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Environmental water allocation required to sustain macroinvertebrate species in ephemeral streams

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Project objectives*

1. To determine the key drought refuges used by macroinvertebrate species in intermittently flowing streams and determine the level of threat to each refuge posed by prolonged drying and unpredictable flow regimes.
2. To determine the role played by different types of drought refuge in restocking macroinvertebrate populations in rivers and therefore the consequences for river communities of loss of each type of drought refuge.
3. To determine the consequences of river habitat fragmentation caused by increased drying for the sustainability of macroinvertebrate populations by quantifying the effects on dispersal and the genetic structure of key aquatic species.
4. Identify biodiversity hotspots among ephemeral stream communities and determine conservation priorities.

* Alteration to original objectives (originally reported in April 2006)

Objectives 1 & 2

The large bushfire in the Grampians National Park in January 2006 burnt all of the original study sites. These streams have since shown marked changes (they are full of ash and are flowing perennially) typical of severe wildfire, making them unsuitable for use in this project. Therefore, we shifted our study sites to the unburnt western part of the Grampians National Park, the Victoria Range. Streams in the Victoria Range contain sandy sections, which were not present in the original study sites. Slight changes were then made to objectives 1 & 2, in that we included dry and damp sand as potential drought refuges.

The experiments originally planned for objective 2 were not supported by the data collected for objective 1. Therefore, objective 2 was modified to determine which qualities of perennial pool refuges were important for sustaining invertebrate biodiversity.

Objective 3

The change to study site described above had the advantage that the drainage networks in the Victoria Range are simpler, which made interpretation easier, enhancing the achievement of this objective. As the interbasin transfer site was one of those burnt, we were unable to pursue this aspect of the objective.

Objective 4

The narrower geographic range of the Victoria Range means that we were less likely to identify biodiversity hotspots. In addition, the very broad area burnt in the bushfire may disrupt normal invertebrate dispersal patterns throughout the region and we may have lost existing (unknown) biodiversity hotspots in the fire. Therefore, while we will still attempt this objective, we may not be able to identify such hotspots as a consequence of the bushfire.

Summary of results against project objectives

Objective 1

To determine the key drought refuges used by macroinvertebrate species in intermittently flowing streams and determine the level of threat to each refuge posed by prolonged drying and unpredictable flow regimes.

Refuges – Drought refuges are places that sustain life during the dry season in ephemeral streams. Dry periods are a natural occurrence but their frequency and length has been increased by both water extraction and supra-seasonal drought in many streams. Climate change predictions for southern Australia suggest that rainfall will continue to decline, also prolonging dry periods for ephemeral streams and some streams that are presently perennial will become seasonally dry. The capability of different parts of the landscape as refuges depends upon how much water has been available annually, and also over longer time periods. In this regard, perennial streams are likely to be the most important refuges against supra-seasonal drought.

The following refuges were listed in the funding application: permanent pools, aestivation (in moist sediments, beneath stones or in leaf accumulations) and drought resistant stages (often eggs). Of these, we have found and sampled the following: permanent pools, beneath stones, leaf accumulations and drought resistant stages in dry sediments. We did not sample moist sediments as none were found in any of the 15 streams sampled. In addition, we also sampled the perennially flowing sections of streams, as there were several throughout the study area.

Permanent pools – found in most of the study streams harboured a large diversity of invertebrates. Invertebrate densities were low and, where fish were present, often very low indeed. We had to change our methodology for sampling in these pools to searching for at least 50 individuals of the most abundant taxa, as taking six Hess samples did not generate sufficient abundances or diversity. All fish observed were native species: *Galaxias olidus* (Mountain galaxid), *Gadopsis marmoratus* (Blackfish), *Galaxias maculatus* (Common Jollytail), *Nannoperca australis* (Pygmy Perch), and *Galaxiella pusilla* (Eastern Little galaxias).

Perennially flowing sections – found in several streams were spring fed. These sections also harboured large densities and low abundances of individuals and were sampled as above.

Aestivation beneath stones – only five taxa were found to use this method. The crayfish *Geocharax* sp.nov., dragonfly (family Telephlebiidae) and damselfly (Megapodagrionidae) nymphs, giant freshwater isopods and the caddisfly *Lectrides varians*. This refuge appears to be used by a far smaller range of taxa than anecdotal information from the literature would suggest. Crayfish were commonly found aestivating in chambers constructed under stones and were found in five of the streams.

Aestivation in dry sediments and leaf packs, desiccation resistant eggs – two reflooding trials were conducted in 2006 and 2008. Six sediment samples were taken from locations on each dry streambed and reflooded in the laboratory. Chironomid midge larvae and stonefly nymphs were observed to hatch but these were in very low numbers. This refuge does not appear to be contributing much to sustaining biodiversity in these streams.

Perennial pools (pools that persist until streams recommence flows) and sections of perennially flowing water are clearly the only refuge type that is comprehensive of stream biodiversity and simultaneously this refuge is also very vulnerable to both drought and the effects of regulation. In particular, regulation mainly comprises water extraction, leading to prolonged drying of streams. Our data show that these streams have very few animal species downstream of offtake weirs and that there are also low numbers upstream of weirs. Fish are the most extreme example of this as fish now do not occur above any of the weirs in the Victoria Range; nor do they occur in the few thousands of metres immediately downstream of weirs.

While some taxa do aestivate, this refuge is a 'polo club' type refuge, that is, it is only available to species with the traits necessary for aestivation. Interestingly, the egg bank that features so predominantly in restocking ephemeral wetlands is of minimal importance here. This is likely because zooplankton are the dominant users of the egg bank and plankton are a negligible component of stream ecosystems (because they cannot tolerate much current).

Conclusions

1. Perennial pools and sections of perennial streamflow sustain a disproportionately large number of invertebrate taxa during dry periods. They are also refuges for fish.
2. While other refuges (most importantly pools) occur in nominally dry stream reaches and contribute to the maintenance of stream biodiversity over summer, their viability is compromised by drought. Perennial reaches are reliable refuges during supra-seasonal drought but are also most vulnerable to increased drying and to water extraction.
3. Over-summering by adult aquatic insects in the terrestrial environment as a refuge has not been quantified here or in other studies. This refuge may be significant if it enables species to recolonise effectively through adults laying eggs when streams begin to flow.

Flow regimes

Flow regimes within the streams were studied in summer 2005–06, 2006–07, 2007–08 and 2008–09. Marked stream-to-stream and year-to-year variation was observed. Perennially flowing streams and stream sections flowed in all summer–autumn periods, however perennial pools were often not present in all years. This depended on both winter–spring rainfall volumes and on the hydrological characteristics of individual streams. In very dry years, even spring-fed pools shrank dramatically in size.

This high degree of spatial and temporal variation in flow regimes is a natural part of ephemeral stream landscapes. It provides opportunities for a variety of species with different flow regime requirements and patterns of drought refuge use. Human activities that artificially increase uniformity in flow regime among streams or years are likely to reduce biodiversity. Increased drying from climate change-induced drought and water extraction will also reduce biodiversity (see below).

There are two important lessons for management from these observations:

1. Ephemeral streams need to be managed as groups, not individually, to ensure that the mosaic of habitat required by different species is maintained.
2. Tight classifications of ephemeral stream flow regimes based, for example, on the frequency of occurrence of pools, will not be useful as they do not properly represent the natural range of variation that typifies these streams.

Level of threat posed by altered flow regimes (drought and/or regulation). The dominance of surface waters as a drought refuge means that alterations to flow regime that prolong dry periods and/or increase their frequency will negatively affect stream biodiversity. Below is the table of proposed flow regime categories given in our grant application. This table proposed components of stream flow likely to create refuges and the questions regarding the impact of stream regulation. Below this, we have modified the table to present our results and conclusions from objective 1.

Table 1. Proposed flow regime categories from funding application.

Water regime	Regulation present (does regulation simply create drier flow regimes within the natural context of a wide range of semi-arid flow regimes? i.e. increased drying induced by regulation transforms third-order streams into headwater streams, in terms of their invertebrate population structure and processes)	Regulation absent	Rationale (water regimes combine level of refuge fragmentation and presence/absence of refuges)
Flowing sections of surface water present	X	X	These sections will provide an optimal drought refuge and source for colonisation
Chains of pools present (separated by single dry riffles)	X	X	These refuges are more fragmented than flowing sections, but may still provide refuge and a source for colonisation
Isolated pools present (separated by multiple dry runs, riffles and pools)	X	X	An isolated refuge may provide a less viable source for colonisation
Single pool present in entire stream length	X	?	Does this severe degree of fragmented habitat still provide a viable source for colonisation?
Surface water absent – streambed retains patches of moist sediment beneath stones	X	X	What is the effect of loss of surface water refuges where aestivation is still possible?
Surface water absent – streambed completely dry	nil	X	What is the effect of loss of both surface water refuges and aestivation refuges?

Table 2. Results from Objective 1.

Water regime	Regulation present	Regulation absent	Rationale
	(does regulation simply create drier flow regimes within the natural context of a wide range of semi-arid flow regimes? i.e. increased drying induced by regulation transforms third-order streams into headwater streams, in terms of their invertebrate population structure and processes)		(water regimes combine level of refuge fragmentation and presence/absence of refuges)
Flowing sections of surface water present	This refuge is absent downstream of weirs. Upstream of weirs, biodiversity is lower than expected compared to unregulated streams	This refuge contains the highest biodiversity of animals (including fish)	These sections do provide an optimal drought refuge and source for colonisation
Chains of pools present (separated by single dry riffles)	This water regime did not exist	This water regime did not exist	This water regime did not exist, therefore no refuge provided
Single, isolated or small groups of pools present – *hard substratum*	Pools often dry out downstream of weirs and generally contain few, transient animals Upstream of weirs, fewer species present than in unregulated streams	This refuge contains the second highest biodiversity of animals (including fish) Mainly a refuge for non flow-dependent invertebrates	Perennial pools provide a refuge for both fish and invertebrates, but invertebrates generally do not disperse out to other areas of streambed when flowing The streambed is often quite bare of invertebrates Stony pools are generally a better refuge than sandy pools for invertebrates
Single, isolated or small groups of pools present – *sand substratum*	Pools generally dry out, leading to fish deaths Dry sand a poor refuge for invertebrates	These pools are mainly a refuge for fish and aestivating caddis flies Large interannual variation in pool longevity	
Spring/groundwater-	Possibly	Similar	Provide an

fed pools on hard substratum	unaffected by regulation when downstream of weirs	abundance and diversity to other pool types	exceptionally constant environment Would be affected by groundwater extraction Valuable refuge but may be functionally disconnected from channel as an artefact of regulation
Surface water absent – streambed retains patches of moist sediment beneath stones	Refuge absent	Refuge very variable in space and time Used by a few aestivating species	What is the effect of loss of surface water refuges where aestivation is still possible? Large effect as most taxa cannot aestivate
Surface water absent – streambed completely dry	Aestivation still possible in dry streambeds, but dry riffles have no aestivating individuals These are all found at the bottom of dry pools in a stony bed Crayfish, mainly in unregulated streams		The effect of loss of both surface water refuges and aestivation refuges is severe

Objective 2

To determine the role played by different types of drought refuge in restocking macroinvertebrate populations in rivers and, therefore, the consequences for river communities of loss of each type of drought refuge. Which qualities of perennial pool refuges are important for sustaining invertebrate biodiversity?

Role played by drought refuges in restocking streams

The results from objective 1 made it clear that perennial pools and sections of perennial flow were the refuges mainly responsible for restocking streams. However, as suggested above, flying adult insects appeared to also play a role in recolonising species into streams after dry periods. This means that both the resistance traits of animals (drought refuge use) and the resilience traits of animals (their dispersal capacity) are important for understanding how ephemeral streams are recolonised (Fig. 1).

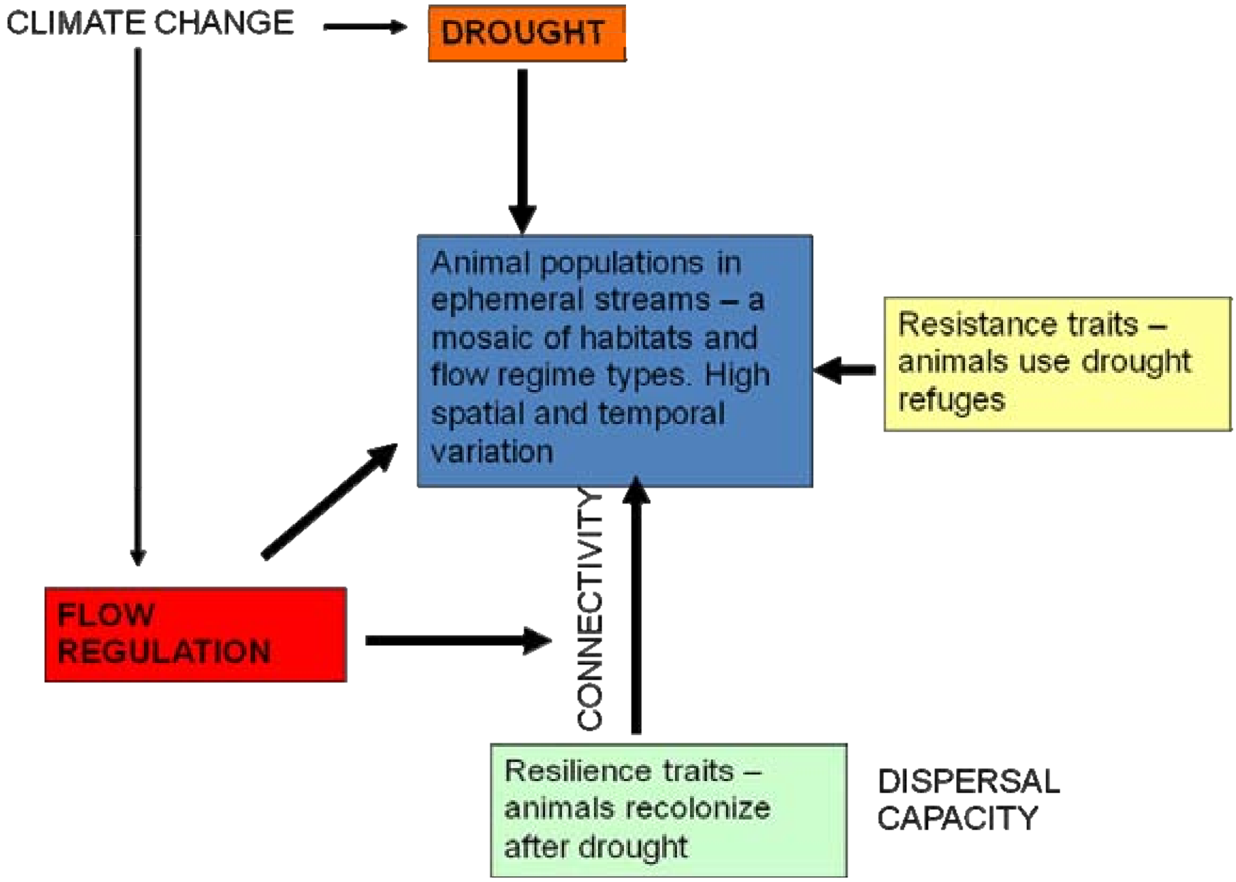

Figure 1. Conceptual model of processes sustaining biodiversity in streams and the impact of increased drying.

Invertebrates were not observed restocking the streambeds during flow periods. That is, individuals present in refuge pools remained there when streams flowed. The exception to this was in Deep Creek, which is nearly perennial and unregulated. In that stream we observed mature larvae moving into runs and riffles once flows resumed. This result was initially surprising, but it may be a response to drought and the idiosyncratic nature of Deep

Creek's discharge pattern. Densities of invertebrates in these streams have been lower than previously observed by us or by Doeg in 1996. The Grampians region has experienced a decade of more or less severe drought and it appears likely that this has caused frequent local extinctions by reducing the number of surface water refuges, and reduced population sizes in general. Therefore, it may be that populations are as yet too small to extend far beyond refuge pools and that a series of average or above average winter rains are needed to truly restock streams. If this is the case, we would predict that invertebrates would recolonise the stream bed from both perennial pools and aestivation refuges over longer time periods than have been observed.

Objective 2 has focused on determining what qualities of perennial pools make them a good refuge for invertebrates. We surveyed stream pools for water quality and the presence of fish, because we had observed that pools with fish contained few invertebrates. Low invertebrate densities could result from predation by fish, poor water quality or both. If the presence of fish dramatically reduces the habitat quality for invertebrates, it is possible that separate pools will be required to provide drought refuges for fish and invertebrates.

Refuge quality

The dominance of pools and sections of perennial flows, and also of aestivating under stones or in litter, is probably due to several factors. Firstly, perennial pools and surface flows are most similar to the flowing stream habitat which best suits the stream invertebrates found in Grampians streams. However, our temperature logger data shows that surface waters also offer a strong temperature buffer against both high and low extremes of temperature on the streambed. Figure 2 shows that while stream bank and dry streambed temperatures in January may range from 10–40°C, temperatures in pools ranged from 12–28°C. Even more strikingly, in April and June, loggers buried under leaf litter recorded a very constant temperature regime of 8–14°C, whereas on the stream bank the range was 2–32°C (Figure 3). Therefore, loggers situated where invertebrates aestivate, under stones or litter in the bottom of dry pools, show a much narrower temperature range. This undoubtedly assists aestivating animals to avoid freezing or overly hot temperatures and enables some species to retain some moisture in an aestivation chamber or case.

Water quality varied greatly among pools and was particularly low in small sandy pools (Figure 4). However, the galaxid fish present in these pools are tolerant to low dissolved oxygen and there was no apparent relationship between dissolved oxygen levels and pool occupancy for fish (Figure 5). Invertebrates were more sensitive to low dissolved oxygen than were fish, therefore, we did not know whether invertebrates were absent from fish-occupied pools owing to water quality or to predation, or both.

A field experiment in Deep Creek was used to address this question. We established 14 streambed pools using pond liner and allowed them to colonise with invertebrates while the stream was still flowing. We also added larvae of the caddisfly *Lectrides varians* to each pool to ensure that this less mobile species was present in the pools. Once streamflow ceased, we added 21 fish to half of the pools, chosen randomly. We then topped up the pools with stream water stored in barrels on the stream bank and ran the experiment for three weeks. During the experiment we measured temperature and dissolved oxygen levels in all pools and at the end we collected all fish and invertebrates. Fish gut contents will be identified and invertebrates identified and counted. The latter data have not yet been analysed, but the water quality results clearly show that the presence of fish reduces dissolved oxygen levels to critical levels (Figure 6). Therefore, for invertebrates, the presence of fish in refuge pools is likely to entail both a predation impact and a negative impact of low dissolved oxygen. Non-air-breathing, pool-dependent invertebrates, such as mayflies and water pennies, would be excluded from these pools by both processes.

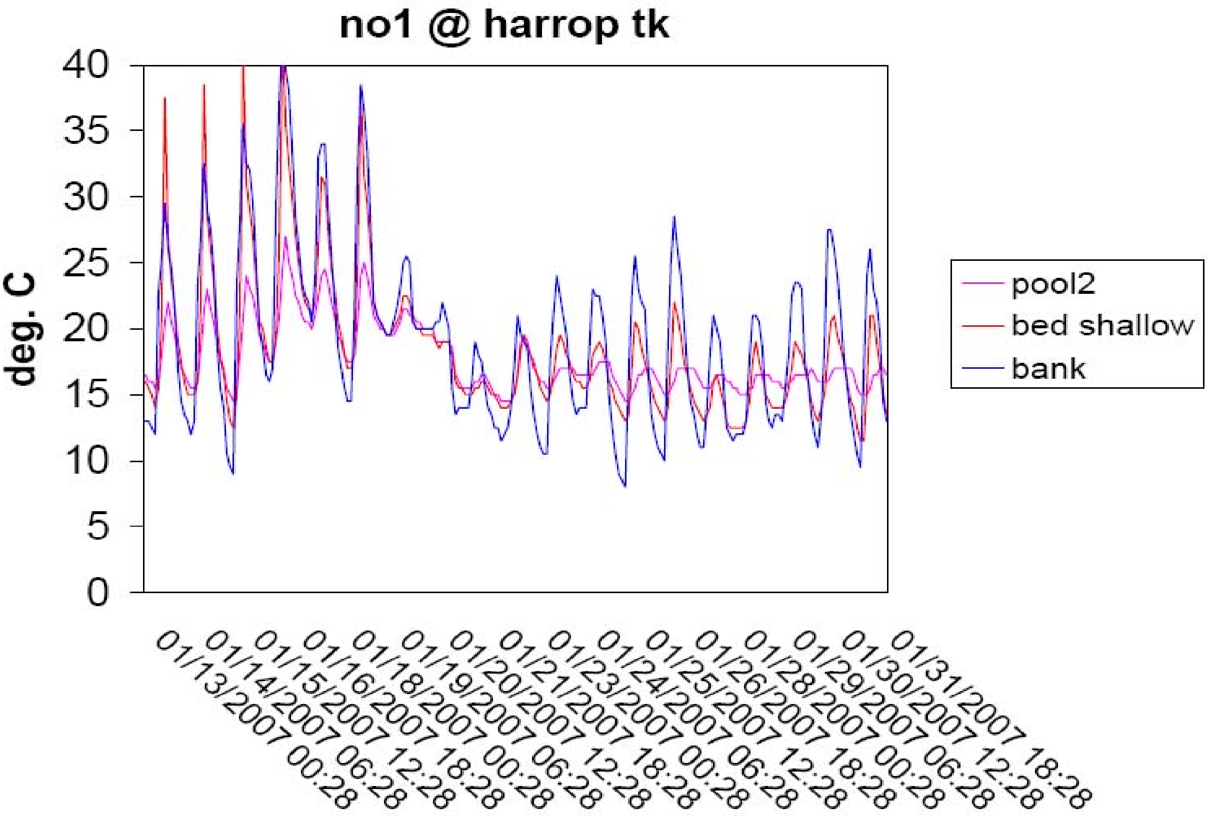

Figure 2. Comparison between adjacent temperature loggers placed on the stream bank, dry streambed and perennial pool during summer.

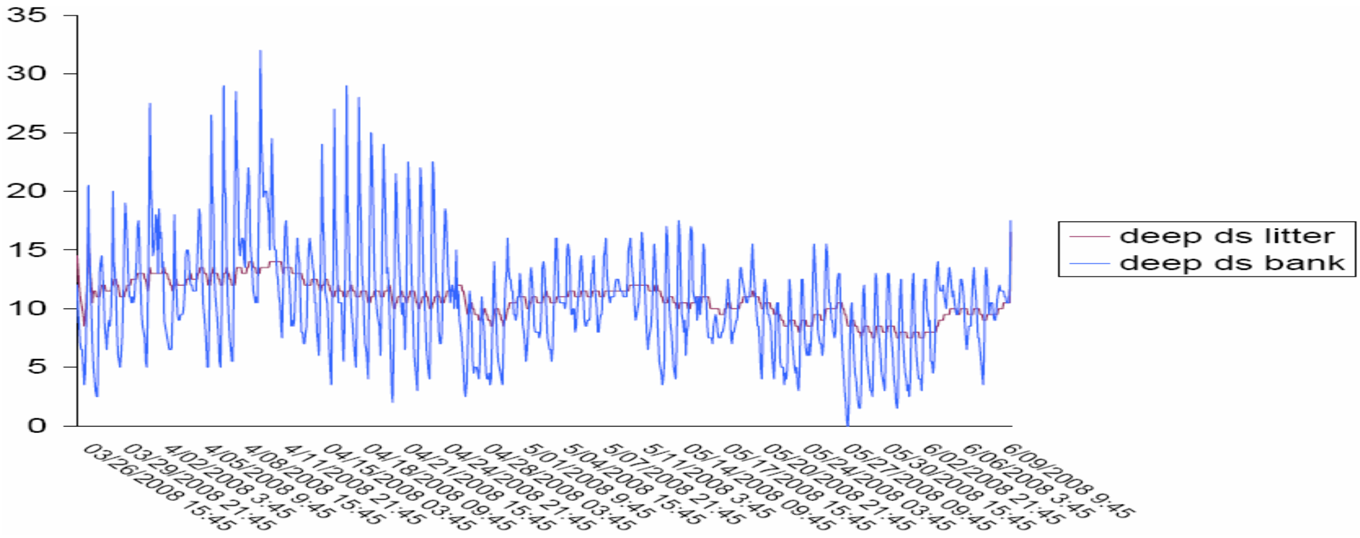

Figure 3. Stream bank and dry streambed litter temperatures in April and June.

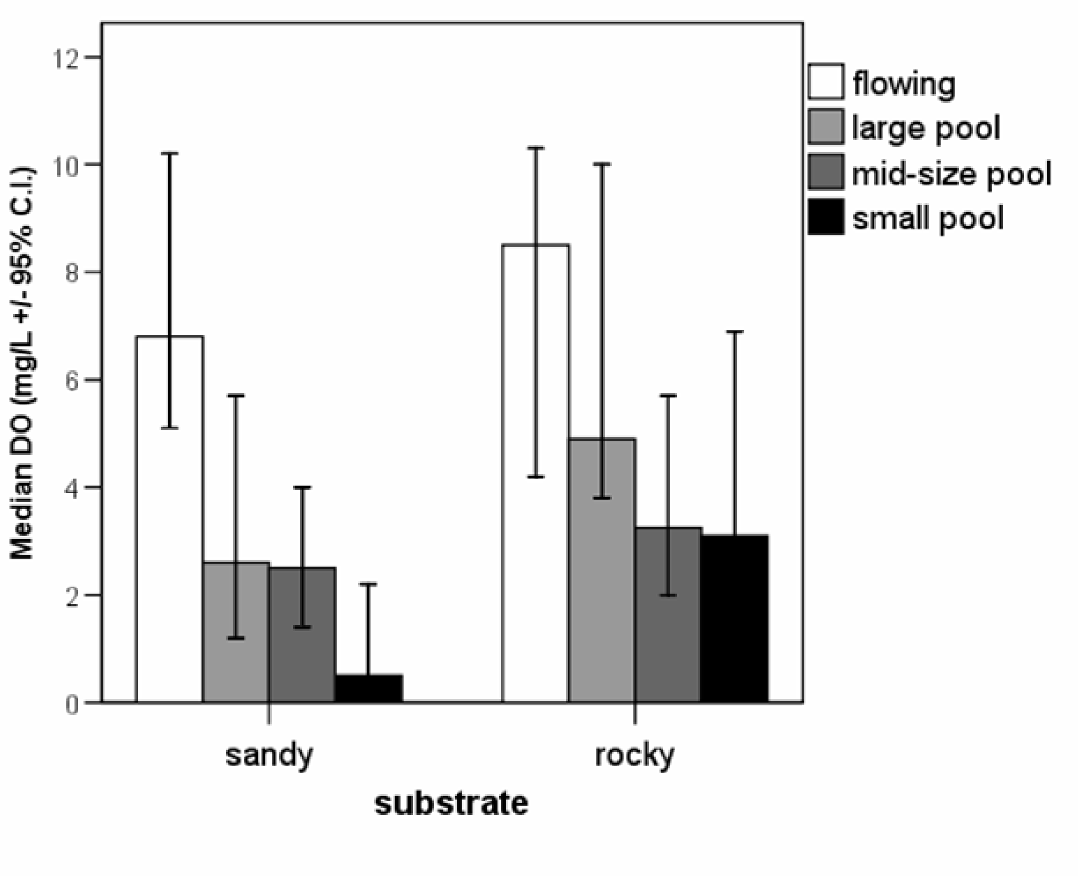

Figure 4. Dissolved oxygen levels in pools and flowing sections in relation to pool size and substratum type. Small pools in sand had significantly lower oxygen levels than others (Wald statistic (6df) = 102.3, $P < 0.001$) but large pools and flowing sections did not differ between substratum types.

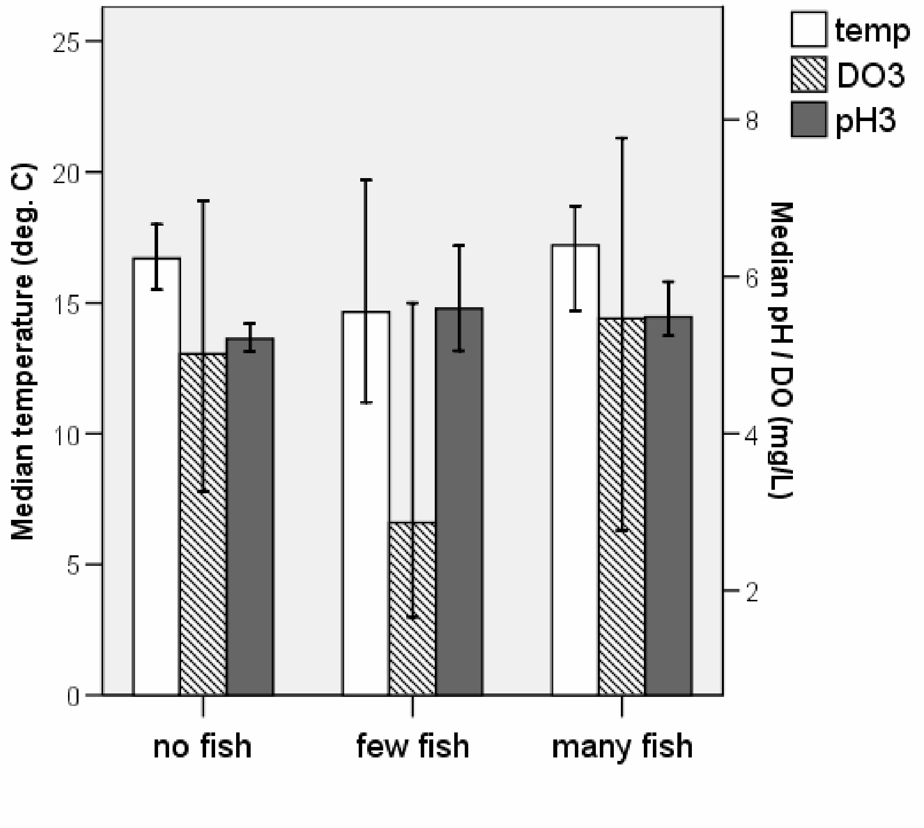

Figure 5. Relationship between pool occupancy by fish and pH, temperature and dissolved oxygen levels.

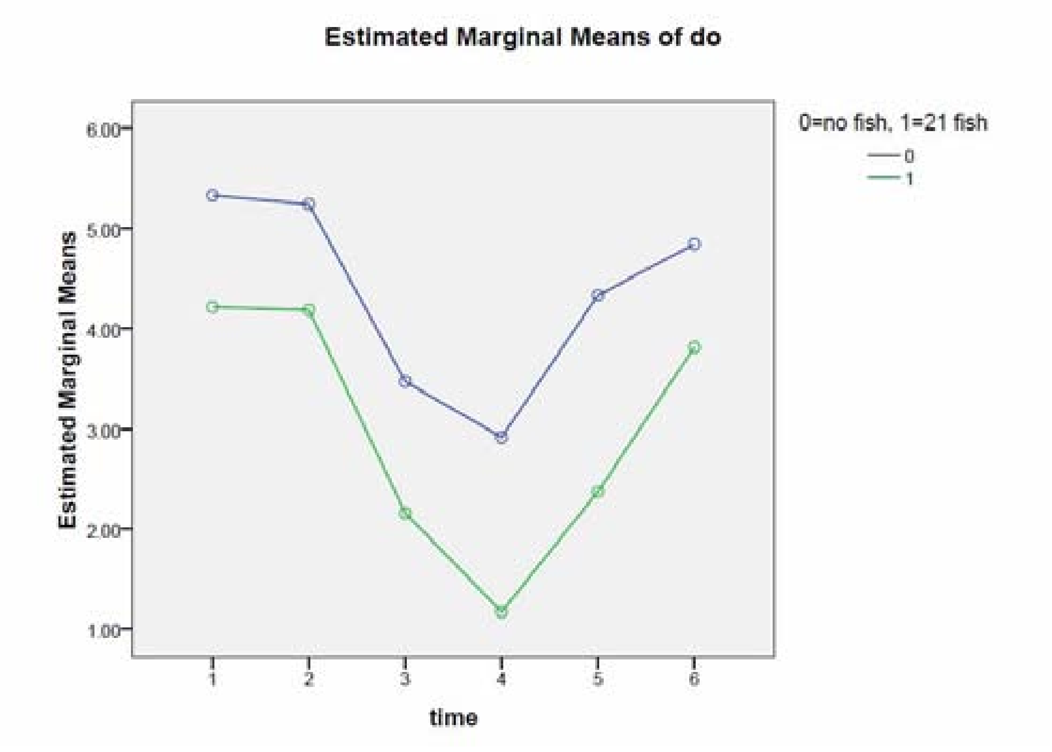

Figure 6. Mean dissolved oxygen levels (mg/L) measured at three-day intervals during the fish manipulation experiment. The presence of fish clearly reduced dissolved oxygen levels.

Field experiment – siltation

Siltation may limit colonisation of stones in pools. Siltation is common downstream of dams and weirs due to reduced flows and most stream invertebrates also avoid it because it clogs their gills. Siltation in pools in these streams may be another limiting factor for invertebrates, which may be exacerbated by stream regulation. Therefore, the aim of this experiment was to determine whether silt was a limiting factor for invertebrates in pool refuges.

Ten stones were used per treatment, with two main treatments and a handling control at some sites. The treatments were: control stones – undisturbed stones covered in silt within the streams; treatment stones – dried, scrubbed and bleached in the laboratory; handling control – stones from the streams, covered in silt but moved. The treatment stones were completely clean and available for colonisation by both algae and invertebrates, compared to the control stones which were already silt-covered. It is possible that the introduction of new stones to the streams is a treatment in itself and so we used a handling control to look at the effect of a newly placed (but otherwise untreated) stone. Seven streams were used in this experiment. Within each one, colonisation on control and experimental stones was to be contrasted upstream and downstream of weirs. If colonisation differed between stone types, it would be an effect of silt. If the results differed between the ephemeral and perennial streams the effect would be due to flow regime. If the results differed upstream and downstream of weirs we would have observed an effect of regulation. Stones were checked monthly for colonists commencing in July 2007, but insufficient numbers of invertebrates colonised any of the stones for analysis. This was probably due to the preceding, extremely dry summer as low invertebrate densities were observed at all sites. Therefore, we were unable to assess the impact of siltation.

Field experiment – aestivation

A laboratory experiment was used to determine how long aestivating caddisflies can survive dry conditions. This type of experiment is important to determine what threat prolonged drying may pose to species that aestivate. This experiment compared the survival rates of continuously inundated caddisfly larvae (control) to some where the sediment remained damp (treatment 1) and to another group where the sediment was allowed to dry out completely (treatment 2). Survival was lower in the aestivation treatments, but did not differ between damp or dry sediments (Figure 7). Survival rates were high in the aestivation treatments (more than four out of every five animals) up until four months of drying, when increased mortality was observed. Interestingly, when animals were re-immersed to test survival, several cohorts of individuals were observed. A large proportion of animals awoke immediately and began to move around, but other groups took between 24–72 hours after re-immersion to respond (Figure 8). This is likely to be a strategy to avoid responding to 'false starts' in stream flows.

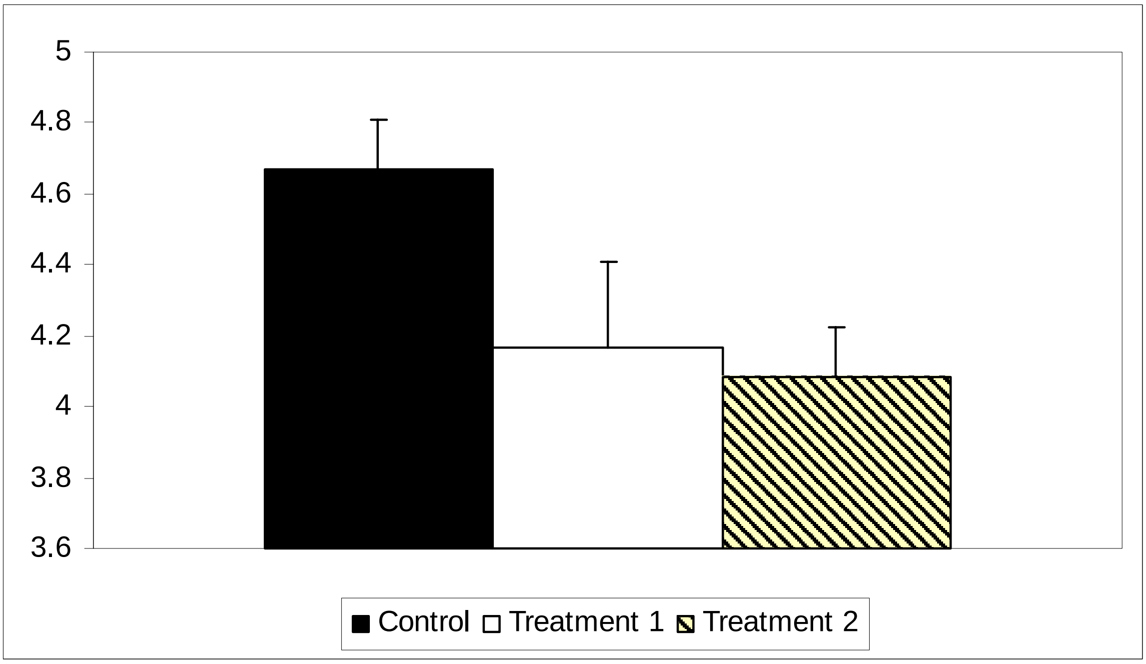

Figure 7. Survival rates of aestivating *Lectrides varians* larvae after four months.

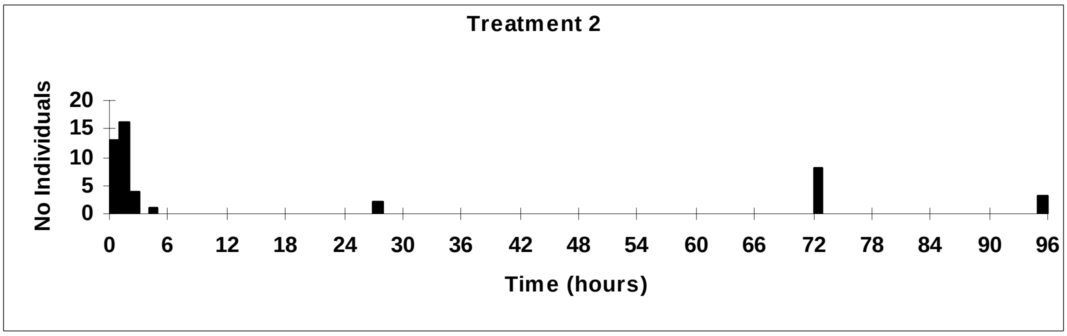

Figure 8. Time in hours after re-immersion of aestivating larvae showing delayed response by some larvae.

Conclusions

1. Drought refuges used during dry periods provide an important buffer against extreme summer–autumn temperatures.
2. Invertebrates present in flowing streams come mainly from pool and perennially flowing drought refuges, and from newly laid eggs brought to streams by flying adult insects. Aestivation and desiccation-resistant eggs make a minor contribution to the assemblage.
3. The presence of fish in pools reduces refuge quality for invertebrates by reducing dissolved oxygen levels and via predation.
4. Increased larval invertebrate mortality is likely in pool refuges as dry periods increase, resulting in fewer species surviving over the summer in that location. However, a subset of species may remain to aestivate where pools have dried. These species have adaptations to protect populations against stop-start flows, but there is probably a considerable energy cost to re-entering torpor if flows cease again.
5. Sufficient refuge pools are required to protect fish and invertebrate populations separately.
6. Animal biodiversity in a stream network is likely to be greatly reduced by the loss of perennial pools and sections of perennial flow.

Objective 3

To determine the consequences of river habitat fragmentation caused by increased drying for the sustainability of macroinvertebrate populations by quantifying the effects on dispersal and the genetic structure of key aquatic species.

Macroinvertebrate focus species

Criteria used to select focus taxa for objective 3 were: a range of dispersal abilities, present in sufficient density to collect 50 individuals, present across most of the 15 streams (Table 3). In general, our hypotheses regarding dispersal capacity were correct. The best disperser was the large caddisfly *Lectrides varians*. This species has strong resistance traits, because it is capable of aestivating and dwelling in pool refuges. It is a good long-distance disperser over tens of kilometres, so it also has strong resilience to increased drought.

The poorest disperser (so far) is the water penny *Sclerocyphon* sp. This beetle has a cryptic terrestrial adult form and genetic data suggest that it is a poor disperser. Larvae are very slow moving, non-drifting algal grazers. The geographic pattern of this species showed distinct populations as well as shared populations in adjacent streams. Non-adjacent streams generally differed in their genetic composition, indicating only short-distance dispersal.

The mayfly Koornonga sp. was the only insect species with any indication of an aquatic dispersal path. Mayflies are known to drift in the current as larvae, but the short-lived adults are also capable of dispersal over kilometres. Within the Victoria Range, northern and southern populations occurred in different watersheds. Therefore, this species has a reasonable dispersal capacity over these shorter distances. It relies on perennial waters as a drought refuge so has weaker resistance traits than *L.varians*. This species therefore shows greater vulnerability to increased drying than the large caddisfly, but is less vulnerable than the water penny.

Table 3. Macroinvertebrate focus species, their hypothesised dispersal capacity, known drought refuge use, known flow regime requirements and actual dispersal pattern derived from mitochondrial DNA. ESU = evolutionarily significant unit. All populations showed significant genetic structure within the Victoria Range except *L.varians* (derived from AMOVA analyses).

Species	Probable dispersal type	Drought refuge use	Presence vs flow regime	Actual dispersal pattern (genetics)
Lectrides varians Caddisfly	Moderate – reliant on flying adults	Pools, adult emergence, aestivation	Perennial streams and streams with pools	Very good aerial disperser – single population throughout Grampians NP
Leptoperla kimminsi, Riekoperla sp. Stoneflies	Good? – reliant on flying adults	Pools, resistant eggs	Perennial streams and streams with pools	Incomplete
Sclerocyphon striatus Water beetles	Poor – crawling	Pools	Perennial streams	Very poor disperser; multiple populations within Victoria Range; likely multiple ESUs
Geocharax sp. nov Freshwater crayfish	Poor-moderate – crawling, some drift	Pools, aestivation in chambers	All stony streams regardless of flow regime	Incomplete
Koornonga AV3 Mayfly	Poor-moderate – reliant on short-lived flying adults	Pools	Perennial streams and streams with pools	Small range disperser; two populations in Victoria Range; possible dispersal by larval drift as well as adult flight
Agapetus sp. Caddisfly	Moderate – reliant on flying adults	Pools	Perennial streams and streams with pools	Moderately good disperser by flight including across mountain ridgeline; deeply incised valleys apparently a barrier to dispersal

The grazing caddisfly *Agapetus* sp. is also capable of dispersing by flight over the top of the mountain range, however deeply incised valleys appear to be a barrier. This species has very specific microhabitat requirements for silt-free stones, which limits the amount of suitable habitat within many streams. This species therefore has poor resistance traits as it needs silt-free perennial pools/flow, it has resilience (dispersal) traits similar to the mayfly *Koornonga*.

Conclusions

1. Species differ strongly in the extent of both their resistance (drought refuge use) traits and their resilience (dispersal) traits with respect to increased stream drying.
2. Species with a greater range of drought refuge options and high dispersal capacity will be the least vulnerable to increased stream drying.
3. Species dependent on surface water as a drought refuge and with limited dispersal capacity will be the most vulnerable to increased stream drying.
4. Some species are mainly dependent on resistance traits for survival; these species will be greatly affected by the loss of drought refuges.
5. Some species are mainly dependent on resilience traits for survival; these species will be less affected by refuge loss and more affected by loss of connectivity among streams (either through vegetation corridors or stream flows).
6. The fragmentation of river flows arising from increased drying will affect species resilience to drought.
7. The loss of refuges arising from increased drying will affect species resistance to drought.
8. For many taxa, it will be possible to predict responses to increased drying by considering their particular combination of resistance and resilience traits, as well as the probable extent of their dispersal capacity.
9. For species with low resilience, ESUs are likely and individual populations are likely to harbour different genotypes. Therefore, the loss of individual populations is more likely to lead to an overall loss of genetic diversity in these species.

Objective 4

Identify biodiversity hotspots among ephemeral stream communities and determine conservation priorities

Following the bushfires, this objective was difficult to meet. Biodiversity hotspots are generally located on a larger spatial scale than the Victoria Range (approximately 25 km long north-south). The genetic analyses did discover a new species of Leptoceridae caddis fly in Deep Creek, but otherwise cryptic species were not found. Therefore, there is nothing further to report against this objective.

Outcomes against project objectives

Objective 1

To determine the key drought refuges used by macroinvertebrate species in intermittently flowing streams and determine the level of threat to each refuge posed by prolonged drying and unpredictable flow regimes

Conclusions

1. Perennial pools and sections of perennial streamflow sustain a disproportionately large number of invertebrate taxa during dry periods. They are also refuges for fish.
2. While other refuges (most importantly pools) occur in nominally dry stream reaches and contribute to the maintenance of stream biodiversity over summer, their viability is compromised by drought. Perennial reaches are reliable refuges during supra-seasonal drought but are also most vulnerable to increased drying and to water extraction.
3. Over-summering by adult aquatic insects in the terrestrial environment as a refuge has not been quantified here or in other studies. This refuge may be significant if it enables species to recolonise effectively through adults laying eggs when streams begin to flow.

There are two important lessons for management from the flow regime data:

1. Ephemeral streams need to be managed as groups, not individually, to ensure that the mosaic of habitat required by different species is maintained.
2. Tight classifications of ephemeral stream flow regimes based, for example, on the frequency of occurrence of pools, will not be useful as they do not properly represent the natural range of variation that typifies these streams.

Objective 2

To determine the role played by different types of drought refuge in restocking macroinvertebrate populations in rivers and, therefore, the consequences for river communities of loss of each type of drought refuge. Which qualities of perennial pool refuges are important for sustaining invertebrate biodiversity?

Conclusions

1. Drought refuges used during dry periods provide an important buffer against extreme summer–autumn temperatures.
2. Invertebrates present in streams when they are flowing come mainly from pool and perennially flowing drought refuges, and from newly laid eggs brought to streams by flying adult insects. Aestivation and desiccation-resistant eggs make a more minor contribution to the assemblage.
3. The presence of fish in pools reduces refuge quality for invertebrates by reducing dissolved oxygen levels and via predation.
4. Increased larval invertebrate mortality is likely in pool refuges as dry periods increase, resulting in fewer species surviving over the summer in that location. However, a subset of species may remain to aestivate where pools have dried. These species have adaptations to protect populations against stop-start flows, but there is probably a considerable energy cost to re-entering torpor if flows cease again.
5. Sufficient refuge pools are required to protect fish and invertebrate populations separately.
6. Animal biodiversity in a stream network is likely to be greatly reduced by the loss of perennial pools and sections of perennial flow.
7. Animal biodiversity in individual streams is likely to be greatly reduced by the loss of perennial pools and sections of perennial flow.

Objective 3

To determine the consequences of river habitat fragmentation caused by increased drying for the sustainability of macroinvertebrate populations by quantifying the effects on dispersal and the genetic structure of key aquatic species.

Conclusions

1. Species differ strongly in the extent of both their resistance (drought refuge use) traits and their resilience (dispersal) traits with respect to increased stream drying.
2. Species with a greater range of drought refuge options and high dispersal capacity will be the least vulnerable to increased stream drying.
3. Species dependent on surface water as a drought refuge and with limited dispersal capacity will be the most vulnerable to increased stream drying.
4. Some species are mainly dependent on resistance traits for survival; these species will be greatly affected by the loss of drought refuges.
5. Some species are mainly dependent on resilience traits for survival; these species will be less affected by refuge loss and more affected by loss of connectivity among streams (either through vegetation corridors or stream flows).
6. The fragmentation of river flows arising from increased drying will affect species resilience to drought.
7. The loss of refuges arising from increased drying will affect species resistance to drought.
8. For many taxa, it will be possible to predict responses to increased drying by considering their particular combination of resistance and resilience traits, as well as the probable extent of their dispersal capacity.
9. For species with low resilience, evolutionary significant units are likely and individual populations are likely to harbour different genotypes. Therefore, the loss of individual populations is more likely to lead to an overall loss of genetic diversity in these species.

Objective 4

Identify biodiversity hotspots among ephemeral stream communities and determine conservation priorities

Insufficient data was collected to conclude anything regarding this objective.

Scope of results

The results of this project should apply to seasonally flowing streams in semi-arid and Mediterranean climate regions of Australia. They will not apply to arid zone or 'dryland rivers' or to larger rivers with floodplains.

The best indicator for application of these results to other systems would be the type of stream fauna. Where the fauna is insect dominated and comprises a 'normal' stream fauna of stoneflies, mayflies, odonates, caddisflies, dipterans, with some crustaceans, particularly amphipods, isopods and decapods; these results should be useful. If the fauna is dominated by microcrustacea and other zooplankton and/or a benthic fauna comprising ostracods, cladocera and dipteran insects; these results will not apply.

Recommendations for managing flow-habitat relationships in ephemeral streams to assist decisions on water allocation and management

1. Ephemeral streams should be managed as groups to allow species to be resilient to drought (so that they have somewhere to colonise from) and so that the mosaic of different habitats is maintained to maximise the opportunities for all species.

2. Healthy, unregulated (often perennial, or with multiple reliably perennial pools) streams are important sources of colonists for other streams and should be a high priority for protection.

3. Sustaining refuge pools is important but not sufficient, connectivity (i.e. flow and terrestrial vegetation) is also necessary. Without connectivity, species relying on resilience to survive drought will not survive. In particular, without flow, many species will not complete their life cycle so their capacity to produce the next generation will be severely limited.

4. Regulation (with no amelioration) reduces biodiversity both upstream and downstream of weirs in ephemeral streams. This occurs because drought refuge pools dry out downstream of weirs and also because weirs and associated stretches of dry streambed block dispersal by species.

5. Environmental water allocation can be used to support resistance to drought by topping up refuge pools or supplementing trickling flows to sustain water quality and pool volume until streamflow recommences naturally.

6. Environmental water allocation can be used to support resilience by providing winter flows in regulated streams (where water extraction otherwise removes 100 per cent of flow or reduces the flow period by weeks to months) that connect refuge pools and flowing stream sections to permit animal dispersal.

Summary of all project knowledge and adoption activities

1. Article introducing this project published in RipRap.
2. Public talk given by B. Robson to GNP threatened species group (community volunteers) on 25 April 2006.
3. Robson B.J., Chester E.T. & Austin C. (2007) Environmental water allocation required to sustain macroinvertebrate species in ephemeral streams. 5th Australian Stream Management Conference, Albury.
4. Robson B.J., Chester E.T. & Austin C. (2007) Environmental water allocation required to sustain macroinvertebrate species in ephemeral streams. 'Biodiversity Across Borders' conference held at the university of Ballarat, 15 June 2007. This one day event consisted of about 350 participants from local environmental management agencies, universities and community groups (e.g. Landcare etc).
5. Robson B.J. & Chester E.T. (2007) Is water extraction a threat to insect populations in intermittently-flowing streams? Royal Entomological Society Symposium and National Meeting, Aquatic Insects: challenges to populations. University of Edinburgh, Scotland.
6. The Fact Sheet entitled "Managing flows for ephemeral streams" was completed and has been released as Fact Sheet No. 2 from the program.
7. Dr Robson attended the LWA workshop in Brisbane 2007 and presented the results to that date.
8. Robson B.J., Chester E.T. & Austin C. (2007) Is an environmental water allocation required to sustain macroinvertebrate species in seasonally-flowing streams? Joint meeting of the NZFSS & ASL, Queenstown, New Zealand.
9. Matthews T.G., Chester E.T., Robson B.J., Johnston K. & Howson T. (2007) Role of fish in the quality of drought refuges for stream invertebrates. Joint meeting of the NZFSS & ASL, Queenstown, New Zealand.
10. Wickson S., Robson B.J. & Chester E.T. (2008) Adaptations to an arid environment – aestivation and diapause in drought-resistant caddisflies. 47th National congress of the Australian Society for Limnology, Mandurah, Western Australia.
11. Chester E.T. & Robson B.J. (2008) Remote sensing of flow-dependent stream habitat condition using temperature loggers. 47th National congress of the Australian Society for Limnology, Mandurah, Western Australia.
12. Dr Robson presented results to the program workshop in Canberra, November 2008.
13. Robson B.J., Chester E.T., Austin C., Wickson S. & Miller A. (2009) EWA required to sustain macroinvertebrate species in ephemeral streams. Final LWA EWA Program workshop, Canberra, May 2009.