 and December 1996. Note: only three data points for conductivity due to equipment failure.

Figure 4. MDS plots showing invertebrate assemblage structure across giant rush sites over five sampling events based upon $\log_{10}$ transformed invertebrate density for A) all sampling events B) events with low or high DO₂ and C) events with high temp/depth or low temp/depth

Appendix I Mean densities (± 1 s.e) (number of individuals per m³ of giant rush surface) of the most abundant taxa (those invertebrates that cumulatively account for > 90% of total abundance on any one date {from SIMPER}) in the giant rush stands of DB. * indicates presence, but low in density.

		Dec 1995	Mar 1996	Apr 1996	Jun 1996	Dec 1996
CNIDARIA	<i>Hydra</i> sp.	39 $\pm$ 5	57 $\pm$ 14	12 $\pm$ 3	1.7 $\pm$ 1.7	49 $\pm$ 8
NEMATODA	Nematoda sp.	17 $\pm$ 3	46 $\pm$ 16	82 $\pm$ 14	342 $\pm$ 58	23 $\pm$ 4
OLIGOCHAETA	<i>Chaetogaster</i> sp.	52 $\pm$ 10	17 $\pm$ 5	72 $\pm$ 14	448 $\pm$ 79	17 $\pm$ 3
	<i>Nais</i> sp.	43 $\pm$ 11	35 $\pm$ 7	252 $\pm$ 32	767 $\pm$ 120	16 $\pm$ 4
	<i>Pristina</i> sp.		8.9 $\pm$ 3.1	20 $\pm$ 5	334 $\pm$ 52	19 $\pm$ 5
	<i>Pristinella</i> sp.		*	*	*	*
	Tubificidae sp.				*	
	<i>Branchiura sowerbyi</i> Beddard			*	*	
HIRUDINEAE	<i>Glossiphonia</i> sp.	*			*	*
MOLLUSCA						
GASTROPODA	<i>Ferrissia</i> sp.	29 $\pm$ 8	35 $\pm$ 6	54 $\pm$ 7	26 $\pm$ 5	183 $\pm$ 22
	<i>Austropeplea</i> sp.	*		*	*	
BRYOZOA	Bryozoa sp.			18 $\pm$ 11	263 $\pm$ 46	41 $\pm$ 10
CRUSTACEA	Chydoridae spp.	*		*	*	*
	Daphniidae spp.	36 $\pm$ 7	4.6 $\pm$ 1.3	256 $\pm$ 49	159 $\pm$ 28	10 $\pm$ 2
	Calanoida spp.	9.4 $\pm$ 3.5	2.7 $\pm$ 0.9	14 $\pm$ 4	770 $\pm$ 110	0.6 $\pm$ 0.3
	Cyclopoida spp.	93 $\pm$ 17	5.1 $\pm$ 1.2	19 $\pm$ 3	68 $\pm$ 12	3.8 $\pm$ 1.0
	<i>Bosmina</i> spp.	*	*	*		*
	Ostracoda spp.	*	*	*	*	*
ARACHNIDA						
HYDRACARINA	<i>Hydrachna</i> sp.	**	*	*	*	*
INSECTA						
EPHEMEROPTERA	<i>Cloeon</i> sp.	*		*		
ODONATA	Amphiterigidae sp.			*		*
	<i>Austrolestes annulosus</i> Selys	*	*			
	<i>Corduliidae</i> sp.			*	*	
	<i>Synlestidae</i> sp.		*			
HEMIPTERA	<i>Hydrometra</i> sp.	*				
	<i>Mesovelgia</i> sp.	**	*	*		*
	<i>Micronecta</i> sp.	*			*	
COLEOPTERA	Dytiscidae sp.		*		*	
	Chrysomelidae sp.	*				
	<i>Hydrochus</i> sp.	*				
	<i>Naucoris</i> sp.	*				
	Hydrophilidae sp.	*				
	Gyrinidae sp.	*		*		*
DIPTERA						
Ceratopogonidae	<i>Bezzia</i> sp1	50 $\pm$ 11	20 $\pm$ 6	81 $\pm$ 20	69 $\pm$ 18	
	<i>Bezzia</i> sp2	*	*	*	*	
	Ceratopogonidae sp3	*	*	*	*	
Chironomidae	<i>Corynoneura</i> sp.	**				
	<i>Dicrotendipes jobetus</i> Epler	50 $\pm$ 23	2.1 $\pm$ 0.8	123 $\pm$ 18	164 $\pm$ 45	28 $\pm$ 7
	<i>Harrisius</i> sp.	*	*			
	<i>Kiefferulus martini</i> Freeman	60 $\pm$ 9	25 $\pm$ 6	377 $\pm$ 46	2660 $\pm$	1240 $\pm$

					440	220
	<i>Kiefferulus intertinctus</i> Skuse	19 ± 4	6.5 ± 2.1	164 ± 33	110 ± 32	3.1± 1.5
	<i>Limnophyes</i> sp.	*				
	<i>Microchironomus</i> sp.	*		*		
	<i>Parachironomus</i> sp.	38 ± 6	16 ± 5	7.5 ± 3.4	3.2 ± 2.2	17 ± 4
	<i>Parakiefferiella</i> sp.	*		*	*	*
	<i>Paratanytarsus</i> sp.		*	*		*
	<i>Polypedilum convexum</i>	162 ± 33	15 ± 3	9.3 ± 3.7	7.8 ± 4.8	7.9 ± 6.5
	Johannsen					
	<i>Polypedilum leei</i> Freeman	74 ± 11	56 ± 6	507 ± 58	508 ± 87	16 ± 4
	<i>Procladius paludicola</i> Skuse	59 ± 9	6.4 ± 2.1	6.9 ± 2.3	6.0 ± 4.3	0.4 ± 0.3
	<i>Stenochironomus</i> sp.			*		
	<i>Tanytarsus bispinosus</i>	*				
	Freeman					
	<i>Xenochironomus</i> sp.			*		*
Psychodidae	Psychodidae sp.				*	
TRICHOPTERA	<i>Ecnomus turgidus</i> Neboiss				*	
	<i>Hellyethira simplex</i> Neboiss	**	*	*	*	*
	<i>Eventlectides australis</i> Navas	*	*	*		*
TOTAL NUMBER OF TAXA		42	31	40	35	31
Total abundance		920 ± 100	326 ± 34	2190 ± 190	6880±750	1750 ± 220
Taxon richness		18.1 ± 0.7	11.9 ± 0.7	17.5 ± 0.5	16.9 ± 0.4	13.3 ± 0.6