OVER-SUMMERING REFUGES OF AQUATIC MACROINVERTEBRATES IN TWO INTERMITTENT STREAMS IN CENTRAL VICTORIA

by A. J. BOULTON*

Summary

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Eight potential refuges for macroinvertebrates were sampled in two intermittent streams in central Victoria, Australia, during summer 1982–83 and summer 1983–84. Ninety-one aquatic taxa, mostly insects, were recorded. Receding pools harboured nearly three-quarters of these taxa; comparatively few were collected from the hyporheos or the water in crayfish burrows. Almost half the taxa were from refuges that did not hold free water. Macroinvertebrates persisted as desiccation-tolerant eggs (mayflies), larvae (chironomids and some beetles) or adults (beetles).

There was remarkable similarity between the broad taxonomic representation in these refuges and those described for intermittent streams in Ontario, Canada.

KEY WORDS: Intermittent streams, over-summering refuges, aquatic macroinvertebrates, Victoria, Australia, pholeteros, hyporheos.

Introduction

Ephemeral (episodic) and intermittent rivers and streams drain over half of the Australian mainland (W.D. Williams 1983) but despite their ubiquity and scientific interest, these systems have attracted little limnological attention (Boulton & Suter 1986; Boulton & Lake 1988). The situation is little better elsewhere (Williams 1987).

In intermittent streams, loss of water during the dry season is probably the most influential environmental parameter affecting the aquatic biota and has led to a wide range of physiological and behavioural adaptations (reviewed by Williams 1987). Behavioural avoidance appears to play a major part in the survival of many stream invertebrates during drought. Williams & Hynes (1977) recognized eight distinct types of refuges that were used by the fauna of a temporary stream in Ontario during summer and suggested that members of certain major taxonomic groups tended to over-summer as similar stages in their life cycle. For example, Ephemeroptera and most Chironomidae over-summered as eggs whereas Gastropoda, some Odonata, Hemiptera and Coleoptera survived the dry period as adults (Williams & Hynes 1977).

In temperate Australian intermittent streams, recolonization pathways and potential over-summering refuges have never been investigated and little is known about the physiological or behavioural adaptations exhibited by the aquatic biota (Boulton & Lake 1988). This study was aimed at elucidating over-summering strategies of aquatic macroinvertebrates in two intermittent streams in Victoria. I also was interested to see how closely the strategies used by biota in the intermittent Victorian streams matched those described by Williams & Hynes (1977) based on work done on intermittent streams in the northern hemisphere.

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Materials and Methods

Study Area

Two study sites were located on the upper reaches of the Werribee River and two more on its main tributary, the Lerderderg River (Fig. 1). Both rivers arise on the southern edge of the Great Dividing Range approximately 100 km north-west of Melbourne and flow south-east before joining near Bacchus Marsh, north-west of Melbourne. Details of flow regime and catchment vegetation are given in Boulton & Smith (1985); other physicochemical data are presented in Boulton & Suter (1986).

The two rivers differ in permanency: the Werribee River ceases flow almost annually whereas the Lerderderg River flows throughout summer for one year in three. On average, the Werribee River does not flow for nine weeks while the Lerderderg ceases flow for six. The Werribee River did not flow at all at one site (Spargo Creek, SC) during the 1982 drought and only flowed for five months (late June to late November) at the site downstream (Werribee Picnic Spot, WPS). The study pool at WPS dried up completely during the ensuing summer. The following year, flow commenced in late June and continued for seven and a half months at both sites.

Flow started in late May 1982 at both sites (Fireplace Ford, FF and Wheeler Road, WR) on the

Lerderderg River and ceased in early December. At FF, the study pool dried to a moist patch of leaves and water did not appear in the depression until mid-March 1983. At WR, the study pool was dry for six weeks before it also refilled in mid-March; flow resumed at both sites in early May, continuing over the following summer.

Physicochemical Monitoring of Potential Refuges

On 20.i.1983, diel ranges of temperature in and around a receding pool at WPS were measured using a 9-channel Miniature Intermittent Temperature Recorder (Grant Instruments, Cambridge, England). Thermistors were placed in shallow (5 cm) and deep (45 cm) water, below leaf litter, beneath a large flat rock, in the water of a crayfish (*Engaeus* sp.) burrow and in exposed grass in direct sunlight (regarded as "air temperature" cf. normal meteorological practise). Recording commenced at 5.00 a.m. and ceased at midnight.

At other times, spot water temperatures (mercury thermometer), dissolved oxygen (oxygen probe, Model 51A, Y.S.I., Yellow Springs, Ohio), conductivity (conductivity meter, Radiometer, Denmark) and pH (Metrohm pH meter, Model CH9100, England) were measured when potential refuges containing free water were sampled. Conductivity data were converted to values at 18°C (K_{18}) (Bayly & Williams 1973) whereas dissolved oxygen was expressed as percentage saturation using the conversion table in Bayly & Williams (1973) and an appropriate correction factor for altitude.

Biological Sampling of Potential Refuges

A variety of collecting techniques was necessary to sample the diverse range of potential refuges:

(a) An F.B.A. pond-net (300 μm mesh) was used to sample fauna in the receding pools. I vigorously shuffled along the bottom of the pool, sweeping the net from side to side across the disturbed path for 30 seconds for each sample. The size of the pool limited the number of samples that could be collected; while I was keen to ascertain the relative abundance of the fauna, I did not want to deplete the remnant populations. A nearby permanent lake (Shaws Lake, Fig. 1) was sampled similarly.

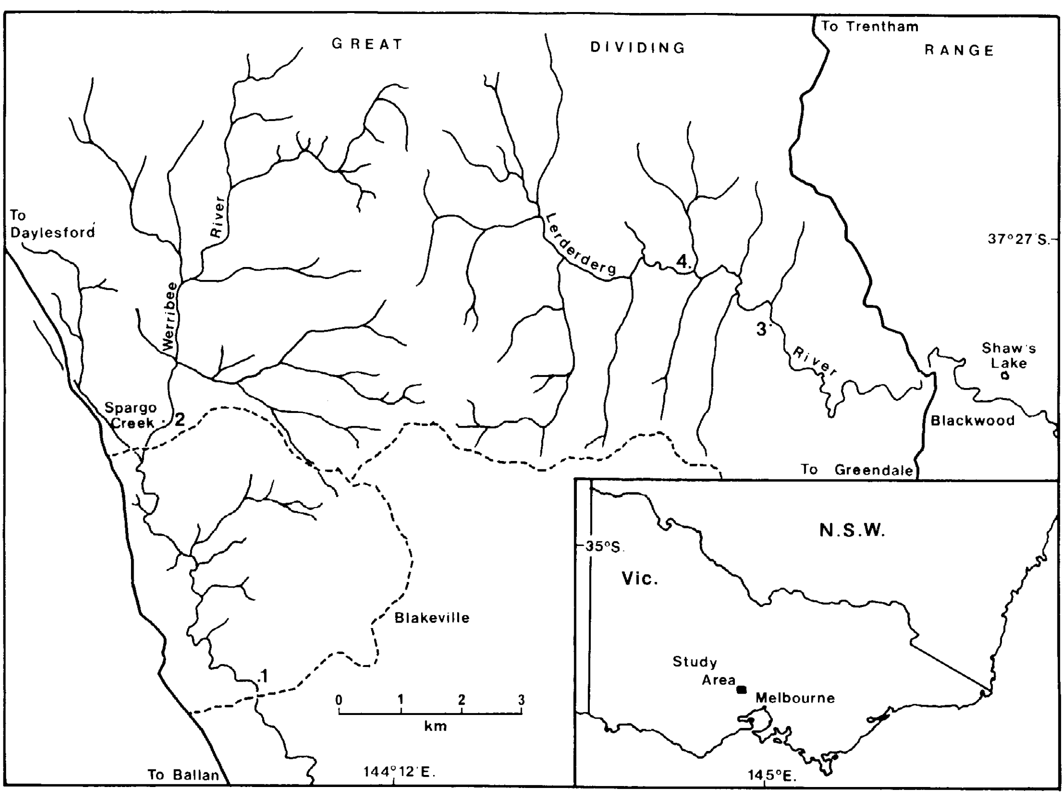

Fig. 1 Map of the study area showing the locations of the four study sites: Werribee Picnic Spot (WPS) = 1, Spargo Creek (SC) = 2, Fireplace Ford (FF) = 3, Wheeler Road (WR) = 4.

(b) Animals residing in the water in crayfish (*Engaeus* sp.) burrows ("pholeteros" *sensu* Lake 1977) were collected by carefully excavating the burrow opening and lowering a flexible plastic tube (6 mm internal diameter) into the burrow water which was sucked out into a plastic bag. In the laboratory, this water was sieved (50 μm) with frequent washing to remove fine silt.

(c) The hyporheos was sampled by digging holes in the dry stream bed and sweeping a small hand-net (50 μm mesh) through the seepage. In some cases, it was necessary to use a plastic tube to collect the water. Quantitative sampling of this habitat was not attempted.

(d) Other potential refuges that were qualitatively sampled while the streams were dry included the humid microhabitats beneath rocks, stumps and mats of leaf litter and dried filamentous algae, and among the roots of riparian plants (e.g. *Carex* spp., *Leptospermum lanigerum*) and stranded *Myriophyllum propinquum* (water milfoil) and *Triglochin procera* (water ribbon). Rotting wood was broken open and examined, and strips of bark were peeled from exposed water-logged snags. Pieces of decomposed wood were brought back to the laboratory for microscopic inspection.

(e) Plastic bags were filled with surface (upper 10 cm) substrata and organic matter collected from the dry beds of riffles and pools. The water content of a subsample of the substratum was determined by subtracting the oven-dry weight (constant weight achieved after 48 h at 100°C) from the initial weight and expressing the value as a percentage. It was assumed that all weight lost during incubation was due to the evaporation of water.

The rest of the sample was emptied into an aquarium immediately upon return to the laboratory and flooded with dechlorinated tap water. Within 30 minutes of immersion of the substrata, a hand-net (50μm mesh) was swept vigorously through the tank and the live contents examined using an Olympus stereomicroscope, and the rank abundance of all invertebrates present was recorded. This process was repeated until no further species were seen. Subsequently, samples were taken at irregular intervals over the next fortnight, always returning the specimens to the tank. Some aquaria were maintained for several months to rear hatchlings through to adults to assist identification.
were identified as far as practicable (see Acknowledgments). Abundance was expressed qualitatively as "present" (1–2 individuals), "common" (3–10) or "abundant" (>10); given the variety of collecting methods and the uneven sampling effort, more precise quantification was inappropriate.

Results

Physicochemical conditions in potential refuges

Means and ranges of spot water temperature, pH, dissolved oxygen and conductivity in two refuges that held free water when they were sampled are listed in Table 1. Not surprisingly, the ranges of these variables were greater in the receding pools than in the burrow water of crayfish (Table 1). Hyporheic water was too disturbed during sampling to obtain reliable physicochemical data and data from Shaws Lake are too few to be useful.

Continuous records of water temperature in a receding pool at WPS illustrated the diel fluctuation of temperatures in various refuges (Fig. 2). Air temperature in direct sunlight near the pool ranged from 3.5°C at dawn to 35°C early in the afternoon (Fig. 2). The day was fine and clear with a light south-easterly breeze starting at 2.30 p.m. Sunrise was at 6.21 a.m. but the pool was shaded by surrounding forest until about 9.00 a.m. Sunset was at 8.41 p.m.

Water temperature in the shallows (5 cm) lagged closely behind air temperature (Fig. 2a) while in deeper water (45 cm) the daily range was far less (Fig. 2b). Water in a crayfish burrow exhibited a diel range of less than 3°C (Fig. 2b). The insulative capacity of several centimetres of eucalypt litter and dried filamentous algal mat approximated that of

TABLE 1. *Means and ranges of water temperature, pH, dissolved oxygen and conductivity in two potential oversummering refuges, based upon n spot measurements.*

Refuge		Water Temperature (°C)	pH	Dissolved Oxygen (% saturation)	Conductivity (K_{18}) (μS/cm)
Receding pools	$\bar{x}$	13	6.4	30.4	164
	range	7–25	4.7–7.2	6–78	90–290
	n	25	23	25	25
Crayfish burrow water	$\bar{x}$	9.5	5.8	63	88
	range	7–12	5.2–6.2	45–79	66–110
	n	8	8	8	8

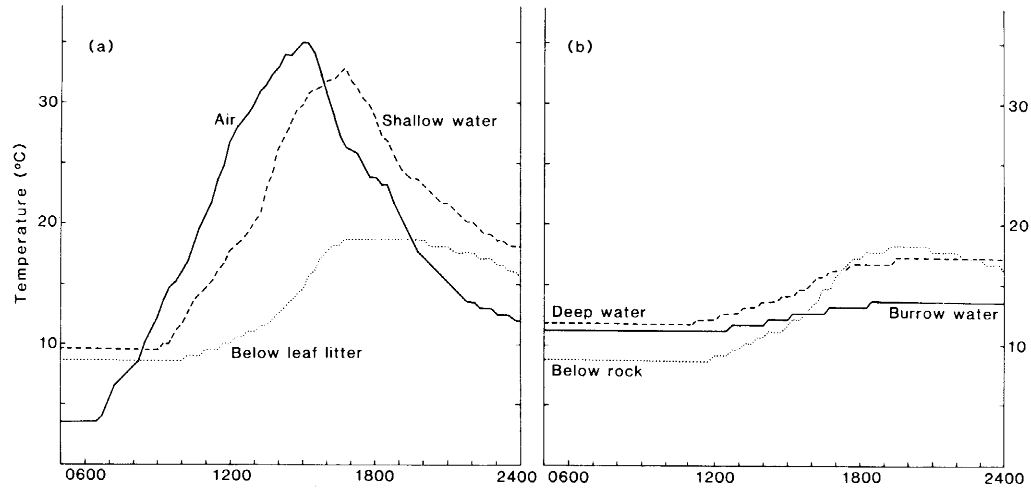

Fig. 2 Variation in water temperature of several potential over-summering refuges in and around the study pool at WPS on 20.i.1983. See text for details.

a flat rock 15 cm thick (cf. Figs 2a and b). During the day, conductivity remained at 270 μS/cm and pH ranged from 5.5 to 6.1 (n = 6 determinations, mean pH = 5.6).

Aquatic macroinvertebrates collected from potential refuges

A total of 91 taxa was collected from the eight over-summering refuges sampled at four sites on the Werribee and Lerderderg Rivers (Table 2). Nearly three-quarters of these taxa over-summered in receding pools along the river beds. These pools also harboured tadpoles of *Litoria ewingi* (Duméril & Bibron) (Hylidae) and *Neobatrachus sudelli* (Lamb) (Leptodactylidae); large numbers of the latter perished when the pool at WPS dried up over the summer 1982–83. Several specimens of *Galaxias olidus* Günther (Pisces: Galaxiidae) were collected from the same pool.

Few taxa were recorded from the hyporheos or crayfish burrow water (Table 2); individuals in these habitats were usually tiny. Decomposed wood yielded small oligochaetes, tipulids and boring chironomids (Orthocladiinae) while amphipods (*Austrochiltonia australis*) were found in curled up strips of *Eucalyptus* spp. bark near the margins of dried out pools. These habitats were not sampled intensively and it is likely that other taxa (e.g. helminthid beetles) may also use rotting wood as a refuge over summer.

Almost half of the taxa recorded were collected from refuges that did not hold free water when sampled (Table 2). Some of these (e.g. *Nousia* spp. and ?*Dinotoperla thwaitesi*) apparently hatched from desiccation-resistant eggs whereas others survived as larvae (chironomids, psephenids, helminthids and case-building caddisflies) or as adults (dytiscids and helminthids) in moist microhabitats below rocks or mats of leaf litter and dried filamentous algae. Large numbers of microcrustacea (ostracods, harpacticoid and cyclopoid copepods) were recovered from dry substrata flooded in the laboratory. The water content of these samples was usually less than 10% by weight (range = 0.19 – 74.00%, mean = 7.71%, S.E. = 0.93%, n = 53) and did not differ significantly between samples collected from the beds of the pool and riffle habitats (Mann-Whitney U-test, $p > 0.05$).

Comparisons among the refuges should be made cautiously because the collecting techniques and the numbers of samples taken from each habitat differed substantially. For this reason, I did not attempt calculations of coefficients of similarity of faunal composition among refuges.

Discussion

The classification of over-summering refuges used by aquatic macroinvertebrates in temporary streams in Ontario (Fig. 3 in Williams & Hynes 1977) may be applied usefully to the data from the Werribee and Lerderderg Rivers. At a broad taxonomic level, the faunal elements over-summering in the various refuges are almost identical and do so at similar stages of their life cycle. This may seem unexpected given the differences in latitude, source of stream flow (snowmelt in Ontario, rainfall in this study) and the difference in the degree of species overlap with nearby permanent streams (Boulton & Suter 1986;

TABLE 2. *Aquatic taxa recorded from potential refuges sampled over the 1982–1983 summer when the streams had ceased flow. Dead specimens were omitted. Abundance categories are qualitative (+ = present (1–)2 individuals), C = common (3–*10 individuals), A = *abundant (more than 10 individuals)) because of the different sampling frequency (n) and methodology (see text). * These individuals did not grow to identifiable size in the laboratory. ** (NMV sp.n) refers to the number of the specimen held in the voucher collection of the Museums of Victoria.*

Refuge	Below dried litter	Crayfish (*Engaeus* sp.) burrows	Receding pools	Shaws Lake	Wood and bark	Dry substrata flooded in laboratory		Hyporheos
						riffle	pool	
(n)	(7)	(12)	(23)	(2)	(10)	(47)	(14)	(5)
TURBELLARIA								
Neorhabdocoela								
?*Mesostoma* sp.			+			C	C	+
Tricladida								
Cura pinguis (Weiss)			C	C				
NEMATODA								
Nematoda spp.	+	C	A	C		A	A	C
GASTROPODA								
Hydrobiidae								
Angrobia sp.			A			C	+	
Glacidorbis hedleyi Iredale						+		
Ancylidae								
Ferrissia spp.	+		C				+	
Planorbidae								
Physastra gibbosa (Gould)			A	A				
BIVALVIA								
Sphaeriidae								
Sphaerium tasmanicum (Tenison-Woods)			C					
OLIGOCHAETA								
Oligochaeta spp.	C	C	A	A	C	A	A	C
CRUSTACEA								
Janiridae								
Heterias sp.		C						+
Ceinidae								
Austrochiltonia australis (Sayce)	A		A	C	C			
Atyidae								
Paratya australiensis Kemp				C				
Parastacidae								
Cherax destructor Clark	+							
Engaeus sp.		C	C	C				
HYDRACARINA								
Limnesiidae								
Limnesia spp.			+	C				
Hygrobatidae								
Australiobates spp.			C					
Corticacarus spp.			C	+		A	+	+
Mesostigmata								
Aquatic sp.						+		
EPHEMEROPTERA								
Leptophlebiidae								
Nousia spp.			C	C		A	A	+
Atalophlebia sp.			C	A				
ODONATA								
Lestidae								
Austrolestes ?*io* (Selys)			+					
Corduliidae								
Hemicordulia ?*tau* Selys			+					

Refuge	Below dried litter	Crayfish (*Engaeus* sp.) burrows	Receding pools	Shaws Lake	Wood and bark	Dry substrata flooded in laboratory riffle	pool	Hyporheos
(n)	(7)	(12)	(23)	(2)	(10)	(47)	(14)	(5)
PLECOPTERA								
Austroperlidae								
Acruroperla atra (Samal)			+					
Notonemouridae								
Austrocerca tasmanica (Tillyard)			A					
Gripopterygidae								
?*Dinotoperla thwaitesi* *Kimmins						C	C	+
HEMIPTERA								
Veliidae								
Microvelia dubia Hale			+	C				
M. distincta Malipatil			C					
Notonectidae								
Anisops deanei Brooks			+	C				
A. ?*hackeri* Brooks			+					
Corixidae								
Micronecta annae illiesi Wroblewski			C					
M. a. tasmanica Wroblewski			+					
COLEOPTERA								
Dytiscidae								
Antiporus blakei (Clark)			C	C				
A. femoralis (Boheman)			A					
Chostonectes johnsoni (Clark)			+					
Chostonectes spp. larvae			C					
Copelatus australiae Clark	C							
Hyderodes schuckardi Hope	+							
Lancetes lanceolatus (Clark)	+		+					
Liodessus shuckhardi (Clark)			+					
Necterosoma penicillatum (Clark)			A	C			+	
Necterosoma sp. larvae			+					
Platynectes decempunctatus (Fabricius)	C		+					
Rhantus suturalis (Macleay)			+	+				
Sternopriscus mundanus Watts			C					
Gyrinidae								
Macrogyrus sp.			+					
Hydraenidae								
Hydraena luridipennis Macleay			+					
H. ?*tricantha* Zwick			+					
Helodidae								
Helodidae sp. larvae						+		
Psephenidae								
Sclerocyphon striatus Lea larvae	+						+	
Helminthidae								
Austrolimnius hebrus Hinton			+			C	+	
A. maro Hinton			+			A	C	
A. "*mormo*" larvae (NMV sp. H_2)**						A	C	
Austrolimnius sp. larvae						C	C	
Simsonia tasmanica (Blackburn) larvae							+	
DIPTERA								
Tipulidae								
Limonia sp.						+		
Ormosia sp.	+				+		+	
Psychodidae								
Psychoda sp. (NMV sp. 3)**						+	C	

Refuge	Below dried litter	Crayfish (*Engaeus* sp.) burrows	Receding pools	Shaws Lake	Wood and bark	Dry substrata flooded in laboratory riffle	pool	Hyporheos
(n)	(7)	(12)	(23)	(2)	(10)	(47)	(14)	(5)
Culicidae								
Aedes spp.			A	C				
Anopheles annulipes Walker			C					
Culex fatigans Weidmann			C					
C. annulirostris Skuse			+					
C. australicus Skuse			+					
Chironomidae								
Ablabesmyia sp. 1 (NMV sp. 7E)**			C	+				
Ablabesmyia sp. 2 (NMV sp. 66E)**			+					
Paramerina spp. (nr NMV sp. 32E)**			C					
Chironomus nr *februarius* (NMV sp. 136E)**			C	+				
Einfeldia sp.			+					
nr *Dicrotendipes* sp. (NMV sp. 34E)**			C					
Riethia sp. (NMV sp. 5E)**			+				+	
Stenochironomus sp. (NMV sp. 3E)**						+		
Calopsectra sp. (NMV sp. 22E)**			C	C			+	
Stempellina nr *bausei*			+			+		
nr *Monodiamesa* sp.					C		+	
Orthocladius-Cricotopus complex (includes NMV spp. 12E and 160E).			C					
Heterotrissocladius sp.	+					C	C	
Tiny chironomids*		+	C	A		+	+	+
Ceratopogonidae								
Bezzia sp.						+		
Nilobezzia sp.						+		
Stratiomyidae								
Stratiomyidae spp.	+		C	+		C	C	
Empididae								
Empididae spp.		+	C			+		
Dolichopodidae								
Dolichopodidae sp.							+	
Muscidae								
Muscidae spp.			C	+		+		
TRICHOPTERA								
Hydrobiosidae								
Ptychobiosis nigrita (Banks)			+					
Hydroptilidae								
Hellyethira ?*simplex* (Mosely)			+					
Calocidae								
Calocidae sp.						+		
Leptoceridae								
Leptorussa darlingtoni (Banks)			C			+		
Oecetis sp.			C					
Lectrides varians Mosely	C		C					
Triplectides similis Mosely			C					
T. truncatus Mosely	+		C					
Tiny leptocerids*			C					
Total number of taxa 91	15	6	68	23	4	27	24.0	8
% of total number of taxa	16.5	6.6	74.7	25.3	4.4	29.7	26.4	8.8

Boulton & Lake 1988). However, physiological and behavioural adaptations employed by animals of common heritage that share gross morphological similarities and that are subjected to similar environmental selective pressures are likely to converge upon a restricted number of solutions (parallel evolution *sensu* Mayr 1963).

In the Werribee and Lerderderg Rivers, several common taxa (*Nousia* sp., some gripopterygid stoneflies) apparently hatched from desiccation-resistant eggs (cf. Lehmkuhl 1971; Snellen & Stewart 1979; Malicky 1982) and were among the first invertebrates to appear when flow resumed. Similar findings have been reported in other intermittent streams (Harrison 1966; Chutter 1968; Hynes 1975; Ladle & Bass 1975; Williams & Hynes 1976, 1977; Abell 1984; Towns 1985). Although simuliids (Diptera) were also common shortly after flow resumed in the Werribee and Lerderderg Rivers, none emerged from the dry substrata flooded in the laboratory, implying that eggs are laid by adults flying in when flow starts (cf. Hynes 1975; Abell 1984).

Microcrustacea (ostracods, cyclopoid and harpacticoid copepods) emerged within hours of flooding dry substrata in the laboratory and harpacticoid copepods were observed mating a day later. Morton & Bayly (1977) recovered ovigerous harpacticoid females only 24 hours after flooding some dried mud from a temporary pool at Clayton, Victoria, suggesting that some species diapause at an advanced stage of development (cf. Cole 1953). Another taxon, common shortly after dry substrata were inundated, was a neorhabdocoel tentatively identified as *Mesostoma* sp.. Bayly (1970) recorded *Mesostoma* from a temporary saline lake in south-eastern Australia and observed thick-shelled eggs in the uteri of some specimens that are apparently released when the animals die. A similar strategy for desiccation-tolerance has been observed in neorhabdocoels from a temporary ditch in England (Cox & Young 1974).

Gastropods in the Werribee and Lerderderg Rivers survive drought either by secreting a protective epiphragm (e.g. *Physastra gibbosa, Ferrissia* spp.) (cf. Kenk 1949; Eckblad 1973; Legier & Talin 1973) or by closing their operculum (e.g. *Angrobia* sp. and *Glacidorbis hedleyi*) (Boulton & Smith 1985). Most tended to aestivate in moist microhabitats under stumps, dry algal mats and leaf litter (cf. Strandine 1941; Klekowski 1959; Casey & Ladle 1976). The bivalve *Sphaerium tasmanicum* probably minimizes water loss by closing its valves. Other members of the Sphaeriidae are ovoviviparous and brood their young while surface water is absent (Heard 1977; Hornbach *et al.* 1980, McKee & Mackie 1981). Aestivating juveniles have been found buried in the substratum (Way *et al.* 1980) but I did not recover any from my study sites.

Parastacid crayfish found in the Werribee River over-summer in their burrows where water temperatures remain quite constant. Surprisingly few other invertebrates (pholeteros *sensu* Lake 1977) appear to use this refuge (cf. Creaser 1931; Williams *et al.* 1974; Williams & Hynes 1976; Wiggins *et al.* 1980). The pholeteros in other Victorian *Engaeus* spp. burrows is also depauperate (Horwitz *et al.* 1985). Nevertheless, this refuge seems to be important for the survival of janirid isopods in the Werribee River. Isopods usually are absent from temporary waters because they lack desiccation-resistant stages and are sedentary (Williams 1985). The water in burrows constructed by fish serves as sources of recolonists after droughts in some streams overseas (e.g. Tramer 1977; Glodek 1978) but this refuge was not evident in the Werribee and Lerderderg Rivers.

Few taxa were abundant in the hyporheos of the study sites during summer. This paucity may reflect the crude sampling methods because amphipods, janirid isopods, stoneflies, molluscs and oligochaetes have been recorded from the hyporheos of the intermittent Brachina River in South Australia (W.D. Williams 1983). Overseas, the hyporheos is considered to be an important refuge from both droughts and floods in some temporary and permanent streams (Clifford 1966; Williams & Hynes 1977; Williams 1977, 1984). However, in desert streams whose beds are mainly composed of unstable sand, hyporheic dormant stages are rare because of high temperatures in the dry streambed and severe scouring of the channel during flash floods (Gray 1981, Fisher *et al.* 1982).

One refuge not considered by Williams & Hynes (1977), possibly uncommon in Ontario, is that provided by decomposing wood debris, abundant along the banks and stream beds of many Australian intermittent streams. In my study, this refuge harboured oligochaetes, amphipods, tipulids and chironomids. More intensive sampling is likely to yield further taxa because other workers have recorded large numbers of xylophilous taxa from permanent streams in Oregon (Anderson *et al.* 1978; Dudley & Anderson 1978) and New Zealand (Anderson 1982).

In the Werribee and Lerderderg Rivers, taxa aestivated under rocks and mats of algae (where temperatures remained constant) as adults (e.g. amphipods, dytiscids) or larvae (e.g. chironomids, stratiomyids). Some larval stages seemed surprisingly tolerant of desiccation; for example, a large water penny larva (*Sclerocyphon striatus*), collected from the exposed surface of a flat rock on the bed of a riffle that had not flowed for 13 weeks, resumed activity immediately after immersion in water from a nearby pool. Similar tolerance of desiccation by larvae of *Sclerocyphon* spp. has been described in Tasmania (Smith 1981) and Queensland (Smith & Pearson 1985).

Adult aquatic Hemiptera (e.g. corixids, notonectids) and Coleoptera (e.g. dytiscids) probably fly in from nearby permanent waters. Such aerial recolonization of temporary pools and streams by these groups is commonplace (e.g. Fernando 1958, 1959; Fernando & Galbraith 1973; Williams & Hynes 1976, 1977; Wiggins *et al.* 1980; Abell 1984; Williams 1985). I also found several species of adult dytiscids over-summering below rocks and dry litter near the margins of pools at SC and WPS. This strategy seems less well-known for this group; only D.D. Williams (1983), Boumezzough (1983) and McKaige (1980)[1] (in a temporary pond near Colac, western Victoria) have reported similar observations.

Although the receding pools harboured most of the taxa that over-summer at the study sites, they appeared to be the most physicochemically "harsh" refuge that I sampled. The pools experienced a considerable diel range in water temperature, oxygen levels were frequently below 20% saturation and pH levels fell to less than 5. Conductivity rises as the water evaporates and the pools are often stained dark brown with eucalypt leachate. Similar conditions have been observed in receding pools in other intermittent streams in Australia (Towns 1983, 1985; Smith & Pearson 1987) and North America (Slack 1955; Larimore *et al.* 1959; Clifford 1966; Harrel & Dorris 1968).

The invertebrates that over-summer in these pools have various adaptations that allow them to tolerate such physicochemical extremes. For example, larval dytiscids come up to the surface of the pool to obtain air through the terminal abdominal spiracle whereas adult dytiscids store air beneath their elytra (Britton 1970). Some chironomid larvae (e.g. *Chironomus* nr *februarius*) are particularly abundant in the receding pools and use haemoglobin to facilitate oxygen uptake (Colless & McAlpine 1970). Mayfly nymphs (*Atalophlebia* sp.), also common in this refuge, have large gills that are constantly oscillated to enhance respiration (Boulton & Lake 1988). Terrestrial oviposition by two species of leptocerid caddisfly common in the Lerderderg River (*Leptorussa darlingtoni* and *Lectrides varians*) may also be an adaptation to low or unpredictably fluctuating oxygen levels (Towns 1983). Development of vulnerable juvenile stages in a physicochemically harsh environment may be avoided or accelerated by ovoviviparity exemplified by the stonefly *Austrocerca tasmanica*, also recorded by Towns (1985) in a South Australian intermittent stream.

Although there is little known about the thermal tolerances of aquatic macroinvertebrates in Australian intermittent streams, it appears that many taxa can cope with short-term exposure to extremes of water temperature. It is likely that they remain near the bottom of the pool where the temperatures may be as much as 15°C cooler than those of the surface water exemplified by the study pool at WPS. Such stratification is uncommon in shallow pools (e.g. Byars 1960; Butler 1963; Moore 1970; Hartland-Rowe 1972). However, Eriksen (1966) recorded surface-bottom differences of 9–16°C in temporary turbid puddles less than 50cm deep, and a shallow (10 cm) rockpool in a stream in the Pyrenees had a surface temperature of 29.9°C while the bottom was 19°C (Chodorowska & Chodorowski 1966). Less marked stratification in pools in North American intermittent streams has been reported by Neel (1951) and Slack (1955).

Isolated pools remaining in the stream bed are important over-summering refuges for aquatic macroinvertebrates in intermittent streams elsewhere (e.g. Slack 1955; Paloumpis 1958; Larimore *et al.* 1959; Williams & Hynes 1976; Abell 1984). In temporary streams in Ontario, they also provide excellent breeding environments due to the ease with which they warm up and the abundant plant food that develops within them, and they enable species with long-lived aquatic stages to complete their life-cycles (Williams & Hynes 1976). Similarly, in the Werribee and Lerderderg Rivers, these pools support a rich fauna although environmental conditons are harsh and predators are numerous (Boulton & Suter 1986).

Taxa whose aquatic life-spans are brief enough to be completed while water is present are under less selective pressure to adopt these strategies than species whose aquatic development takes longer than the period that water persists. Unfortunately, we lack information on the duration of aquatic stages of many Australian macroinvertebrates and few generalizations may be drawn. Most crustaceans and molluscs listed in Table 2 probably live longer than a year and this may account for their ability to survive in refuges other than the pools. Although many other taxa (e.g. chironomids, culicids) can complete their aquatic stages in a matter of weeks, their survival in intermittent streams depends upon when their eggs hatch and how long water persists afterwards. Interpretation of the significance of many of these refuges will be possible when more information on the life histories of

[1] McKaige, M.E. (1980) Emergence and development of aquatic invertebrate communities from dried mud after flooding. B.Sc. Hons thesis, Department of Zoology, Monash University, (Unpubl.).

macroinvertebrates in Australian intermittent streams is available.

In summary, there appear to be five major over-summering strategies employed by the fauna of these two rivers:

i) tolerating extreme and variable environmental conditions in the remaining pools,

ii) surviving in moist microhabitats below stones, stumps and mats of dried algae and leaf litter, and in rotting wood,

iii) over-summering in microhabitats where environmental conditions are relatively mild and constant such as in the hyporheos or the burrow water of crayfish,

iv) surviving as desiccation-resistant stages in the dry substratum, and,

v) living in nearby permanent water-bodies and flying in and ovipositing when flow resumes.

The relative contributions from each of these refuges reflects the nature of the substratum (e.g. Clifford 1966; Gray 1981), the amount and pattern of discharge during the previous spring and the severity of the summer. This last was illustrated by the 1982 drought when all the pools in the upper reaches of the Werribee River dried completely, extinguishing several common taxa (e.g. the shrimp *Paratya australiensis*) that I never recorded the following year. Differential survival of fauna in these various refuges undoubtedly influences the community composition of the stream and has a profound effect upon its ecological succession during the ensuing period of flow.

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