

FACTORS INFLUENCING THE COMPOSITION OF FAUNAL ASSEMBLAGES IN RAINFOREST STREAM POOLS

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ABSTRACT

Previous research has shown that a range of physical and biological drivers can influence the composition of faunal assemblages occupying localities within streams. There is much debate in the literature about which of these is more important. Descriptive and experimental field studies were conducted in two relatively undisturbed, second order rainforest streams in southeast Queensland, Australia. The principal objectives were to describe spatial and temporal patterns in pool fauna and explore relationships between these patterns and physical attributes of habitat, disturbance and biotic interactions.

The macroinvertebrate and vertebrate fauna of 12 small stream pools were sampled approximately monthly over a period of 15 months. Samples were collected from all major within-pool habitat types and concurrent measurements of potentially important environmental parameters were made at landscape scales of stream, pool and habitat patch.

Faunal assemblages were consistently different between the two streams and between the various within-pool habitat types, although the latter may partially be explained by differences in sampling protocols applied in the different habitat types. However, spatial and temporal variation in faunal assemblages within habitat types was large at the scales of whole pools and within-pool habitats, and this variation occurred apparently independently of variation in physical habitat attributes. These results indicated that very little of the local scale faunal variation could be explained by abiotic drivers and that some other factors must be responsible for the observed faunal patterns.

Previous research had indicated that atyid shrimps can play a significant ecological role in rainforest streams, where they act as "ecosystem engineers" by removing fine sediment from hard surfaces. This subsequently alters algal dynamics and faunal composition in streams. A pool-scale manipulative experiment was conducted to investigate the role of the atyid *Paratya australiensis*, which is an abundant and conspicuous component of the fauna. Removal of shrimp from pools had no effect on

sediment accrual on hard surfaces and consequently did not affect algal biomass or faunal assemblages. The lack of effect on sediment accumulation was attributed to the low rate of deposition in these streams, which was an order of magnitude lower than in streams where atyids have been demonstrated to play a keystone role.

The fish *Mogurnda adspersa* was found to be the primary predator of pool fauna in the study streams, where it preyed on a wide variety of taxa. Dietary analyses revealed that an ontogenetic shift occurred in both diet and the within-pool habitat where fish fed. Within this general framework, individual fish had strong individual prey preferences. Significant correlations were found between the natural abundance of *Mogurnda* in pools and faunal assemblage patterns in both gravel habitat and pools in general, indicating that predation had an effect on pool fauna. The nature of this effect varied between habitats. A direct density dependent response was observed in gravel habitat. In contrast, the response in pools varied considerably between individual pools, perhaps reflecting the differing prey preferences of individual fish. Despite these correlations, an experimental manipulation of the density of *Mogurnda* at a whole-pool scale did not conclusively identify a predation effect. This may have been due to problems with fish moving between treatments, despite attempts to constrain them, and low experimental power due to the inherent high variability of pool fauna.

Overall, the results of the study indicated that there was considerable spatial and temporal variation in pool fauna despite similarities in the physical attributes of pools and their close proximity. This variation appeared to occur at random and could not be explained by abiotic or biotic factors. Predation had a small effect, but could not explain the overall patterns, whereas disturbance by spates had very little effect at all. Stochastic processes associated with low level random recruitment were identified as a possible and plausible explanation for observed patterns.

These conclusions are discussed in terms of their implications for our understanding of the ecology and management of streams.

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STATEMENT OF ORIGINALITY

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Jonathan Coid Marshall

March 2001

CHAPTER 1: GENERAL INTRODUCTION

1.1 The physical habitat – habitat template

The relative contribution of physical habitat and biotic factors in influencing the structure and functional organisation of biotic assemblages is a fundamental issue of ecology. The importance of both abiotic and biotic factors and interactions between them has long been recognised. Physical environment provides the template within which occur the evolutionary processes generating species with particular traits (Southwood, 1977; 1988). Localities with similar environmental properties should be populated by species with similar traits and therefore display similar assemblage structure in terms of functional organisation (Orians, 1980). The assemblage of species that occurs at a location is a subset of all available species, governed by the tolerances and preferences of each species for ambient environmental conditions (Hutchinson, 1957). Given that a location has conditions within the tolerances of a given species and provides necessary resources, there is potential for that species to maintain a viable population there. Whether or not this occurs depends upon the species' ability to colonise the site and, even then, its persistence may be influenced by biotic interactions with other species.

Each species can be considered to have a specific range of tolerance and an optimal range of preferences for environmental factors and the availability of resources (Stearns, 1989). The concept of the ecological niche (Hutchinson, 1957), as a multi-dimensional hyper-volume defined by the range of each important environmental parameter in which a species can maintain a viable population, depends critically upon the relationship between organisms and environmental conditions.

In streams, it has been widely demonstrated that interactions among chemical and physical processes create environmental conditions at a range of scales that strongly influence the distribution and abundance of species, and thus the composition of assemblages (*e.g.* Hynes, 1970; Townsend, 1980; Vannote *et al.*, 1980; Minshall and Petersen, 1985; Sweeney, 1984; Resh *et al.*, 1994; Statzner and Borchardt, 1994; Townsend and Hildrew, 1994; Downes *et al.*, 1995). The distributions of individual aquatic taxa can be strongly influenced by physiological tolerances to abiotic conditions. For example the distribution of the parastacid crayfish genus *Euastacus* in eastern Australia is primarily constrained by its intolerance of warm water.

Consequently at the high latitude parts of its range with cooler climates, *Euastacus* species occur at sea level. As latitude decreases, its distribution becomes more and more restricted to high altitude (cooler) streams. At the limits of its range in tropical north Queensland, species are restricted to the peaks of the very highest mountains, as these are the only locations where temperature tolerances are not exceeded (Riek, 1969; Morgan, 1986; 1988; 1989; 1991; Ponniah and Hughes, 1998).

Water chemistry can also influence biotic composition of streams and wetlands at a landscape scale (e.g. Townsend *et al.*, 1983; Bunn *et al.*, 1986; Rosemond *et al.*, 1992; Clenaghan *et al.*, 1998). For example, there is a suite of species with distributions confined to low pH water bodies within south eastern Queensland, including the so-called “acid frogs”, “acid fish” and some species of macroinvertebrates and algae. Most species that are widespread in the more typical non-acid water bodies throughout the area do not occur at these sites (Riek, 1969; Arthington and Marshall, 1991; 1993; Ingram and Raven, 1991; Arthington, 1996; Queensland Department of Natural Resources, *unpublished data*). Changes to biotic assemblages following anthropogenic modification to stream water chemistry provides additional evidence of its influence (e.g. Armitage, 1980; Norris *et al.*, 1982; Lake and Marchant, 1990).

Different channel units within streams, such as pools and riffles, which can be defined in purely physical terms (Jowett, 1998), are inhabited by distinctly different biotic assemblages (e.g. Jenkins *et al.*, 1984; Ormerod and Edwards, 1987; Ormerod, 1988; Beisel *et al.*, 1998) providing evidence of the important role of abiotic drivers at a smaller spatial scale. Abiotic drivers also influence assemblage properties within habitat units. Many studies have identified substrate composition, complexity and heterogeneity as major determinants of in-stream biota (e.g. Flecker and Allan, 1984; Richards *et al.*, 1993; Beisel *et al.*, 1998; Downes *et al.*, 1998a; Minshall and Robinson, 1998). For example, detailed studies of abiotic influences upon occurrence patterns of Ephemeroptera and Odonata species in Hong Kong streams found substrate composition and heterogeneity to be the strongest correlate with population sizes of almost all species and thus also with assemblage structure (Dudgeon, 1992). Further evidence of the importance of substrate is provided by studies demonstrating large changes in the faunal composition of streams subject to substrate modifications as a

consequence of increased sedimentation (*e.g.* Richardson, 1985; Wood and Armitage, 1997).

Flow is another important abiotic driver of faunal assemblages at a local scale (*e.g.* Barmuta, 1990; Extence *et al.*, 1999; Kefford and Lake, 1999; Lancaster, 1999; Choy *et al.*, 2000). Many species can feed, maintain position and respire only within a narrow and specific range of hydraulic conditions (such as velocity and turbulence), which can vary over very small spatial and temporal scales (*e.g.* Statzner and Higler, 1986; Davis and Barmuta, 1989; Bouckaert and Davis, 1998).

Poff (1997) proposed a hierarchical series of landscape filters to explain the distribution and abundance of biota at various spatial scales, based on species level functional relationships with abiotic and biotic selective forces. This model considers environmental conditions as filters through which species in a global pool must "pass" to be potentially present at a given locality. The absence of a species at a locality reflects its inability to pass through at least one of the selective filters. This provides a useful framework in which to conceptualise abiotic influences on biotic patterns in streams.

1.2 Biotic processes

Often, the distributions of species are considerably more restricted than would be predicted by their physiological tolerances to abiotic factors alone. In part, this can be due zoogeographical factors (*e.g.* Bunn and Davies, 2000) and zoogeography was recognised by Poff (1997) as a critical factor determining the regional pool of species available to colonise a stream within his hierarchy of landscape filters. However, biotic processes can also result in such departures from predicted patterns or even a lack of predictive success.

1.2.1 Food resource availability – bottom up influences

The influences of food resource availability on assemblages of organisms differ from those of abiotic habitat features because the organisms themselves influence food availability through consumption. Food webs in headwaters streams are driven by allochthonous carbon in the form of leaf litter and other plant detritus and by

autochthonous algal production. Associations between detritus quality and quantity and assemblages of stream macroinvertebrates have been well documented (*e.g.* Cummins, 1974; Cummins and Klug, 1979; Vannote *et al.*, 1980; Richardson, 1991; Davies, 1993). Limitation of consumer density by food resource availability is termed “bottom-up control”. For example, the productivity, density and biomass of primary consumers can be limited by the availability of algal food resources (*e.g.* Lamberti and Moore, 1984; Rosemond *et al.*, 1994). Heavy grazing by insects can alter and deplete assemblages of epilithic algae (Power *et al.*, 1988; McCormick *et al.*, 1994; Huryn, 1996; 1998). However, intermediate levels of grazing can also stimulate new algal growth and increase primary productivity (*e.g.* Lamberti and Resh, 1983; Mosisch, 1995). In some circumstances bottom up control can cascade through several trophic levels (*e.g.* Flecker and Townsend, 1994; Huryn, 1998).

The availability of autochthonous and allochthonous food resources in a stream can also govern the diversity of stream fauna (Bunn and Davies, 1990). Where food availability is high there is a large amount of energy available and this results in a high diversity of stream fauna. Two mechanisms have been proposed to explain this (Bunn and Davies, 1990). Firstly, productive habitats with a high density of available food have more potential for dietary specialisation than unproductive habitats and in the former, each species will utilise fewer of the variety of food types available. Thus the same spectrum of food resources will support more species (Pianka, 1983). Secondly, some food sources in unproductive habitats may be too sparse to support species that utilise those resources, while in highly productive systems the same resources may be dense enough to support such species (MacArthur, 1965).

The activities of stream fauna can indirectly provide food and nutrients to other organisms. For example, the feeding activity of shredders breaks up leaf litter producing fine particulate matter, which generates food for filter feeders and collectors (Richardson and Neill, 1991) and the metabolic by-products released by consumers act as nutrients promoting algal growth (*e.g.* McCormick, 1990; Power, 1991).

1.2.2 Competition

Competition is believed to be a relatively unimportant force in streams in comparison with other ecosystems (Hildrew and Townsend, 1987; Lampert and Sommer, 1997;

Bunn and Davies, 2000). Environmental heterogeneity in space and time at various scales is pronounced in streams, and this is thought to permit species with identical requirements to coexist (Dudgeon, 1992; Lampert and Sommer, 1997). There are however, some examples that suggest competition can influence the distribution and abundance of stream organisms, and that competitive exclusion can occur (Hart, 1983; Hemphill and Cooper, 1984; Power, 1990; Douglas and Lake, 1994; Morgan and Ringler, 1994; Closs, 1996; Kohler and Wiley, 1997). Competitive interactions in streams appear to be strongest within periphyton grazing guilds during periods of environmental stability (Dudgeon, 1992; Kohler, 1992; Negus, 1995; Kohler and Wiley, 1997).

1.2.3 Predation – top down influences

Consumption by a predator is the predominant biotic cause of mortality and almost every organism is potential food for some other organism. Predation can destructively change the composition of assemblages by reducing prey abundance, or even eliminating species that are particularly susceptible, either because of predator preferences, or differential vulnerability of prey species.

Fish are often the predominant predators in stream ecosystems (Healey, 1984). Studies of the effects of fish predation on the abundance and assemblage structure of their invertebrate prey have produced contrasting results, with some showing strong interactions (*e.g.* Cooper, 1988; Gilliam *et al.*, 1989; Morgan and Ringler, 1994) and many others showing no effects at all (*e.g.* Allan, 1978, 1982; Holomuzki and Stevenson, 1992). The strength of predation effects identified in studies such as these is very much determined by attributes of the fish predators, their prey and the environment.

Complex substrates provide prey with shelter, which in turn reduces the predation efficiency of fish, so in highly heterogeneous environments predation is unlikely to exert strong effects on the distribution and abundance of prey taxa (*e.g.* Allan, 1982; Flecker and Allan, 1984; Cook and Streams, 1984).

Strong interactions are also unlikely in stream systems where there are high rates of prey immigration. In such circumstances individuals lost to predation can be replaced

with little net change in assemblage structure (Reice and Edwards, 1986; Cooper *et al.*, 1990; Dahl and Greenberg, 1998). Where the mortality of prey species resulting from predation is low in comparison with the overall abundance of prey it is also unlikely that predation will exert much overall influence on prey assemblages (Reice, 1991b).

Invertebrate predators are also capable of reducing the abundance of some prey taxa (Peckarsky *et al.*, 1990), as is mortality stemming from infection/infestation by pathogens and parasites (Kohler and Wiley, 1997).

1.2.4 “Keystoneness” – functional importance

While all species in an assemblage have the potential to affect other species in some way or another, the strength of such interactions varies markedly. The presence or absence of some species can have a strong influence on the structure and functional organisation of the remainder of the assemblage and these have been termed “keystone species” (Paine, 1969). Rather than a categorical division between keystone and non-keystone species, the functional importance of species in an assemblage may actually range from high to low with some at intermediate levels (Hurlbert, 1971; 1997).

Certain fish predators in streams have been demonstrated to influence entire assemblages, rather than just the abundance of their prey. These fish are responsible for dramatic “trophic cascade” effects (Paine, 1980; Carpenter *et al.*, 1985) in stream ecosystems. For example, in some stream systems the presence or absence of large predatory fish has been shown to dramatically influence algal biomass (Power, 1990). Similar effects have been demonstrated through fewer trophic levels (*e.g.* Power *et al.*, 1985; Power, 1987; Gelwick *et al.*, 1997).

The activities of some organisms can generate and modify habitat patches for other organisms, in a process termed “ecosystem engineering” (Mills *et al.*, 1993; Jones *et al.*, 1994). For example, Hart (1985b) demonstrated that small patches dominated by epilithic diatoms persisted as a result of the behaviour of the larvae of a species of caddisfly. In the absence of caddisfly larvae, the diatom patches were rapidly overgrown by filamentous cyanobacteria. The caddisfly larvae did not actually eat the cyanobacteria, but rather removed and discarded them, thus allowing better growth of the diatoms that provided them with their food. Other examples of these effects include

benthivorous fish, the foraging behaviour of which can alter the composition and abundance of phytoplankton in rivers by modifying physical habitat (Breukelaar *et al.*, 1994; Gehrke and Harris, 1994; King *et al.*, 1997) and subsequently influence the entire food-web via “bottom-up” mechanisms (McCauley and Kaliff, 1981; Mills and Schiavone, 1982; Canfield and Watkins, 1984). The foraging behaviour of Atyid shrimp can also modify the environmental properties of streams by generating patches with reduced quantities of fine deposited sediment. These patches grow an increased biomass of epilithic algae, which in turn alters the composition of insect assemblages (Pringle *et al.*, 1993; Pringle and Blake, 1994; Pringle, 1996).

1.3 Disturbance

The physical nature of environments are rarely stable in either space or time and this is especially the case in streams, which are considered to be patchy environments (*e.g.* Townsend, 1989; Lampert and Sommer, 1997). Fluctuations in environmental attributes vary in their magnitude from small to large and in their duration from short-term to long-term. A disturbance is a physical event causing rapid environmental changes that can disrupt “normal” patterns and processes in ecosystems, assemblages and populations (White and Pickett, 1985). Disturbances can prevent resources becoming limiting by reducing population densities and preventing species from excluding other species by interrupting potential competitive interactions. In many respects predation can be viewed as a form of disturbance (*see* Section 1.2.3).

Spates are a major form of disturbance in streams and can influence stream fauna directly by reducing the total number of individuals and species via mortality (*e.g.* Resh *et al.*, 1988; Reice, 1991a; Palmer *et al.*, 1996). They can also indirectly influence fauna by generating habitat patches of different types, sizes and ages, providing a range of habitats for a variety of species (Townsend, 1989), and by reducing the influence of predators and competitively dominant species, thus permitting the persistence of some species (*e.g.* Lancaster, 1990; Peckarsky *et al.*, 1990; Hemphill, 1991). Spates can also drastically reduce the availability of algal and detrital primary food resources in streams (*e.g.* Mosisch, 1995; Mosisch and Bunn, 1997; Lancaster and Hildrew, 1993b), which can result in alterations to the composition and functional organization of stream fauna via “bottom up” mechanisms (*see* Section 1.2.1).

Droughts have not been as well studied in streams as have spates and are not as easily defined. They develop gradually with a deficiency in rainfall and vary greatly in their predictability and duration (Lake, 2001). Droughts lead to the constriction of available habitat and disruption of connectivity. Biota can be killed if the water dries completely from the location where they are living (Extence, 1981; Smock *et al.*, 1994), resources can become limiting and concentrations of toxic substances can increase (Lake, 2001). The intensity of biotic interactions can also increase as prey species are forced into close proximity to predators in shrinking habitats (Dudgeon, 1992; Closs, 1996) and there is also potential for competition for limited resources to become more prevalent

Spates and droughts are part of the normal hydrological regime of upland streams and in most cases their occurrence is inevitable. However, their timing and magnitude over a given interval is erratic and unpredictable. They occur with sufficient frequency to be considered “disasters” rather than “catastrophes”, in that they exert selective pressure on populations to evolve traits that enable them to persist (*see* Bergon *et al.*, 1990). In fact, many aquatic species have evolved such traits, which increase their capacity to cope with the inevitable disturbance of spates and droughts. These enable them to either recolonise from elsewhere if local populations are eradicated, or else survive the disturbance *in situ* (Townsend *et al.*, 1997).

There is evidence that streams contain “flow refugia” which are locations within streams that are not subject to raised hydraulic stress during high discharge events (*e.g.* Hildrew *et al.*, 1991; Lancaster and Hildrew, 1993a; 1993b), and “drought refugia” which are locations within streams that are subjected to reduced desiccation stress during drought (Boulton, 1989; Boulton *et al.*, 1992b; Stanley *et al.*, 1994). The mortality of fauna caused by spates and droughts is diminished if they utilise refugia and it has been suggested that the presence of refugia may be critical to the persistence of stream fauna (Hildrew *et al.*, 1991).

Individuals have been demonstrated to actively migrate to refugia in response to the onset of spates (Borchardt and Statzner, 1990; Lancaster and Hildrew, 1993b; Dole-Olivier *et al.*, 1997) but little is known about movement of individuals into drought refugia. Several types of flow refugia within streams have been proposed including large particles such as boulders and large woody debris (Townsend, 1989),

hydraulically dead areas with low sheer stress (Lancaster and Hildrew, 1993b; Palmer *et al.*, 1996; Mattheai *et al.*, 2000), the edges of streams (Bishop, 1973; Poole and Stewart, 1976) and the hyporheic zone (Williams and Hynes, 1974; Matthaei *et al.*, 1999). Comparatively little is known about drought refugia but they are known to include water in remnant pools, the hyporheic zone and crayfish burrows, plus coarse woody debris, litter and stones in the dry streambed (Boulton, 1989; Boulton *et al.*, 1992b; Stanley *et al.*, 1994). Individuals in refugia are able to recolonise disturbed sections of the stream via a variety of dispersal mechanisms when conditions there once again become tolerable (*e.g.* Williams and Hynes, 1974; 1976; Morrison, 1990; Smock *et al.*, 1994).

1.4 Relative importance of biotic and abiotic processes

1.4.1 Harsh and benign environments

The likelihood of biotic effects having a greater influence on assemblage characteristics than abiotic effects is thought to be higher when physical environmental conditions are benign, stable and predictable, and vice versa in severe, variable or unpredictable environments (Paine, 1966; Connell, 1975; Menge and Sutherland, 1976; Menge *et al.*, 1986). The basis for these predictions is that when conditions fluctuate or are harsh, abiotic drivers of the occurrence and abundance of species assemblages predominate, mediated via the tolerances of individual species. In such circumstances mortality of individuals resulting from abiotic stress is thought to be high enough to maintain populations at levels below those at which resources become limiting. On the other hand, when conditions are relatively stable or benign, mortality due to abiotic stress is thought to be comparatively low, and population sizes (and subsequently assemblage composition) are more likely to be driven by resource availability, governed via biotic processes such as competition and predation (Paine, 1966; Connell, 1975; Menge and Sutherland, 1976; Menge *et al.*, 1986).

In streams, this equates to a higher likelihood of biotic effects being important in pools rather than riffles, and under base flow conditions rather than during or shortly after spates (*e.g.* Peckarsky, 1983; Power *et al.*, 1985; Peckarsky *et al.*, 1990).

1.4.2 Applied community ecology – predicting “response” and managing water resources

The empirical and theoretical concepts discussed in preceding sections of this chapter have led to practical applications based on the principle that assemblage structure and dynamics can be predicted if the biotic and abiotic drivers are understood and quantified. It is however, often assumed that principles or theories derived from one system or region or at particular spatial and temporal scales, can be applied elsewhere, and this is not necessarily the case (Lake and Underwood, 1995; Downes *et al.*, 2000). Examples of applied community ecology based on prediction include biomanipulation of water quality (*e.g.* Carpenter *et al.*, 1985; Van Donk *et al.*, 1989; Morin, 1999), bioassessments of the ecological “health” of waterways and rehabilitation of degraded stream habitats to restore assemblage composition and function.

The idea that local species assemblages are a consequence of local environmental features is paramount to the many biomonitoring programmes increasingly incorporated into water resource management practices throughout the world (Norris and Norris, 1995). Empirical models have been developed to predict the occurrence of macroinvertebrate taxa based on their association with environmental variables (*e.g.* Wright, 1995; Reynoldson *et al.*, 1997; Chessman, 1999; Simpson and Norris, 2000) and some of these models can predict the occurrence of taxa with accuracies of 80% or greater (Hoang *et al.*, 2001). This concept has been taken even further with the development of models to predict local environmental features based on catchment level features, and thus predict both the habitat types and associated fauna that *should* be present at degraded sites (Davies *et al.*, 2000). A common feature of these models is that they do not incorporate biotic interactions when making predictions, and thus make the assumption that assemblages can be accurately predicted based on physical habitat alone.

The notion that habitat can predict biota has been further applied in the field of stream restoration. The principle evoked here is that restoring habitat in a degraded stream will subsequently result in restoration of a more “natural” biotic assemblage. Examples of the application of these ideas include the restoration of modified river flow regimes (so called “environmental flows”) (*e.g.* Arthington *et al.*, 2000) and the rebuilding of riffles in previously channelised stream reaches (*e.g.* Newbold *et al.*, 1983; Newbury and

Gaboury, 1993). Once again, these projects tend to make predictions of ecological outcomes while ignoring the possibility that some species may fail to return to restored sites because of biotic effects such as competition and predation from species already present, (notably exotic species that often live in degraded areas), or limited opportunity for dispersal to the restored habitat.

The problems and deficiencies raised above in relation to practical applications of ecological theory for water resource management, highlight the necessity for a better understanding of the roles of biotic and abiotic processes in structuring assemblages of aquatic organisms. Improved understanding will permit more accurate predictions to be made concerning the ecological consequences of management options and enhance our capacity to sustainably manage aquatic ecosystems in the face of increasing consumptive demands placed upon water resources.

1.5 Aims of this study

The overall aim of this study is to identify biotic and abiotic processes that underlie spatial and temporal patterns in pool faunal assemblages in rainforest streams in south east Queensland, Australia. The following descriptive and experimental field studies were conducted to address this aim:

Chapter 2 describes the study area, streams and pools in terms of climate, geology, topography, geomorphology and biology to provide context for the remainder of the study.

Chapter 3 describes spatial and temporal patterns in pool fauna and explores relationships between these, physical habitat and primary food resource levels. The relative significance of physical habitat and primary food resource levels in determining the composition of fauna is investigated across spatial scales of habitat within pools, whole pools and streams.

In Chapter 4 the ecological role of the shrimp *Paratya australiensis* is investigated. This species is a conspicuous component of pool fauna and has potential as an “ecosystem engineer”. The chapter investigates whether or not the foraging activities of

this shrimp modifies physical habitat, and if so whether or not this directly or indirectly influences algal biomass and faunal assemblage composition in pools.

Chapter 5 explores the influence of predation by studying the most likely contender to be a strongly interacting predator in the study pools, the fish *Mogurnda adspersa*. Confirmation is made that this species is a predator of pool fauna and then investigations of the effects of fish predation on pool faunal assemblages and the abundances of individual prey species are presented.

The final chapter draws conclusions from the overall body of work and discusses implications for our understanding of stream ecology and management of waterways.

CHAPTER 2: THE STUDY AREA

2.1 The Conondale Range

This study was conducted in two small tributaries of Stony Creek in the southern portion of the Conondale Range in south east Queensland, Australia. The Conondale Range is situated approximately 100km north west of Brisbane in the Sunshine Coast Hinterland (Figure 2.1). The range was formed from a deeply dissected basalt plateau (Murphy *et al.*, 1976). Foot-hills rise from an altitude of approximately 200 m above sea level to a peak of 876 m at Mt Langley. The area forms the upper catchments of two major river systems; the Mary River draining to the north and the Brisbane River to the south. Stony Creek is a tributary of the Stanley and subsequently Brisbane Rivers.

2.1.1 Climate and Stream Flow

The Brisbane River has been described as a dry but flood-prone catchment (Stock, 1990). It has a low average rainfall to runoff ratio with nett evaporation equal to average rainfall and occasional severe droughts with zero stream flows. Occasional severe floods are also a feature of the river (Stock, 1990).

The climate of the area is “sub-tropical humid”, characterised by a hot wet humid period from November to April and a mild dry period from May to October (Figure 2.2) (Australian Bureau of Meteorology, 1983). Rainfall is seasonal, however total annual and total wet season rainfall varies markedly between years, without a particularly strong pattern in relation to the El Nino Southern Oscillation (ENSO) (Auliciems, 1990).

Figure 2.1. Map indicating location of study streams and key features in the area. Further details are provided in figures 2.3 and 2.5.

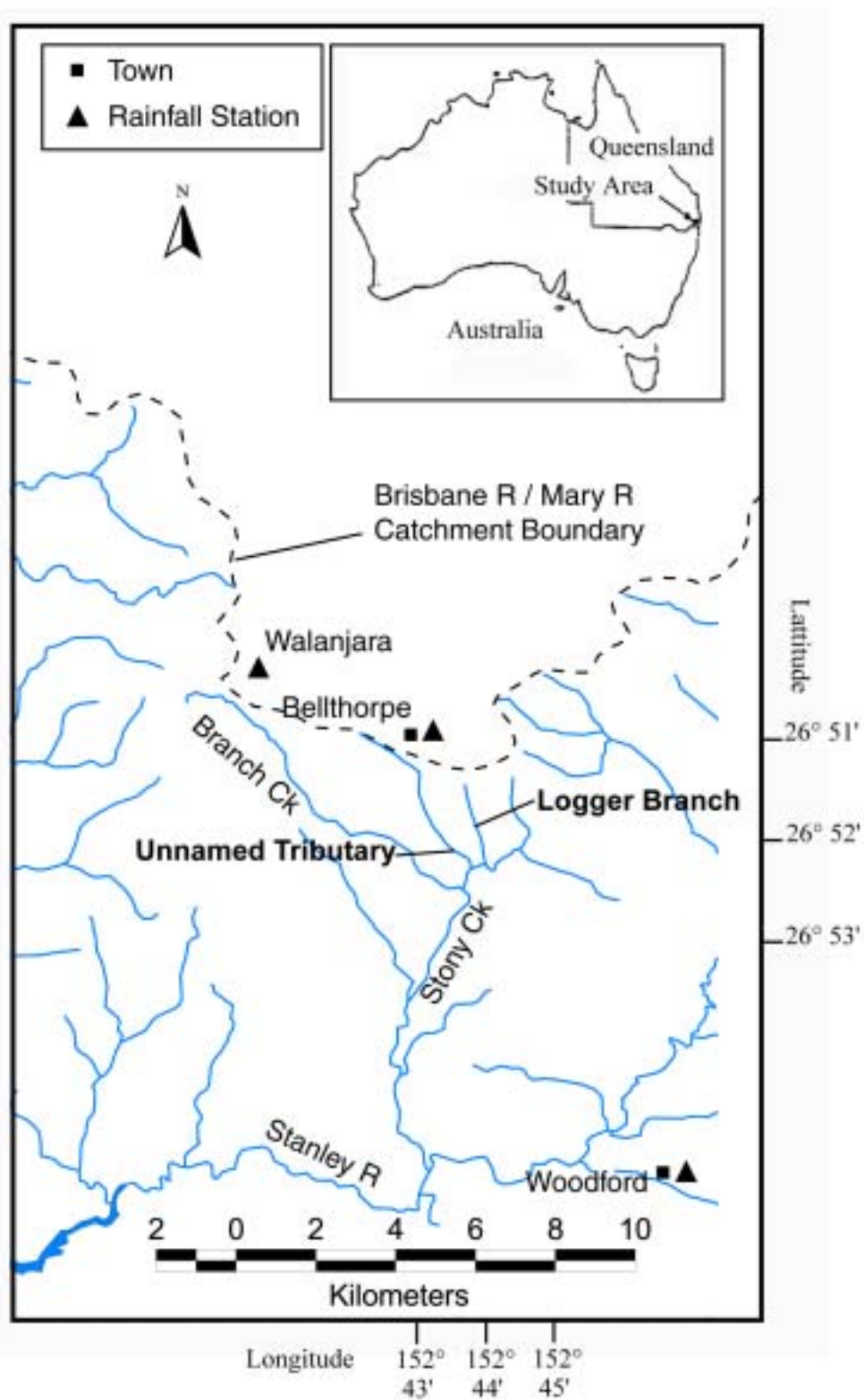
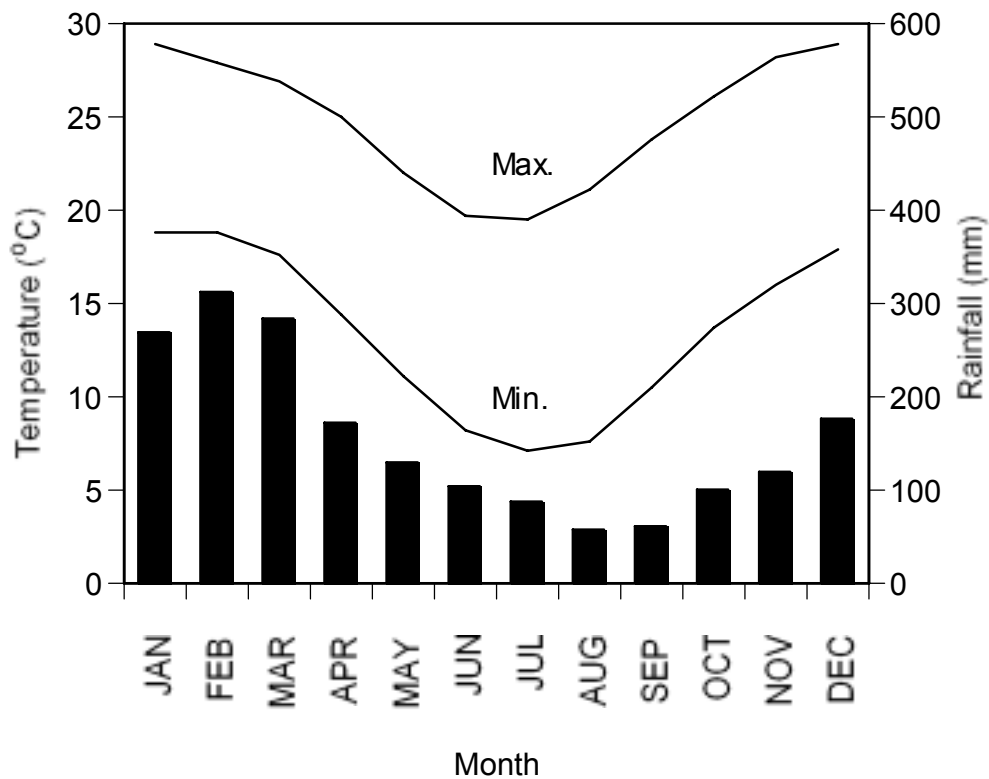


Figure 2.2. Average rainfall (columns) and maximum and minimum daily air temperature (lines) for each month at Crohamhurst, approximately 20 km NW of the study area (Australian Bureau of Meteorology Station: 040062, Latitude: 26.81° S, Longitude: 152.87° E, Elevation: 200 m).



Within this general climatic setting, streams in the area are prone to unpredictable, large-volume floods and severe drought. During the wet part of the year, much of the rainfall is heavy and frequently associated with thunderstorms. This form of rainfall can be spatially patchy in occurrence, and result in flash flooding, particularly in small streams. More significant flooding events are associated with periods of continuous rainfall of greater than 24 hours in duration. Major flooding has occurred in the Brisbane River at least once every 80 years since European settlement. This type of event is associated with cyclones which have a greater probability of affecting the area in years with a high southern oscillation index (SOI) (Auliciems, 1990).

In summary, stream flow is predictable in the sense that there are distinct wet and dry seasons corresponding to periods of elevated flows and periods of base flow. However, the timing and magnitude of high flow events is highly unpredictable because wet season rainfall is patchy and varies tremendously from year to year.

2.2 Study Streams

The two small streams from which sites were chosen for this study have no official names. In past studies they have been referred to by the unofficial names of Unnamed Tributary and Logger Branch (Hancock, 1995). This convention will be adhered to for the purposes of the current study.

Unnamed Tributary and Logger Branch, together with other Conondale Range streams, have been the subjects of several ecological studies investigating algal community dynamics (Mosisch, 1995; Mosisch and Bunn, 1997), stream drift (Kerby, 1991; Kerby *et al.*, 1995), population genetics and dispersal of aquatic species (Kingston, 1993; Hancock 1995, 1998; Schmidt *et al.*, 1995; Bunn and Hughes, 1997; Hughes *et al.*, 1995, 1998), community dynamics of grazers (Negus, 1995 and the life history of atyid shrimp (Hancock 1995, 1998; Hancock and Bunn, 1997; Hancock and Hughes, 1999). Further description of the study streams may be found in these publications.

The headwaters of the two streams are approximately 250 km from the sea via the channel network. The streams are short with steep gradients and drain small catchments within deeply excised and heavily vegetated valleys (Table 2.1; Figures 2.3 and 2.4). Both are second order streams (Strahler, 1963) as determined from a 1:50 000 scale topographic map (Kilcoy, Queensland, Australia 1:50 000 Topographic Survey, Series R733, Sheet 9444-111, Edition 1-ASS, 1982). The catchments are adjacent and separated by a ridge rising to a height of 200 - 250 m above the stream beds over a distance of approximately 500 m (Figure 2.4).

Table 2.1. Geomorphological features of the study streams.

	Unnamed Tributary	Logger Branch
Catchment Area	3.55 km ²	1.86 km ²
Stream Length	5.3 km	3.1 km
Stream Order	2	2
No. First Order Tributaries	11	3
Lowest Elevation	170 m	
Highest Elevation	590 m	520 m
Average Gradient	1 : 12.6	1 : 8.9
Geology	Neurum Tonalite	Neurum Tonalite
Riparian Vegetation	Notophyll Vine Forest	Notophyll Vine Forest

The majority of this study was conducted in the lower reaches of the two streams as indicated on Figure 2.4. A detailed survey of the major habitats in these reaches was undertaken using a dumpy level (Figure 2.5).

There are two major impoundments downstream of the study reaches; Somerset Dam on the Stanley River and Wivenhoe Dam on the Brisbane River. The only potential influence these dams may have on the study area is a reduction in the recruitment of catadromous fish species such as the long finned eel (*Anguilla reinhardtii*) as a consequence of impaired migration (Kennard *et al.*, 2000), though eels are present in the study streams.

Figure 2.3. Composite aerial photograph of the study area. Catchment boundaries of Unnamed Tributary and Logger Branch are marked from the Kilcoy, Queensland, Australia 1:50 000 Topographic Survey, Series R733, Sheet 9444-111, Edition 1-ASS, 1982. Photographs were taken from 4310 m above sea level on 18/8/97. North point and scale bar are approximate. Raw images were supplied by Queensland Department of Natural Resources.

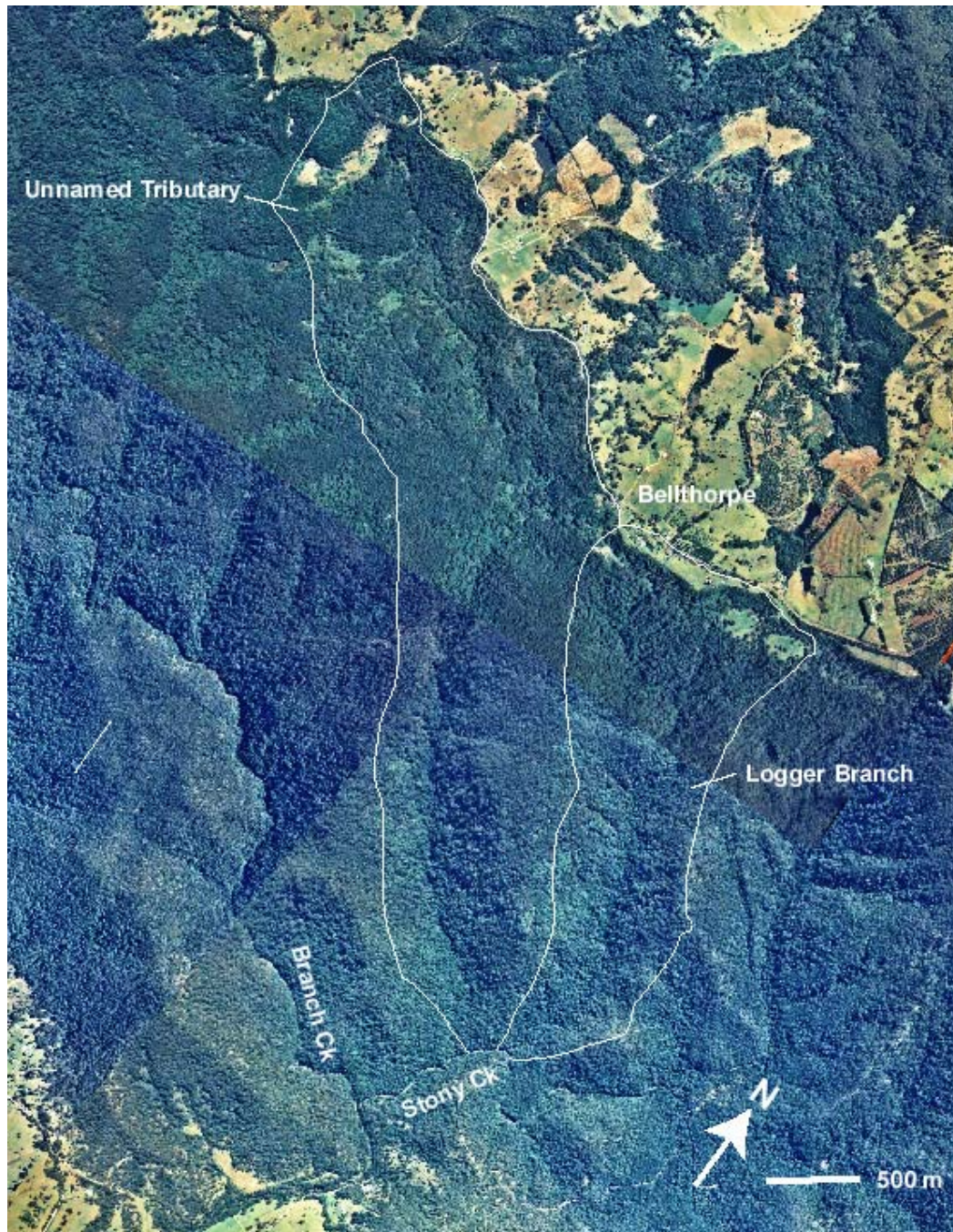


Figure 2.4. Stream profiles of (A) Unnamed Tributary and (B) Logger Branch (Australia 1:50 000 Topographic Survey map, Kilcoy Queensland, series R733, sheet 9444-111, edition 1-AAS, contour interval 20 m) indicating the elevations of the stream beds and the top of the ridge dividing their catchment basins. Asterisks on the horizontal axes indicate the upper and lower extremities of reaches used for the majority of this study. Dashed vertical lines indicate the location of a cross-section through the two streams presented in (C).

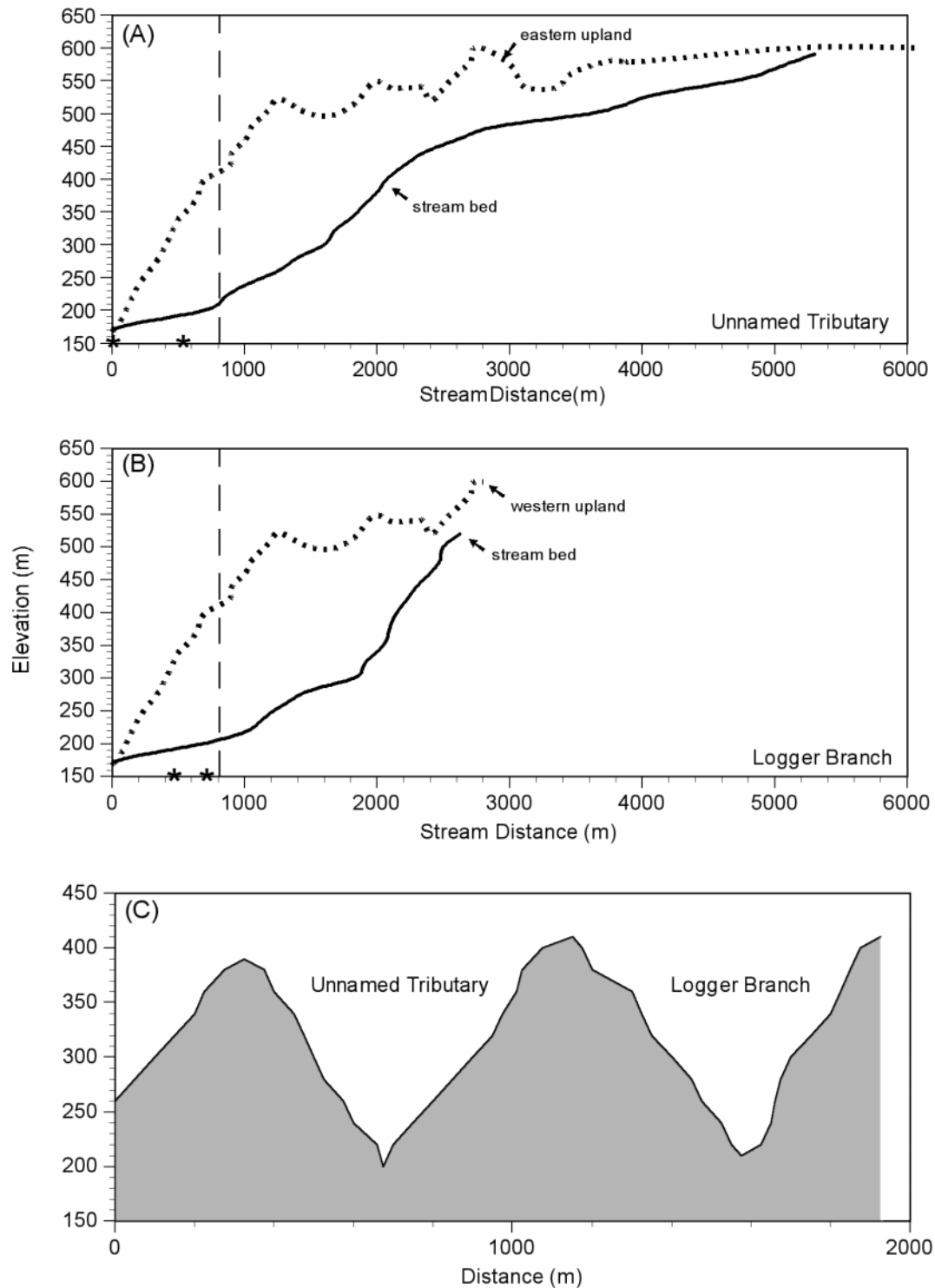
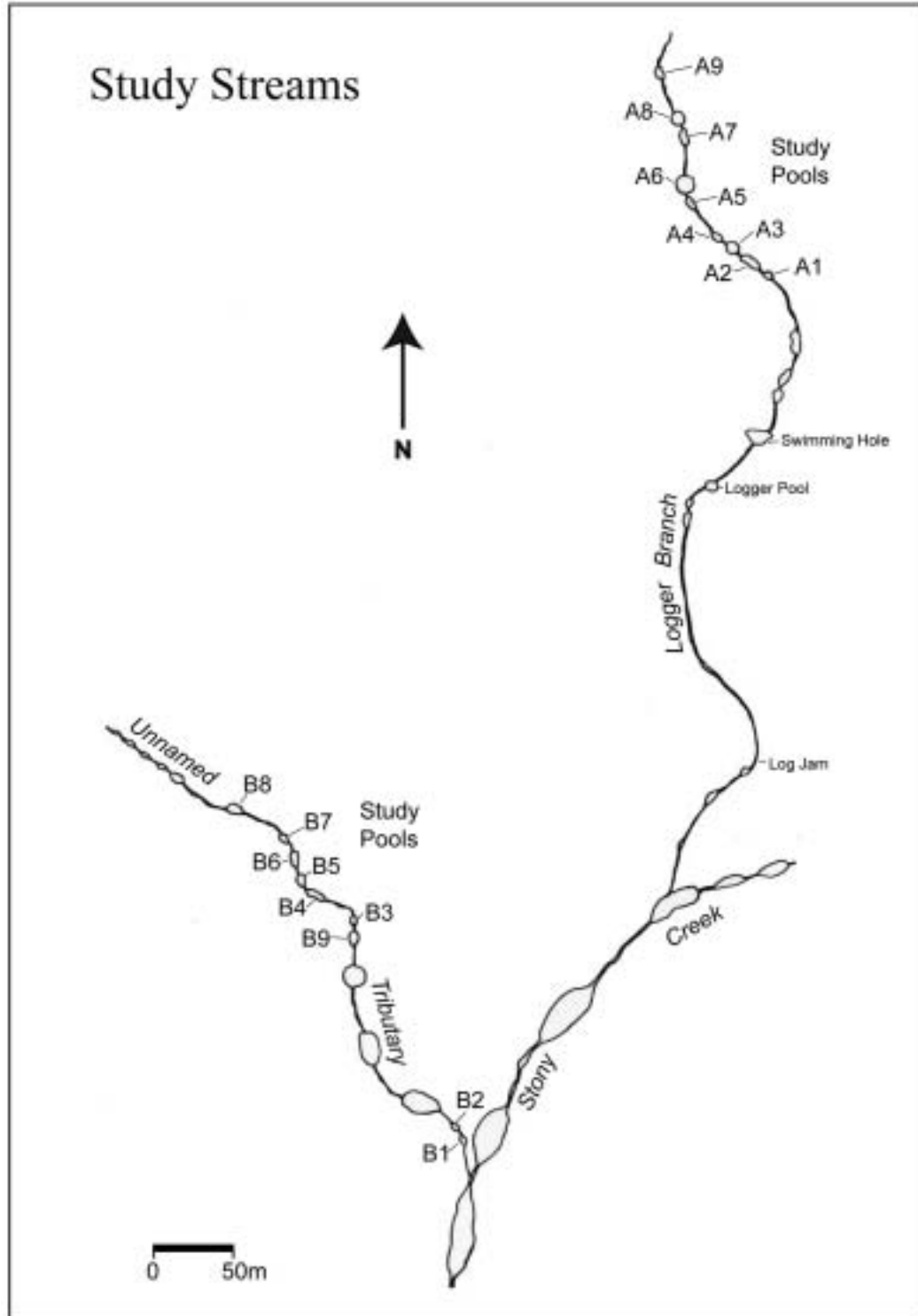
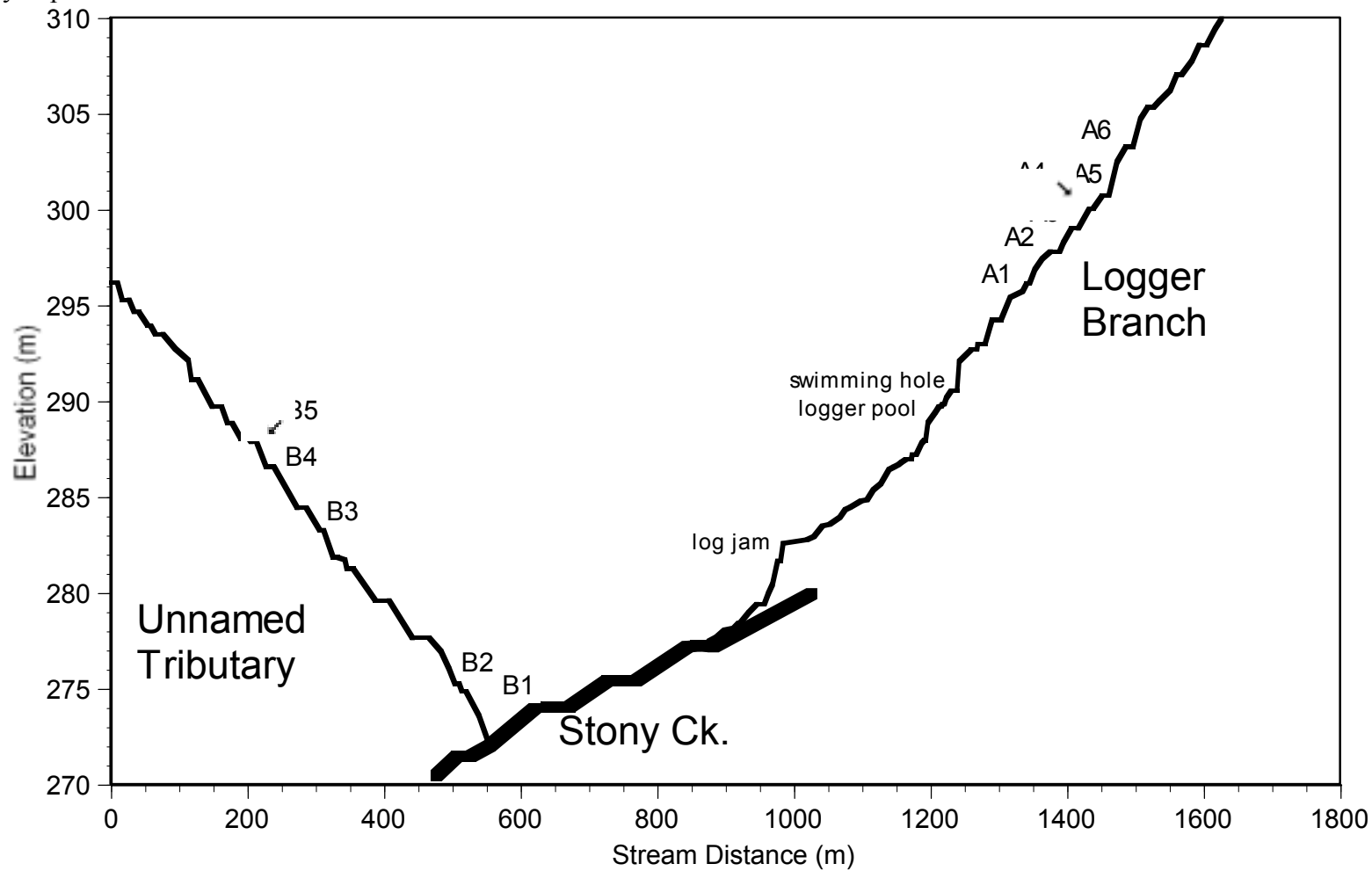


Figure 2.5. Surveyed map (a) and profile (b) of the study reaches of Unnamed Tributary and Logger Branch, plus a section of Stony Creek between their confluences. The locations of key features are indicated, as are the positions of pools used in Chapter 3 (e.g. A1, B3 etc).

(a) Surveyed map.



(b) Surveyed profile.



2.2.1 Geology

The geology of the study streams is dominated by igneous formations. The uppermost reaches of the catchments of the two streams consist of Bellthorpe Andesite, which dates from the lower Permian. The majority of the catchments, including the reaches associated with this study, consist of Neurum Tonalite. This formation contains tonalite, granodiorite and porphyritic tonalite dating from the lower to middle Triassic (Murphy *et al.*, 1976). A coarse grained granodiorite-like rock forms the predominant bed material in the study streams.

2.2.2 Geomorphology and Stream Flow

The study streams consist of small pools alternating with shallow riffles. Typically, pools are associated with intrusions of bedrock into the stream channel (Figure 2.6). In places, the channels of the streams are modified by the presence of log jams formed against large fallen trees during previous flood events (Figure 2.6).

Most pools are 5 to 10 m long and 3 to 5 m wide with a maximum depth of 0.3 to 1.0 m. Some larger pools are also present (Figure 2.5).

The streams are characterised by an armoured bed of boulders, cobbles, pebbles, gravel and sand in varying proportions, and areas of exposed bedrock. Many pools contain accumulations of coarse particulate organic matter (CPOM), particularly leaf litter, throughout the year and some also contain large woody debris.

Flow patterns in the study streams are consistent with those of the region, with marked seasonality and considerable inter-annual variability. For much of the year, streams are reduced to a series of “discrete but connected pools” (Bunn and Hughes, 1997). There was continual discharge from both streams throughout the period of this study, although under typical baseflow conditions riffles amounted to little more than trickles and pools were effectively isolated. During baseflow conditions, the wetted area of the streams is only a small proportion of the active channel width (Bunn and Hughes, 1997). A drought in 1990 (before this study began), led to cessation of stream discharge and some pools totally dried up. The streams can therefore be considered intermittent with respect to flow.

Negus (1995) recorded a daily fluctuation in the water level of pools in Logger Branch of up to 50 mm. The highest levels occurred in mid-afternoon and the lowest just before sunrise. This form of tidal fluctuation has rarely been recorded in streams and may reflect daily fluctuation in the transpiration rate of riparian plants (Bren *et al.*, 1979).

Wet season storms result in short-lived spates in the study streams, which can cause major physical disturbances to the stream bed. Tractive forces estimated to be greater than 20 kg m⁻² have been recorded during a spate in Logger Branch (Mosisch and Bunn, 1997). Sustained elevated levels of discharge follow longer periods of rainfall. Pools become more connected during these periods.

2.2.3 Vegetation

Soils of basaltic and other basic rock derivation support subtropical rainforest along the valleys of the streams in the Conondale Range. This type of rainforest has been categorised as “complex notophyll vine forest” and is dominated by species of the families Cunoniaceae, Escalloniaceae, Meliaceae, Monimiaceae, Myrtaceae, Proteaceae and Sterculiaceae (Young and McDonald, 1987). A vegetation survey conducted along the two study streams by members of the Queensland Naturalists Club in November 1995, identified over 300 species of plant (A. Moran, D. Boucharde and P. Williams, *pers comm*, 1995). Families recorded were consistent with complex notophyll vine forest but also included elements typical of “simple notophyll vine forest”. These elements include members of the families Elaeocarpaceae and Lauraceae and the piccabeen palm, *Archontophoenix cunninghamiana* (Figure 2.6). Rainforest of this type is common along gullies in south east Queensland and includes many bird-dispersed species (Young and McDonald, 1987).

Figure 2.6. Photograph of Logger Branch just above pool A6 (see Figure 2.5) showing typical riparian vegetation with prominent piccabeen palms (*Archontophoenix cunninghamiana*). Note also the bedrock intrusion in the foreground and the pool formed immediately upstream of it plus the large tree fallen across the stream. Photograph by Jon Marshall.



The tops of ridges are vegetated with dry sclerophyll forest dominated by *Eucalyptus* species, with an understorey of shrubs and grasses. This vegetation type is susceptible to fire and is intentionally burnt-off at regular intervals as part of forestry management practices (M. Venz, Beerburrum Forestry Office, *pers comm.*, 1995).

Very little incident sunlight reaches the streams because of shading by the dense canopy cover of the fringing rainforest and the deeply dissected nature of the stream valleys. Average riparian canopy cover in Conondale Range streams is approximately 70 % (Bunn *et al.*, 1999). Consequently aquatic macrophytes are absent from the study streams. Small clumps of the filamentous algal genus *Batrachospermum* occur infrequently, as do small colonies of aquatic or semi-aquatic epilithic liverworts and small epilithic colonies of the cyanobacterium genus *Coccochloris* (Mosisch, 1995). Most plant life within the streams consists of unicellular epilithic diatoms in mixed species assemblages. In Logger Branch and Booloumba Creek (another Conondale Range stream in the Mary River catchment), assemblages were dominated by the genera *Cocconeis*, *Navicula*, *Rhicosphenia* and *Tabellaria*, in decreasing order of cell density (Mosisch, 1995).

Input of allochthonous carbon into the streams in the form of litter fall (leaf, fruit, flowers, bark and other components of terrestrial plants) occurs throughout the year. Peak litter fall in Conondale Range rainforests occurs in spring and summer with 10% to 15% of annual fall occurring in each month from September to December (Paul Ryan, Queensland Department of Natural Resources, Gympie, *unpublished data*). In each of the months from March to July only approximately 4% of annual fall occurs. Litter fall is dominated by foliage, but both foliage and reproductive structures show the same seasonality of fall. Branch fall occurs sporadically and without seasonality. Severe drought conditions result in increased litter fall as the rainforest canopy becomes sparser (Paul Ryan, Queensland Department of Natural Resources, Gympie, *unpublished data*).

2.2.4 Land Use and Anthropogenic Influences

Historically, the dominant land use in the Conondale Range has been timber production. The study streams are within State Forest number 832 in the Beerburrum Forestry District. Despite the undisturbed appearance of the vegetation surrounding the streams

(Figure 2.3), there has been documented selective logging within these catchments on three occasions. The eastern portions of both catchments were logged for hardwood species for the first time in 1955. In 1972 forest to the east of Logger Branch and in 1977 forest on the ridge separating the two catchments was again selectively logged. These operations did not infringe within 50 m of the banks of the streams (M. Venz, Beerburrum Forestry Office, *pers comm*, 1995). Remaining evidence of these activities are old logging tracks and stumps of felled trees in the dry forest along ridges. One such logging track runs parallel to the eastern bank of Logger Branch approximately 30 m above the stream. This facilitated access to the stream, and may have been the source of some fine clay run off into the stream (Mosisch, 1995). A better maintained dirt road, known as Branch Creek Road, follows Unnamed Tributary about 50 m above its eastern bank for some distance. It is also likely that some fine clay reached this stream from the road above. There was however, no evidence during the course of this study that excessive or detrimental siltation occurred as a result of road run off. In general the streams, and in particular Logger Branch, tended to have more silt evident in reaches upstream of the influence of the roads.

Under the 1999 South East Queensland Regional Forestry Agreement the study area will be protected from further logging activity and will be fully reserved as an “icon area” (Conondale Range Committee, 1999).

In addition to the logging outlined above, there is evidence of much earlier selective felling of large trees close to the streams themselves. Markings on remaining stumps suggest these trees were felled by hand. Logs must have been extracted, with considerable difficulty, down the stream channels.

Another major land use in the area is leasehold cattle grazing. The density of cattle on these leases is low, and throughout the study no evidence was found of cattle entering the streams or their steep banks. The very uppermost tributaries of both streams infringe to a minor extent into areas of more intensive freehold grazing. It is unlikely that the minor exposure of the catchments to this form of land use had any detrimental effects during the course of the study.

Stony Creek State Forest Park is a popular day-use recreational facility situated 300 m downstream of the confluence of Unnamed Tributary and Stony Creek. The majority of visits are during the summer months when swimming is popular. A small number of the visitors to this park explore the lower reaches of the study streams. The activities of park visitors may represent minor disturbances to the streams (*e.g.* harvesting *Euastacus* crayfish, littering), but most people encountered during the course of this study presented no threat to the streams or their biota.

Bee-keeping within State Forests is another minor land uses in the area but this did not appear to take place in the catchments of the study streams.

2.2.5 *Water Quality*

Spot readings of water chemistry have been taken from Logger Branch and Stony Creek both upstream and downstream of the confluences of the study streams (Arthington and Marshall, *unpublished data*). Comparison of these results with water quality data relating to other sites within the Brisbane River catchment (Table 2.2) (Queensland Department of Natural Resources, *unpublished data*) reveals that the Stanley River sub-catchment, including Stony Creek and the study streams, have lower levels of hardness and total dissolved ions than the rest of the catchment. The concentrations of most major ions are also lower than the remainder of the Brisbane River. This is likely to result from the geology of the Stanley River catchment and its relatively undisturbed condition with respect to much of the remainder of the Brisbane River. Nutrient levels were low in Logger Branch reflecting the undisturbed nature of the catchment.

Table 2.2. Water chemistry of Logger Branch and other sites on Stony Creek, Stanley River and elsewhere in the Brisbane River Catchment.

	Conductivity ($\mu\text{S}/\text{cm}$)	pH	Total Hardness ($\text{mg}/\text{L CaCO}_3$)	Alkalinity	Total Dissolved Ions (mg/L)	Total Dissolved Solids (mg/L)	Turbidity (NTU)	Total Suspended Solids (mg/L)
Stony Creek upstream ¹	143	7.2	44	44	-	104	1.22	2
Logger Branch ¹	187	7.5	52	48	130	112	1.848	2
Stony Creek downstream ¹	193	7.5	54	47	82	115	1.766	2
Stanley River ²			40		94			
Kilcoy Creek ²			91		204			
Reedy Creek ²			209		409			
Cooyar Creek ²			327		677			
Emu Creek ²			630		1182			
Brisbane River ²			256		562			

	Silica (mg/L)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Iron (mg/L)	Copper (mg/L)
Stony Creek upstream ¹	-	12	1	11	5	-	-
Logger Branch ¹	22	17	1	10	6	0.02	0.05
Stony Creek downstream ¹	17	17	1	11	7	0.02	0.05
Stanley River ²		13		8	5		
Kilcoy Creek ²		28		19	10		
Reedy Creek ²		42		51	21		
Cooyar Creek ²		94		61	42		
Emu Creek ²		159		84	98		
Brisbane River ²		79		47	34		

	Bicarbonate (mg/L)	Carbonate (mg/L)	Chloride (mg/L)	Fluoride (mg/L)	Nitrate (mg/L)	Sulphate (mg/L)	Total P (mg/L)
Stony Creek upstream ¹	44	-	20	-	0.3	-	0.04
Logger Branch ¹	53	0.1	24	0.1	0.6	5	0.03
Stony Creek downstream ¹	52	0.1	26	0.1	2.1	6	0.02
Stanley River ²	46		19	0.1		2	
Kilcoy Creek ²	104		51	0.1		1	
Reedy Creek ²	195		84	0.3		12	
Cooyar Creek ²	188		280	0.3		7	
Emu Creek ²	270		536	0.2			
Brisbane River ²							

¹ Arthington and Marshall, *unpublished data*; ² Queensland Department of Natural Resources, *unpublished data*.

CHAPTER 3: THE INFLUENCE OF LANDSCAPE FILTERS ON SPATIAL AND TEMPORAL PATTERNS IN POOL FAUNA

3.1 Introduction

3.1.1 *Abiotic vs biotic influences on biota*

The notion that attributes of the physical environment govern the distribution and abundance of species is a central tenet in ecology. Spatial and temporal patterns in faunal assemblages can be driven by environmental fluctuation at a range of scales. The substantial body of evidence that abiotic environmental conditions influence the distribution and abundance of species and the composition of biotic assemblages in stream ecosystems was summarised in Section 1.1. Key abiotic drivers of stream assemblages included disturbance from high discharge events, substrate composition, flow velocity and water chemistry (*see* Section 1.1).

Despite these well-established relationships, the actual species present in an assemblage, results from the interactive effects of both abiotic and biotic factors acting at multiple spatial and temporal scales (Orians, 1980). The complexities of multiple drivers acting at multiple scales were explained conceptually by Poff (1997) as an hierarchical series of landscape filters governing the distribution and abundance of stream biota. Abiotic and biotic environmental conditions were considered as filters through which species in a global pool must "pass" to be potentially present at a given locality. Successful passage of a species through a filter at a locality depended upon the environmental attribute represented by the filter falling within the range of conditions in which the species can maintain a viable population. This reflects the preference and tolerance traits of the species. A species present at a locality reflects its ability to pass through all selective environmental filters operating at all scales at the locality. A four level hierarchy of spatial scale was proposed: a) basin/watershed, b) stream/stream reach, c) channel unit, and d) habitat. The relative influence of factors acting at local and regional scales on species distribution, abundance and community composition is largely unknown (Poff, 1997).

The pool of species available to colonise a habitat type within a stream is thus determined by the prevalent abiotic attributes of the habitat, channel unit, stream reach, catchment and bioregion. Although stream biota generally respond predictably to variations in physical habitat, this can be over-ridden by biological processes that

generate departures from predicted patterns or even a lack of predictive success (Bunn and Davies, 2000).

The role of biotic interactions in structuring stream assemblages was discussed in Section 1.2. Predation can dramatically affect the biotic composition of streams by directly reducing the abundance of prey species, and via “trophic cascade” effects, modify entire aquatic food webs (*see* Section 1.2.3). Despite these potentially strong interactions between predators and prey, some studies have found predation to have no effects at all (*see* Section 5.1), so the influence of predation on the composition of stream biota is variable.

There is little evidence to suggest that interspecific competition typically results in major changes to the structure of stream assemblages. Empirically demonstrated strong competitive interactions in streams at a large scale are restricted to periphyton grazing guilds during periods of environmental stability (*see* Section 1.2.2).

Biotic effects have been considered more likely to drive assemblage composition when conditions are relatively stable or benign and abiotic factors when conditions are fluctuating or harsh (*see* Section 1.4).

3.1.2 Aims

In this chapter, spatial and temporal patterns in pool fauna are described from several key habitat types within pools in the study streams. The aims of the chapter are to determine how much of the observed spatial and temporal faunal variation can be accounted for by variability in environmental attributes. Assessment will be made of the relative importance of local and catchment scale attributes to investigate how well faunal patterns comply to Poff’s (1997) hierarchical landscape filters.

3.2 Methods

3.2.1 General

Six pools in Logger Branch and six in Unnamed Tributary were each sampled eleven times between September 1992 and December 1993. For logistical reasons, pool

samples were collected in the two streams on consecutive days. The order in which the two streams were visited was determined at random, by the toss of a coin, on each occasion. Within each stream the order in which pools were sampled was determined by their position and was thus the same on all occasions. The pool furthest downstream was sampled first, then the next upstream and so on until all six pools were sampled. This mode of sampling was adopted so that disturbance to pools during sampling did not affect other pools before they themselves were sampled. Locations of pools within the study streams are detailed in Chapter 2 (Figures 2.5 and 2.6).

Sampling methods employed were as non-destructive to the pool communities as possible, so that sampling-induced community alterations were minimised. This was a particularly pertinent consideration in this study as pools were generally small and sampling relatively frequent. Minimally destructive sampling was achieved by the development and application of a photographic sampling procedure whereby collected fauna could be released back to the pool from which it was collected. Fauna collected in samples were identified in the field and identifications verified from the resultant photographic transparencies (Marshall, 1994, Hancock, 1995, *see* Appendix I). Taxonomic resolution from photographed samples was almost as high as that obtained from conventional preserved samples. Trials of the method indicated that specimens in photographic samples could be identified to species level for 64 of 78 taxa (82 %) in the study area and that those that could not be identified to species could readily be identified to genus or family. The use of a comprehensive reference collection of preserved specimens from the study streams enhanced the identification accuracy of photographed specimens (Marshall, 1994).

In cases where non-destructive sampling was impossible (gravel and leaf litter samples), sampling frequency was reduced to only four occasions (Table 3.1).

Table 3.1. The dates and types of samples collected on each sampling occasion.

Sample	Date	Non-destructive Samples	Destructive samples
9209	8-9 September 1992	✓	
9210	13-14 October 1992	✓	
9212	4-5 December 1992	✓	✓
9301	27-28 January 1993	✓	
9302	20-21 February 1993	✓	
9303	30-31 March 1993	✓	✓
9305	27-28 May 1993	✓	
9306	24-25 June 1993	✓	✓
9308	5-6 August 1993	✓	
9309	10-11 September 1993	✓	✓
9312	12-13 December 1993	✓	

3.2.2 Habitat Characteristics of Pools

Selected environmental variables were measured on each sampling occasion. Some were recorded from habitats within pools, some from each pool, some for each stream and some for the study area in general (Table 3.2). These variables defined the habitat characteristics prevalent at the particular moments when samples were collected. A summary of all variables is presented in Table 3.3 with details described below. Spatial and temporal variation in pool fauna was later assessed in relation to fluctuations in habitat characteristics at these landscape scales.

Table 3.2. The landscape spatial scales (*sensu* Poff, 1997) at which environmental variables used in the study are relevant.

Landscape Scale			
Habitat	Pool	Valley/Reach	Catchment
cobble attributes	pool size	stream discharge	photoperiod
gravel mineral fractions	pool flow velocity	average pool variables per stream	rainfall
gravel organic fractions	pool water chemistry		
litter organic fractions	pool substrate composition		
	pool CPOM		
	patch-weighted habitat scale variables		

Table 3.3. Summary of environmental variables used in the study with abbreviated names used in some tables, units of measurement, sampling frequency (a = every sampling occasion, b = only those sampling occasions where destructive samples were collected, c = September 1992), and relevant landscape scale (H = habitat, P = pool, V/R = valley/reach, C = catchment). Scaled-up variables are not presented: Patch-weighted habitat scale variables relate to the scale of pools and have the same units and sampling frequency as the original variables. Pool scale variables averaged per stream relate to the scale of valley/reach and have the same units and sampling frequency as the original variables.

Variable Name	Abbrev.	Units	Sampling Freq.	Scale
Cobble Epilithon Organic Dry Mass	epilithon	mg	a	H
Cobble Surface Area	cobble area		a	H
Dry Mass of Gravel Sample Sediment Fraction >4 mm	4 mm	g	b	H
Dry Mass of Gravel Sample Sediment Fraction 1-4 mm	1 mm	g	b	H
Dry Mass of Gravel Sample Sediment Fr. 0.5-1 mm	0.5 mm	g	b	H
Dry Mass of Gravel Sample Sediment Fr. 0.25-0.5 mm	0.25 mm	g	b	H
Total Dry Mass of Gravel Sample Sediment	total gravel	g	b	H
Proportion of Gravel Sample Sediment Fraction >4 mm	%4 mm	%	b	H
Proportion of Gravel Sample Sediment Fraction 1-4 mm	%1 mm	%	b	H
Proportion of Gravel Sample Sediment Fr. 0.5-1 mm	%0.5 mm	%	b	H
Proportion of Gravel Sample Sediment Fr. 0.25-0.5 mm	%0.25 mm	%	b	H
Gravel Sample Sediment Heterogeneity	gravel het	-	b	H
Dry Mass of Gravel Sample FPOM	gravel FPOM	mg	b	H
Dry Mass of Gravel Sample CPOM (Leaves)	gravel leaves	mg	b	H
Dry Mass of Gravel Sample CPOM (Sticks and Fruit)	gravel sticks	mg	b	H
Dry Mass of Gravel Sample CPOM (Total)	gravel CPOM	mg	b	H
Total Dry Mass of Gravel Sample POM	gravel organic total	mg	b	H
Dry Mass of Litter Sample FPOM	litter FPOM	mg	b	H
Dry Mass of Litter Sample CPOM (Leaves)	litter leaves	mg	b	H
Dry Mass of Litter Sample CPOM (Sticks and Fruit)	litter sticks	mg	b	H
Dry Mass of Litter Sample CPOM (Total)	litter CPOM	mg	b	H
Total Dry Mass of Litter Sample POM	litter organic total	mg	b	H
Pool Length	length	m	a	P
Pool Width	width	m	a	P
Pool Cross-sectional Area	x area	m ²	a	P
Pool Wetted Area	area	m ²	a	P
Pool Volume	vol	m ³	a	P
Pool Minimum Flow Velocity	min flow	m sec ⁻¹	a	P
Pool Water Temperature	temp	°C	a	P
Pool pH	pH	-	a	P
Pool Turbidity	turbidity	NTU	a	P
Proportion of Boulder Habitat in Pools	%B	%	c	P
Proportion of Bedrock Habitat in Pools	%BR	%	c	P
Proportion of Cobble Habitat in Pools	%C	%	c	P
Proportion of Gravel Habitat in Pools	%G	%	c	P
Pool Substrate Heterogeneity	pool het	-	c	P
Area of Boulder Habitat in Pools	B	m ²	a	P
Area of Bedrock Habitat in Pools	BR	m ²	a	P
Area of Cobble Habitat in Pools	C	m ²	a	P
Area of Gravel Habitat in Pools	G	m ²	a	P
Pool CPOM Wet Mass	pool CPOM	g	a	P
Stream Discharge	discharge	l sec ⁻¹	a	V/R
Photoperiod	phot	hours	a	C
Rainfall in Previous Month	rain	mm	a	C

a) Variables relevant at the habitat scale

Cobble Epilithon - A square of 900 mm² (30 mm x 30 mm) was marked with pencil using a plastic template on the upper surface of the cobbles sampled for fauna (*see* Section 3.2.3). A fixed blade scalpel was used to carefully scrape the marked area for 60 seconds. Matter scraped loose was washed into labelled vials with distilled water via a funnel. Samples were kept cool until they were processed in the laboratory. Samples contained small fragments of rock, which had been scraped from the surfaces of the cobbles as the samples were collected. It was not possible to distinguish the inorganic mass of epilithon from the mass of these fragments. Thus, only the organic mass was calculated. Samples were rinsed with distilled water into porcelain crucibles, which had been pre-ashed at 460 °C for four hours and individually pre-weighed using a Mettler AE240 analytical balance (accurate to 0.01 mg). The balance was calibrated before each session of use. Samples were oven dried for 24 hours at 60 °C, weighed, ashed at 460 °C for four hours and then re-weighed. All weights were recorded after crucibles had cooled to room temperature within a vacuum desiccation chamber filled with silica gel to prevent atmospheric re-hydration. Sample organic weight was calculated as the difference between its dry weight and ashed weight.

Cobble Surface Area - Cobble surface area was determined from stones collected for faunal analysis (*see* Section 3.2.3), by tracing each onto plastic paper in its two largest dimensions. The area of each tracing was later calculated using BIOQUANT digitising software. This form of measurement has been demonstrated to be highly correlated with total cobble surface area and can be used as an index of surface area (McCreadie and Colbo, 1991).

Mass of Gravel Size Fractions - The mineral fraction of gravel samples (*see* Section 3.2.3), was oven dried at 60 °C and separated into particle size fractions using soil sieves and mechanical agitation for 5 minutes. Fractions used were >4 mm, 1 - 4 mm, 0.5 - 1 mm and 0.25 - 0.5 mm. Each fraction was weighed with an accuracy of 0.1 g.

Total Gravel Mass - Calculated as the sum of the masses of all gravel size fractions in a sample.

Gravel Heterogeneity - Gravel size heterogeneity was calculated based on the proportional mass of each size fraction in a sample (Equation 3.1, after Zar, 1984).

Equation 3.1
$$\text{Heterogeneity} = 1 - (H' / \log_{10} k)$$

H' - Shannon Wiener Diversity index (Shannon, 1948)

k - number of substrate categories

Gravel FPOM Mass - The organic matter from each gravel sample (*see below*) that washed through a 1 mm mesh sieve was oven dried for 24 hours at 60 °C and weighed using a Mettler AE240 analytical balance (accurate to 0.01 mg).

Gravel CPOM Leaf Mass and Gravel CPOM Stick and Fruit Mass - The organic matter from each gravel sample (*see Section 3.2.3*) which did not wash through a 1 mm mesh sieve was sorted by hand into two fractions; leaves and non-leaves. The non-leaf fractions were composed mostly of sticks and bark with some fruits. Each fraction was oven dried for 24 hours at 60 °C and weighed using a Mettler AE240 analytical balance (accurate to 0.01 mg).

Gravel Total Organic Mass - The total organic matter mass from gravel samples was calculated as the sum of the masses of the three component fractions.

Litter FPOM Mass - The organic matter from each leaf litter sample (*see Section 3.2.3*) that washed through a 1 mm mesh sieve was oven dried for 24 hours at 60 °C and weighed using a Mettler AE240 analytical balance (accurate to 0.01 mg).

Litter CPOM Leaf Mass and Litter CPOM Stick and Fruit Mass - The organic matter from each leaf litter sample (*see Section 3.2.3*) which did not wash through a 1 mm mesh sieve was sorted by hand into two fractions; leaves and non-leaves. The non-leaf fractions were composed mostly of sticks and bark with some fruits. Each fraction was oven dried for 24 hours at 60 °C and weighed using a Mettler AE240 analytical balance (accurate to 0.01 mg).

Litter Total Organic Mass - The total organic matter mass from leaf litter samples was calculated as the sum of the masses of the three component fractions.

b) Variables relevant at the pool scale

Pool Size – pool length and width were measured on each occasion and used to calculate wetted area. Pool depth at the deepest point was measured and used to calculate cross-sectional area and, with wetted area, pool volume. Cross-sectional area was divided by stream discharge (*see part (c) below*) to calculate pool minimum flow velocity.

Physico-chemical Water Properties - Water temperature, pH and turbidity were measured on each sampling occasion in each pool at a depth of 0.2 m near the middle of the pool. Turbidity and pH were measured using calibrated meters (Hach Model 16800 PortaLab Turbidimeter, Hanna Instruments HI8314 membrane pH meter), and temperature using a 0 – 40°C alcohol thermometer.

Pool Substrate Composition - Substrate classes were recognisable habitat types and were named after their predominant particle size class (*sensu* Cummins, 1962). Boulder and bedrock classes were highly uniform with other substrate sizes present only as traces of silt/clay. Cobble class was dominated by cobbles but also included finer substrates that formed a matrix between the cobbles and in which they were variably embedded. Areas of gravel/sand accumulation generally included some pebbles and traces of silt/clay. Pebbles and silt/clay were not present in pools to the extent that they formed specific habitat types.

The proportions of substrate classes were determined from one or more photographs (ISO 400 35mm transparencies taken with a 50 mm lens) of pools taken in September 1992. These were superimposed with a 1 mm grid. The dominant substrate class in each grid was recorded and the proportions of all grids composed of each substrate class used as an estimate of pool substrate composition. The area of substrate classes in each pool on each occasion was calculated by multiplying proportions by the pool wetted area.

Pool substrate heterogeneity was calculated based on the proportions of pool substrate classes (Equation 3.1, after Zar, 1984).

Pool CPOM - the wet mass of Coarse Particulate Organic Matter (CPOM) collected in the sweep sample (*see* Section 3.2.3) was measured. Samples of CPOM were washed through a 1mm sieve to remove fine organic matter, towel dried, and weighed in a plastic bag using a calibrated Salter spring balance. After weighing organic matter was returned to the pool. As flow velocities were very low, material returned to pools was not lost downstream.

Patch-Weighted Habitat Scale Variables - The values of all environmental variables relating to habitat samples (*see* part (a) above), were patch weighted to apply to entire pools using the methods applied to composite fauna samples (*see* Section 3.2.3). This was achieved by multiplying the sample value by an estimation of the total number of potential samples in the pool (*see* Table 3.4).

c) Variables relevant at the valley/reach scale

Stream Discharge - calculated at one location on each stream on each sampling occasion. The locations used were narrow stream portions flowing over bedrock substrates. Depth transects were measured and flow velocity estimated as the water depth was inevitably too shallow to make use of a flow meter. The time taken for a coloured liquid (milk), released into the centre of the stream, to travel a predetermined distance (1.0m or 0.5m) was recorded five times. Mean times were calculated from these records and a cross-sectional area of the location estimated from the depth transects. Discharge was calculated as the product of flow velocity and cross-sectional area and expressed in litres per second.

Pool Scale Variables Averaged per Stream - The values of all environmental variables relating to pools (*see* part (b) above), were averaged for all pools in each stream on each sampling occasion.

d) Variables relevant at the catchment scale

Photoperiod - the latitude and longitude of the study area was used to calculate sunrise and sunset times for the study area for each sampling occasion using data provided by the Australian Bureau of Meteorology (*pers comm*). Photoperiod was calculated as the time between sunrise and sunset.

Rainfall in Previous Month - daily rainfall records from the most relevant proximal rainfall station (Bellthorpe, *see* Chapter 2) were summed for the thirty day period preceding each sampling occasion.

3.2.3 Faunal samples

Sampling was randomly stratified by depth and/or position within pools, to enhance the validity of comparisons between spatial and temporal replicates. Different methods were required for each habitat type.

a) Sweep Samples

Sweep samples were collected from each pool on all occasions. A hand held “D” shaped net (area 525 cm², nylon gauze mesh, 250 µm) was swept through pools to collect pool fauna. Samples began at the downstream end of pools and proceeded in an upstream direction for 15 seconds while sweeping the net from side to side. Sweeps were conducted close to the pool bed, but did not make direct contact with it, in water of approximately 0.3 m depth. After 15 seconds the direction of sampling was reversed and the area that had previously been sampled was re-swept for a further 15 seconds. This aimed to capture animals and CPOM displaced from the pool bed into the water column by the first pass of the net. The area of pool bed covered by this procedure was approximately 5 m². The contents of the net were emptied into a white plastic tray with approximately 10 mm of clean water from the stream. Leaf litter and other CPOM was carefully checked for animals and removed for weighing (*see* Section 3.2.2). Animals were live picked from the tray for a maximum period of one hour or until no more were found after 10 minutes of searching and kept alive. Taxa targeted by this method were restricted to a subset of all the taxa potentially present. Those collected were fish, Anuran tadpoles, Decapod crustaceans, Odonata, Hemiptera, and Coleoptera. These groups include nektonic and large mobile benthic taxa that were not adequately sampled

by the other methods used. Other taxa collected in sweep samples but not recorded, such as Ephemeroptera, Diptera and Trichoptera were considered to be sampled more effectively (and quantitatively) by the other methods employed (*see below*). Furthermore the taxa recorded were conspicuous and often large and thus were relatively easy to live pick from the sample. Taxa not included were mostly small and cryptic and difficult to live pick.

Animals picked from the sweep samples were identified, counted and photographed alive, then later returned to the pool from which they were collected. Enumerations and identifications were confirmed from the resulting photographs.

b) Cobbles

On each sampling occasion, three cobbles from each pool were randomly selected from a standardised depth and position within the pool (*viz* 0.25 m to 0.35 m deep and at least 2 m downstream of the pool inflow and 1 m upstream of the pool outflow). Cobbles were carefully lifted into a 250 µm mesh net placed immediately downstream of them to capture any invertebrates dislodged by the act of lifting. They were removed from the water in the net and invertebrates were picked from both the stones and the net until no more were found, and kept alive. Fauna from the three cobbles were pooled. Cobbles were processed for epilithon and surface area calculation (section 3.2.2) then returned to the pools as close as possible to the position and orientation from which they were collected. Fauna were identified, counted and photographed and later returned to the pools immediately over the cobbles from which they were collected. Enumerations and identifications were confirmed from the resulting photographs. Faunal abundances were expressed as the mean number per cobble and rounded up to the nearest whole number.

c) Boulder and Bedrock Samples

A boulder that protruded from the water was randomly selected in each pool on each sampling occasion. A 0.3 m length of the water/air interface on the downstream side of the rock was randomly chosen and 0.1 m immediately above and below the water was searched for invertebrates. Sampling was conducted above the water line in this manner, as several species of Trichoptera (*Tasiagma ciliata*, *Tasimia palpata?*, *Triplexa*

villa and *Antipodoecida* sp.AV2) were known to frequently venture out of the water on hard substrates (Negus, 1995).

Any animals that were found were removed with forceps, identified, counted and photographed, before being released back onto the rock from which they were collected. Enumerations and identifications were confirmed from the resulting photographs. Fast moving mayfly nymphs (Leptophlebiidae and Baetidae), which could not easily be caught with forceps, were not included in these samples. This procedure was repeated in each pool for an area of bedrock protruding from the water.

d) Pneuston Samples

These samples consisted of a simple count of the number of adult Gyrinidae present on the surface of each pool on each sampling occasion. Counts were conducted over a period of one minute. Other pneustonic taxa such as Veliidae, Mesoveliidae and Gerridae were too small to be counted in this way and were not sampled by this or any of the other methods.

e) Gravel Samples

The bed material of study pools was comprised largely of cobbles, boulders and bedrock, surrounded by, and to varying extents, embedded in, a matrix of finer gravel and sand. These patches of gravel and sand were generally too small to sample independently of the larger substrate types. There were however larger patches of gravel and sand that were located immediately downstream of large boulders present in all pools. The location of these patches corresponded to pockets of low pressure and thus low flow velocity that form behind boulders during periods of high discharge (Ward, 1992).

Samples were collected using a small, modified Hess sampler (Hess, 1941). This consisted of a 110 mm internal diameter PVC “T” piece with a rubber glove clamped onto the top and a 250 μ m nylon gauze mesh collecting net ending in a plastic screw topped jar clamped to the side. The bottom of the “T” was open with an area of 95 cm² and was pressed into the gravel to a depth of approximately 50 mm. Gravel and water

were scooped into the collecting net by a hand inserted into the attached glove for a period of one minute. This methodology was designed to collect all of the gravel and associated animals within the 50 mm deep volume enclosed by the sampler. A single sample was collected from each pool on each occasion, labelled and preserved in plastic bags using 10% buffered Formalin.

Although these samples were destructive, and thus had the potential to modify pool fauna in subsequent samples, it is estimated that the area of gravel sampled on each occasion represented less than 1% of the mean area of gravel habitat in pools. Sampling is therefore unlikely to have significantly modified subsequent pool fauna.

In the laboratory, samples were thoroughly rinsed in a 250 μm mesh sieve under running water in a fume hood to remove the Formalin. They were placed into a saturated solution of calcium chloride and gently agitated. In this solution particulate organic matter present, including collected fauna, floats to the surface and can be decanted off leaving only the mineral component behind (*see* Hauer and Resch, 1996). This procedure was repeated twice to ensure all particulate organic matter was removed. Both the organic and mineral fractions were thoroughly rinsed in a 250 μm mesh sieve under running water to remove residual calcium chloride. The mineral fraction was retained for particle size analysis (section 3.2.2). The organic fraction was examined under a dissection microscope and all fauna removed and stored in 70% ethanol with 5% glycerol. The mineral fraction was also scanned under a microscope to search for stone-cased Trichopterans and other taxa that may not have been buoyant in the calcium chloride solution. In practice very few such animals were found. Remaining organic matter was retained for mass determination (section 3.2.2). Fauna samples were later identified and enumerated under a dissection microscope.

f) Leaf Litter Samples

Patches of accumulated leaf litter were sampled using the modified Hess sampler described above. The sampler was placed over the leaf litter patch and a single handful of litter grabbed through the glove of the sampler and released into the sampling bag. Samples were preserved in plastic bags using 10% buffered Formalin.

It is estimated that the area of litter sampled on each occasion represented less than 5 % of the mean area of litter habitat in pools. Sampling is therefore unlikely to have significantly modified subsequent pool fauna.

In the laboratory samples were thoroughly rinsed in a 250 µm mesh sieve under running water in a fume hood to remove the Formalin. They were then examined under a dissection microscope and all fauna removed and stored in 70% ethanol with 5% glycerol. Remaining organic matter was retained for mass determination (section 3.2.2). Fauna samples were later identified and enumerated under a dissection microscope.

g) Composite Pool Samples

The abundances of all taxa from each type of fauna sample were patch weighted by a factor reflecting the proportion of the total available habitat type in the pool represented by the sample. The abundance of each taxon in the entire pool was then estimated as the sum of patch weighted abundances across all sample types. The precise means of patch weighting for each sample type is outlined in Table 3.4. In each case the algorithm used represents the product of the sampled abundance and the number of samples that could potentially be collected in the pool.

A number of points pertaining to Table 3.4 require clarification. The calculation for cobble fauna includes multiplication by a factor of 0.3 to reflect the proportions of the pools that is actual cobble rather than the gravel and sand matrix surrounding cobbles. This factor was not used to adjust up the area of gravel in pools as the gravel matrix between cobbles may represent a different habitat type with different fauna from the gravel habitat actually sampled. The fauna of this gravel matrix between cobbles thus remains unknown. The number of potential leaf litter samples in a pool was expressed in terms of the dry mass of leaf litter in a sample. This is because the area of leaf litter accumulations in pools was not recorded. The dry mass was multiplied by 5 to estimate the wet weight, assuming 80% water content (*see Villee et al.*, 1968).

Table 3.4. Algorithms used to calculate the patch-weighted abundances of taxa collected by each sampling method. A = abundance in original sample.

Sample Type	Algorithm
Sweep Sample	$A \times (\text{pool area} / 5 \text{ m}^2)$
Cobble Sample	$A \times [\{\text{pool area} \times (0.3 \times \% \text{ cobble})\} / \text{cobble area}]$
Boulder Samples	$A \times (\text{total length emergent boulder} / \text{length of boulder sample})$
Bedrock Samples	$A \times (\text{total length emergent bedrock} / \text{length of bedrock sample})$
Pneuston Sample	A
Gravel Samples	$A \times [\{\text{pool area} \times \% \text{ gravel}\} / \text{gravel sample area}]$
Leaf Litter Samples	$A \times [\{\text{CPOM sweep sample mass} \times (\text{pool area} / 5 \text{ m}^2)\} / (5 \times \text{CPOM litter sample dry mass})]$

h) Taxonomy

Most taxa were identified to species or “morphospecies” level. A reference collection of specimens collected from other sites within the study streams and where necessary, from the sampling pools themselves, was established to aid identification. Appropriate taxonomists confirmed identifications where possible (*see Acknowledgements*). Chironomidae were identified to morphospecies within subfamilies and other Diptera and Hemiptera to morphospecies within families. Some Coleoptera were identified to morphospecies within genera and Oligochaeta, Nematoda, Dugesiidae, Copepoda, Ostracoda, Cladocera and Nematomorpha were identified no further.

i) Adequacy of Taxon Richness Estimates

The pools used in this study were generally very small (see Chapter 2) and it was not possible to collect multiple replicates of most sample types without causing excessive physical damage to the pool assemblages, thus compromising temporal aspects of the study. In the case of the sweep samples, almost the entire area of smaller pools was represented, so there was no capacity for replication.

One of the problems with relying upon small numbers of replicates or single samples to represent the fauna of a pool at a time was that the samples might have underestimated the true taxon richness of the pool habitats (Rahel *et al.*, 1984; Gotelli and Colwell, 2001). This problem was largely overcome by excluding rare taxa from analyses (see Section 3.2.4a; Clarke and Warwick, 1994), which improves the fidelity of taxon richness estimates when comparing samples from pools. Furthermore, quantitative data collected in a related study of these streams confirms that estimates from a small number of samples are adequate when rare taxa are excluded (Figure 3.1).

Ten randomly chosen cobbles were sampled from riffle/run habitats within Stony Creek each month between September 1992 and December 1993 (Bunn, *unpublished data*). The location and timing of sampling thus corresponded closely with the collection of cobble fauna data presented in this study. The focus of this study was on algal grazers, which represent most of the taxa on cobble habitats. Although there may be some expected habitat differences between riffle and pool samples, it is important to note that flows were very low throughout much of this period and the composition of the biota was very similar. The EstimateS software package (Colwell, 2000) was used to generate randomised species accumulation curves (with 50 randomisations) using the 10 cobble samples for each month. These were calculated using all taxa and with rare taxa removed and in both instances averaged across the 16 months of samples.

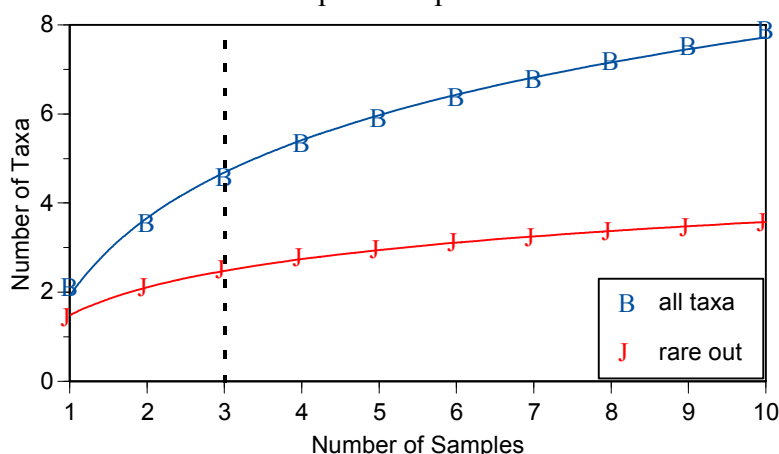
The resulting taxon accumulation curve indicates that most species on cobbles are presented within a few samples, once rare taxa have been removed from the dataset (Figure). It is apparent that with rare taxon removal, adequate estimates of richness for comparative purposes can be made with a small number of samples (for example the three cobbles sampled in this study appears adequate) or even with a single sample. Sampling 10 cobbles added only a little over half a taxon on average compared with sampling a single cobble and added even less compared to sampling three cobbles.

The sweep sample procedure employed in this study was similar in many ways to that used by the AusRivAS rapid bioassessment protocol (*see* Chessman, 1995; Simpson and Norris, 1999). Replication trials using this protocol have shown that a single sweep sample accurately represents the fauna of a site if rare taxa are excluded (Metzeling and

Miller, 2001; Nichols *et al.*, *in prep*). This suggests that once rare taxa were excluded, the sweep samples employed in this study adequately estimated the taxon richness of pools.

It can be concluded from this that the additional effort of increased sample replication would result in little improvement in taxon richness estimates when rare taxa are excluded. Additional sampling was therefore not necessary and would have been impractical given its destructive effects discussed above (see also Section 3.2.1). It can be concluded that the level of sampling effort employed adequately represented the biota in any pool at any time.

Figure 3.1. Randomised taxon accumulation curves from 10 cobble samples for datasets including all taxa and with rare taxa removed. The dotted vertical line is at the three cobble level which was used for pool samples.



3.2.4 Describing Variation in Pool Fauna and linking it to Environmental Gradients

Many analytical procedures were employed to investigate the degree to which observed spatial and temporal patterns in pool fauna could be explained by measured environmental variation.

a) Data Preparation

Data were analysed separately for each pool habitat type with the exceptions of the boulder, bedrock, leaf litter and pneuston samples. Sampling times and pools respectively were treated as replicates of spatial and temporal patterns in faunal assemblages. For each replicate (*i.e.* sampling time for all pools and pool for all

sampling times) rare taxa were excluded from the data. Rare taxa were considered to be inadequately sampled to be included in analyses of faunal assemblages. The presence or absence of rare taxa in individual samples is a matter of chance as a result of their low occurrence frequency. They thus do not contribute information to patterns of faunal occurrence evident from samples, but rather generate “noise” which has the effect of masking patterns (Clarke and Warwick, 1994). Rare taxa were defined as those contributing less than 1% of the total number of individuals in a data set and contributing less than 5% of the total number of individuals in any single sample in the data set. This definition of rare was used as it identified taxa that were rare both globally (*i.e.* in the data set) and in all samples comprising the data set. A definition of rare taxa based only on global rarity was not used because taxa that may be abundant in even a single sample, but be globally rare, could potentially be important contributors to faunal patterns (Clarke and Warwick, 1994).

Following the removal of rare taxa, taxon abundance data were $\log_{10}(x+1)$ transformed. This transformation had the effect of down-weighting the contribution of numerically dominant taxa within the data set. This form of down weighting is recommended when generating multivariate descriptions of species assemblage patterns. Without down weighting, association measures between samples tend to reflect only the differences in the abundance of common taxa. After down weighting, association measures reflect differences in the overall assemblage composition (Clarke and Warwick, 1994).

b) Analysis of patterns

Multivariate analyses were performed using PATN (Belbin, 1995), PRIMER (Carr, 1996) and STATISTICA (StatSoft Inc., 1995) software packages.

The transformed species data sets were used to calculate association measures between samples (ASON in PATN). The Bray Curtis distance coefficient (Bray and Curtis, 1957) was used as it has been considered the most appropriate for species/samples data sets. This is because shared absences of taxa do not render two samples similar and shared high abundances are given more significance than shared low abundances (Clarke and Warwick, 1994; Belbin, 1995).

For each spatial and temporal replicate, the mean Bray Curtis difference between samples and the standard error of the mean were recorded. Pearson's correlation coefficients were calculated between the mean values and environmental variables, both overall and within streams. This established whether or not the average magnitude of faunal difference between samples was explained by environmental differences.

Differences in the fauna of the two streams at each sampling time were assessed using pools within the streams as replicates. This was achieved using analysis of similarity (ANOSIM in PRIMER). ANOSIM is a simple non-parametric permutation procedure that tests for differences between predetermined groups of samples based on the Bray Curtis difference matrix. The null hypothesis in such tests is that there are no differences in faunal composition between the groups of samples (Clarke and Green, 1988, Clarke and Warwick, 1994). A maximum of 10 000 permutations was used for these tests. Pearson's correlation coefficients were calculated between the ANOSIM statistic (R) from each sampling time and measured differences in the values of environmental variables between the streams. This established whether or not the magnitude of the faunal difference between the streams was explained by environmental fluctuation.

Taxa contributing to faunal differences between the streams were identified at sampling times where the difference was significant ($p < 0.05$) using Similarity Percentages (SIMPER) in PRIMER. SIMPER calculates the contribution of each taxon to differences between two groups of samples for each individual Bray Curtis difference. This is then averaged across Bray Curtis differences to give the average contribution of each taxon to group differences. The average contribution is expressed as a percentage (Clarke and Warwick, 1994).

c) Ordination

Replicate association matrices were ordinated using Semi-Strong Hybrid Multi Dimensional Scaling (SSH MDS). For details of this algorithm *see* Belbin (1991 and 1995). This form of ordination constructs a “map” in a specified number of dimensions, which attempts to represent the dissimilarity matrix. The accuracy with which the association matrix is represented on an ordination plot is expressed as the stress of the

ordination. Fifty random starts were used for these ordinations with the stopping rules set for a maximum of 500 iterations per start and a minimum stress difference of 0.0005 between iterations (SSH in PATN). The ratio/ordinal cut-off was changed from the default value of 0.9 where perusal of a histogram of association measure distribution suggested it was necessary. The cut-off was set to a level corresponding to the point on the histogram where the distribution departed from normality. If Bray-Curtis differences are greater than the prescribed cut-off, the rank-order of the differences are used by the MDS. For those below the cut-off, the actual values of the differences are used. This dichotomy generates ordinations of superior accuracy (Belbin, 1995).

Where possible, two-dimensional ordinations were performed. If the stress of such an ordination was greater than 0.2, it was considered necessary to use three or more dimensions. Ordinations with stress values of greater than 0.2 are considered to be inaccurate representations of the underlying association matrix (Clarke and Warwick, 1994). In cases where three or more dimensions were required to achieve an acceptable level of stress, ordinations were Varimax rotated to simple structure to maximise the displayed variation in two of the three dimensions using PCR in PATN (Belbin, 1995).

All ordinations with the same number of dimensions were rotated to similar configuration using generalised Procrustean Rotation (PROC in PATN). The procedure is used to compare two ordinations of the same objects (*e.g.* pools or sampling times). In all cases one arbitrarily chosen ordination was used as the target ordination to which others were rotated without standardisation of the target ordination (as per Belbin, 1995).

In some situations, particular samples may be classed as extreme outliers, meaning that they are very different from all other samples. This results in elevated stress levels and an ordination plot with all points, except that representing the extreme outlier, grouped into a tight clump with the outlier some distance away. In such circumstances little can be interpreted from the ordination other than there is an extreme outlier. When this situation arose, extreme outliers were noted and removed from subsequent analyses. This permitted interpretations to be made concerning the remaining samples.

Principle axis correlations (PCC in PATN) were calculated for the logged abundances of all taxa contributing to each ordination. This procedure is a multiple linear regression programme that determines how well attributes can be fitted to ordination space. These are plotted on the ordination as linear vectors of a standard arbitrary length indicating the direction of best fit of the correlation. Correlation coefficients are also calculated (Belbin, 1995). The significance of the correlations was determined using a Monte-Carlo randomisation procedure with 1000 permutations (MCAO in PATN).

3.2.5 Calculation of the Proportions of Spatial and Temporal Environmental Variation Explained by Environmental Factors

Measured environmental variables were summarised into a reduced number of environmental factors using Principle Components Analysis (PCA) (Bishop, 1995) in STATISTICA. PCA outputs were used to partition the spatial and temporal components of variation in these factors.

The form of PCA used was based on the correlation matrix calculated between the original attributes, and can be termed a correlation PCA. PCA was carried out on environmental variables associated with each pool habitat type. PCA factors with eigenvalues greater than 1.0 were included in subsequent analyses. Eigenvalues indicate the variance explained by the PCA factor and those with values less than 1.0 explain less of the variation than any of the original variables (Kaiser, 1960, StatSoft Inc., 1995). The percentage of total variation explained by each remaining PCA factor was recorded. After Varimax normalised rotation, the loadings of the original environmental variables for each of the PCA factors were investigated. The aim of rotation was to obtain a clear pattern of loadings of the original variables on factors (StatSoft Inc., 1995). Loadings of greater than 0.7 or less than -0.7 were considered indicative of variables closely associated with a factor.

Scatter plots of all samples were generated for pairs of factors to illustrate the distribution of sample scores for each factor. Samples on these plots were coded to indicate pools and the temporal trajectory (*i.e.* samples from a pool linked in temporal

sequence) of each pool was plotted. The aim of this was to determine the way in which each factor varied spatially and temporally.

The range of sample score values for each factor over all samples was used to quantify the amount of variation that was distributed spatially between streams, spatially between pools, temporally over all pools in a seasonal cycle, temporally over all pools with non-seasonal change and temporally within pools. Sample score ranges for each of these categories were determined from the distributions of pools and sampling times on the scatter plots. The proportion of the total variance explained by each factor which was distributed in each of the spatial and temporal categories was calculated by multiplying the percentage of total variation explained by the proportion of the factor's variation in each category as expressed by the range in sample scores (Equation 3.2).

Equation 3.2.
$$c_{ij} = r_{ij}T_i$$

c_{ij} - the proportion of total environmental variance explained by PCA factor i in category j

r_{ij} - the proportion of variation in factor i expressed in category j

T_i - total variation explained by factor i

In some situations, factors varied simultaneously in relation to more than one spatial/temporal category. Factor one from the sweep sample analysis presents an example of this effect (Figure 3.2). The full range of variation of this factor was expressed as spatial differences between pools but nested within this was temporal variation within individual pools. The full proportion of total variation explained by this factor was therefore attributed to differences between the pools but a nested fraction was also attributed to temporal change within pools. As a consequence of this, the sum of the variation for the factor across all categories appears to be greater than the total variation explained by the factor. This means of partitioning factor variation into spatial and temporal components was considered to better reflect the nested nature of the variation between categories than merely using the sum of the ranges to partition the variation.

Total explained variation was partitioned into its spatial and temporal components by calculating the total variance explained by each factor distributed in each of the spatial and temporal categories and summing these across all factors (Equation 3.3). Because of the influence of nested variation discussed above, the sum of the proportions of total explained variation that was spatial and temporal may not equal 100%, but rather may be a little higher.

Equation 3.3
$$p_{s \text{ or } t} = \sum (c_{ij})_{s \text{ or } t}$$

$p_{s \text{ or } t}$ - the proportion of total explained environmental variation which is spatial (s) or temporal (t)

$(c_{ij})_{s \text{ or } t}$ - the proportion of total environmental variance explained by PCA factor i in category j , for spatial (s) and temporal (t) categories

Finally, the percentages of total explained spatial and temporal variation attributable to each PCA factor were calculated. This was achieved by dividing the sum of total variation for each factor in either the spatial or temporal categories by the percentage of total variation that was either spatial or temporal (Equation 3.4). These figures were then used for comparison with the total spatial and temporal faunal variation explained by each PCA factor. Comparisons are of the form: PCA factor z accounted for x % of explained environmental spatial variation. What % of faunal spatial variation did factor z explain?

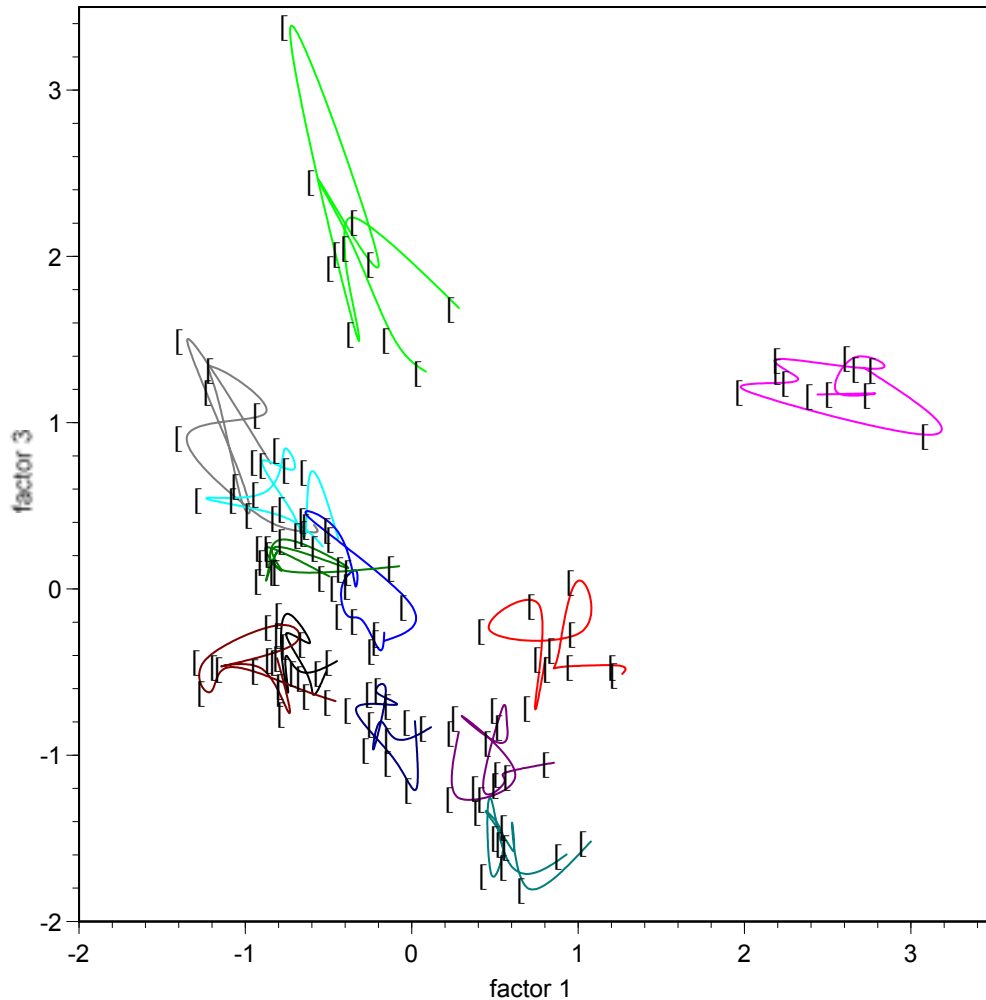
Equation 3.4
$$(f_i)_{s \text{ or } t} = (c_{ij})_{s \text{ or } t} / p_{s \text{ or } t}$$

$(f_i)_{s \text{ or } t}$ - the percentage of total explained environmental variation which is spatial (s) and temporal (t) attributable to PCA factor i

$p_{s \text{ or } t}$ - the proportion of total explained environmental variation which is spatial (s) or temporal (t)

$(c_{ij})_{s \text{ or } t}$ - the proportion of total environmental variance explained by PCA factor i in category j , for spatial (s) and temporal (t) categories

Figure 3.2. Plot of environmental PCA factors 1 vs 3 for variables associated with sweep samples. Each colour represents an individual pool. Lines indicating temporal trajectories of environmental change join consecutive samples. Note that most of the variation is spatial (between pools), but nested within that is temporal variation within pools.



3.2.6 Calculation of the Proportions of Spatial and Temporal Faunal Variation Explained by PCA Factors

a) Spatial Variation

The proportion of faunal spatial variation explained by the PCA factors used above was calculated using the BIOENV routine in PRIMER.

BIOENV is a procedure that links multivariate faunal patterns to multivariate environmental patterns by rank correlating the Bray Curtis faunal association matrix with multiple Euclidean distance matrices derived from environmental variables.

Matrices derived from all possible combinations of environmental variables are considered; Spearman's correlation coefficients between each of these environmental matrices and the target biological matrix are generated and the subset of environmental variables generating the highest correlation or "best fit" with the biological matrix is identified (Clarke and Ainsworth, 1993).

BIOENVs were calculated for each replicate sampling time between the Bray-Curtis faunal dissimilarity matrix between individual pools (calculated following the removal of rare taxa and $\log_{10}(x+1)$ transformation) and multiple Euclidean distance matrices derived from PCA sample scores for all possible combinations of PCA factors for each pool. The weighted Spearman's correlation coefficient for matrices derived from each single PCA factor alone was recorded. As many of the resulting coefficients were approximately zero, a randomisation procedure (RELATE in PRIMER using 10 000 random starts, (Clarke and Warwick, 1994)) was utilised to determine which were significantly different from zero ($p < 0.05$). Coefficients that were not significantly different from zero are indicative of the absence of any relationship between faunal and environmental difference matrices. Coefficients of determination (r^2) were calculated as the square of the correlation coefficients. The coefficient of determination indicates the amount of variability in one variable (faunal variation) accounted for by correlating that variable with a second variable (environmental variation) (Zar, 1984). These were used as a measure of the total faunal spatial variation explained by each individual PCA factor at each time. The overall total faunal spatial variation explained by each individual PCA factor was calculated as the mean coefficient of determination across all times. Variation in the importance of factors was expressed as the standard error of the mean.

Maximum correlation coefficients and the PCA environmental factors contributing to the environmental matrix of "best fit", were recorded from each of the BIOENVs calculated (*i.e.* for each sampling time). Maximum coefficients of determination were calculated from the correlation coefficients. These figures indicated the *maximum* proportion of faunal spatial variation explained by measured multivariate environmental variation. Remaining faunal variation could be considered to be unrelated to measured environmental variables.

b) Temporal Variation

The overall faunal temporal variation explained by each individual PCA factor and the *maximum* proportion of temporal faunal variation explained by measured multivariate environmental variation, were calculated in the same way as for spatial variation. In this case BIOENVs were calculated between faunal and environmental difference matrices in each pool.

3.2.7 Additional Data Exploration

Many additional analytical procedures were employed to explore the degree to which observed spatial and temporal patterns in pool fauna could be explained by measured environmental variation. This additional data exploration generated results and interpretations of patterns that were in concordance with those stemming from the analyses described in detail above. The results of additional analyses are thus not presented.

Analyses described above and presented here (section 2.3) were performed on logged abundance data. In addition, preliminary investigations were carried out on untransformed abundance data, proportional abundance data and on presence/absence of taxa. Results obtained from analyses conducted on these additional data sets were generally similar to those conducted on logged abundance data. Logged abundance data are presented because of the theoretical benefits of logging discussed above (Section 3.2.4).

The strength of relationships between faunal and environmental variation was also investigated in pools with and without the predatory fish *Mogurnda adspersa*, as it was shown in Chapter 5 that the presence or absence of the species could have an influence on pool assemblage composition. The degree to which observed spatial and temporal patterns in pool fauna could be explained by measured environmental variation was no different in these analyses from analyses conducted on all pools combined.

Analytical methods which were utilised but which provided no additional or important information are not described in detail and the results of these analyses are not

presented. In general these additional analyses identified no consistent relationships between faunal and environmental variation. Additional techniques included: calculation of correlation vectors with environmental variables for each ordination (PCC in PATN); correlations of BIOENV scores with environmental attributes of pools; Mantels tests between all pairs of times, ordination of the matrix of Mantels correlation statistics between the times, plotting with temporal trajectories marked, calculation of correlation vectors with temporally variable environmental factors and calculation of BIOENV statistics between the Mantels matrix and environmental variables. Also, for each time, Mantels tests were performed between faunal difference matrices and difference matrices based on the geographical distance, stream distance, and altitudinal distance between the pools. This was then correlated with the strength of the difference between the streams and with environmental variables.

3.3 Results

3.3.1 Environmental Variation

During the course of the study, peak rainfall occurred in late summer, however, there were no large-scale rainfall events, and some rain fell consistently throughout the period (Figure 3.3). Rainfall in the thirty days preceding sampling reflected the daily rainfall patterns, with peak values in early autumn and at least some rainfall in most other months. Values for the three nearest rainfall stations (Bellthorpe, Woodford and Wallanjara, *see* Figure 2.1) are presented to give an overall indication of the rainfall in the area of the study streams (Figure 3.4A). It is evident that Woodford received less rainfall than, Bellthorpe and Wallanjara, which are near the upper portions of the catchments of the study streams (*see* Figure 2.1). Bellthorpe was considered to give the closest approximation of the rainfall influencing the study streams, and was used for subsequent analyses.

Stream discharge was not closely linked to rainfall patterns. At the beginning and end of the study period, discharge in Logger Branch was greater than that Unnamed Tributary, but this reversed during the middle portion of the study (Figure 3.4B). The average minimum flow velocity of water through pools, which was calculated based on discharge, showed temporal patterns in the two streams that were indistinguishable from discharge (Figure 3.4C).

Pools varied in length from an average of 5 to 12 m and the length of individual pools was fairly static over time. There was no difference between streams in the length of pools with an overall average of 8 m. The average width of pools varied between streams, with pools in Logger Branch on average 1 m wider than those in Unnamed Tributary. Individual pools had a fairly consistent width over time. The overall range of pool width was from 3 to 10 m with a mean of 5 m. The depth of Logger Branch pools was on average greater than those in Unnamed Tributary, however, the depth of individual pools varied considerably over time. The overall average pool depth was 61 cm (Table 3.5).

Figure 3.3. Daily rainfall totals recorded at Bellthorpe during the sampling period and the months immediately preceding it. For comparison with mean monthly rainfall see Figure 2.2.

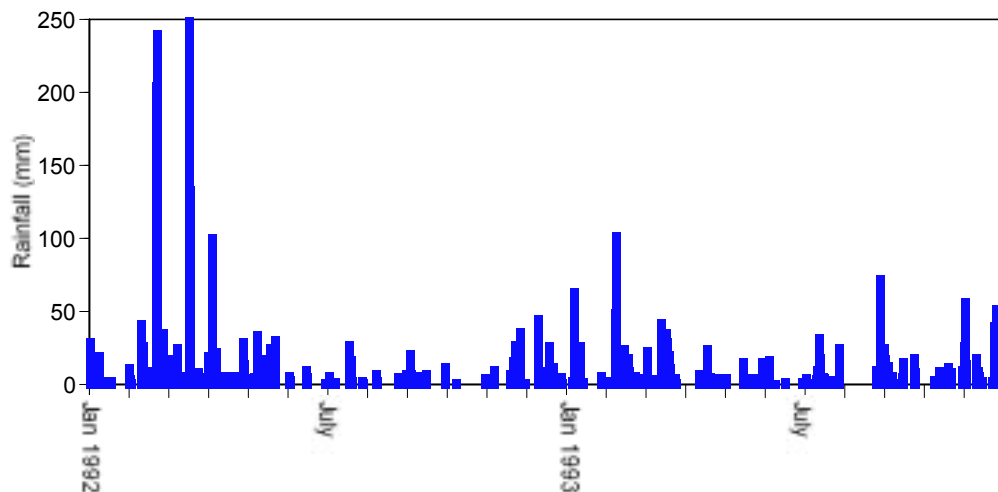
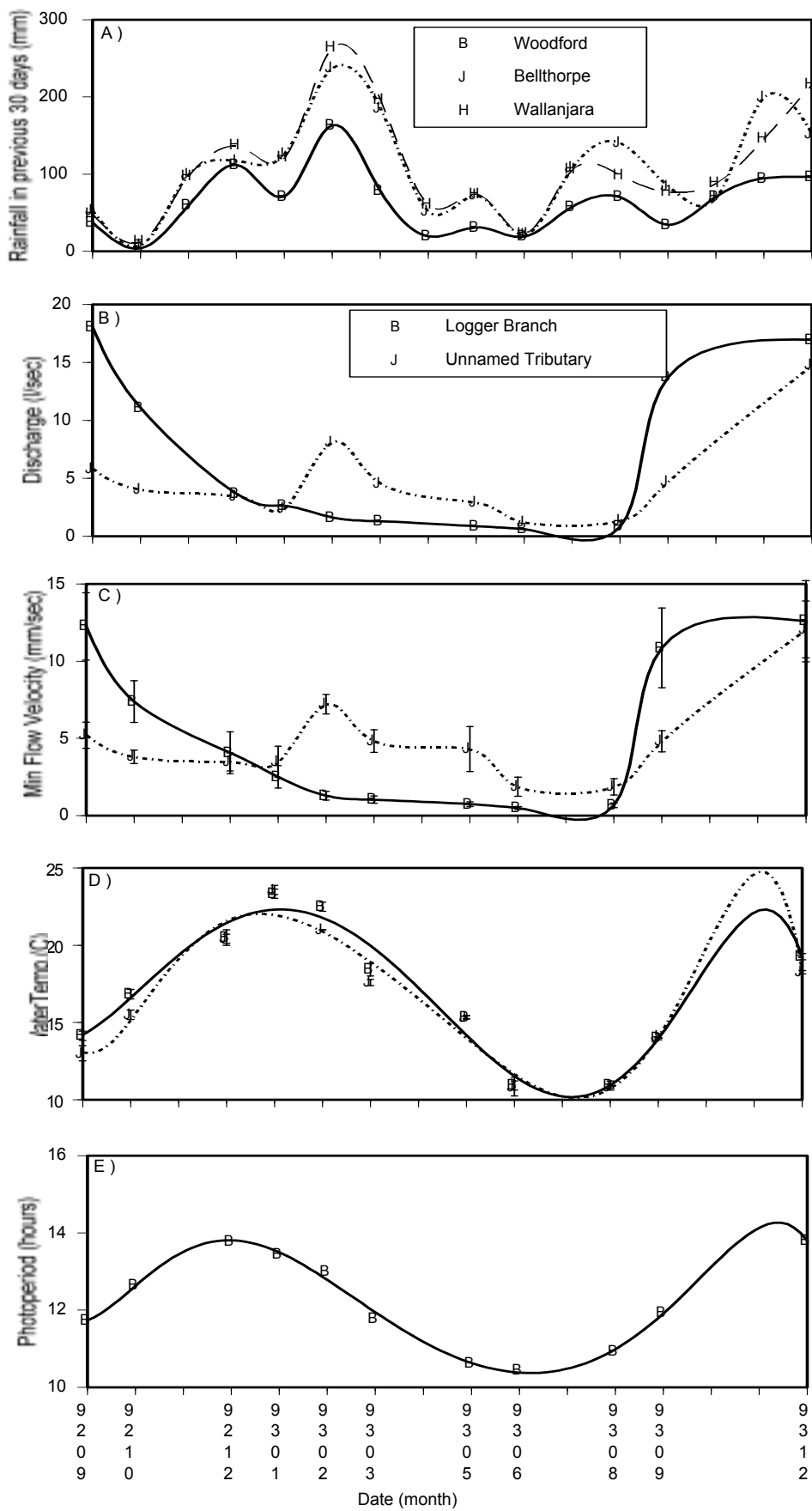


Figure 3.4 (*over page*). Temporal fluctuations in environmental variables recorded during the study on each sampling occasion. A) rainfall during the 30 days preceding each sampling date at the 3 nearest recording stations; B) Discharge recorded in the two streams; C) Mean minimum flow velocity in pools in each stream; D) Mean water temperature in pools in each stream; E) Photoperiod on each sampling occasion; F) Mean pH in pools in each stream; G) Mean turbidity in pools in each stream; H) Mean CPOM mass in pools in each stream; I) Mean epilithon organic mass on cobbles (per unit area of 900 mm²) in pools in each stream. Bars indicate standard errors of mean values.



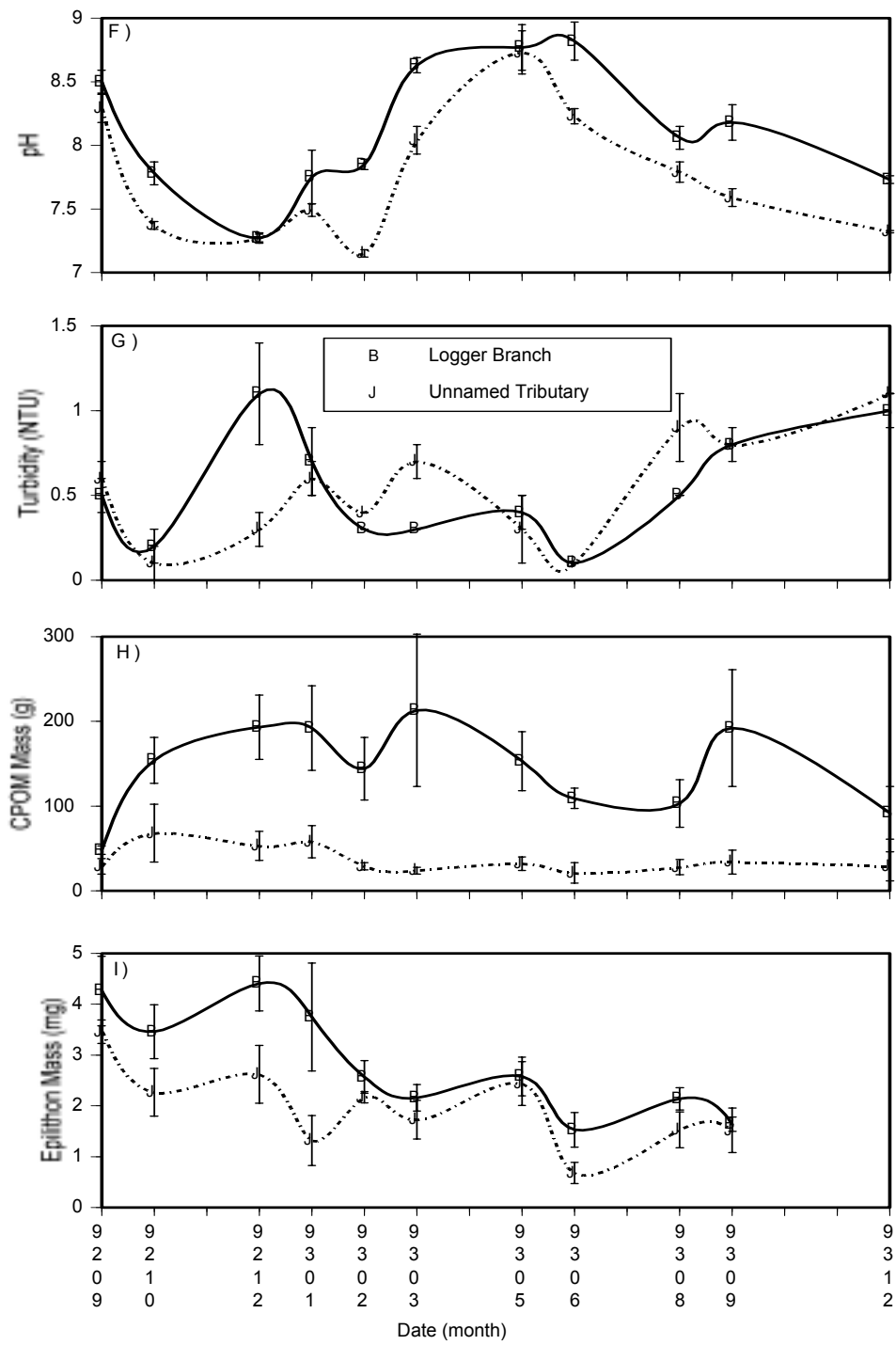


Table 3.5. Mean values and standard error (in brackets) of environmental parameters for each pool, pools in Logger Branch (A) and Unnamed Tributary (B), and overall. For pools n = 11, for streams n = 66 and overall n = 132. G = gravel, C = cobble, B = boulder and BR = bedrock.

Pool	Length (m)	Width (m)	Depth (cm)	Area (m ²)	Cross Sectional Area (m ²)	pH	Water Temp (°C)	Turbidity (NTU)	CPOM (g)	Cobble Epilithon (mg/)	%G	%C	%B	%BR	Substrate Heterogeneity
A1	5 (0)	5 (0)	31 (1)	23 (2)	0.8 (0.1)	8.0 (0.2)	16.0 (1.3)	0.6 (0.1)	210 (35)	3.0 (0.4)	15.5 -	26.1 -	23.3 -	35.1 -	0.03 -
A2	12 (0)	5 (0)	81 (1)	64 (2)	2.2 (0.0)	8.0 (0.2)	16.4 (1.3)	0.7 (0.2)	73 (10)	3.2 (0.6)	13.0 -	59.2 -	19.8 -	8.0 -	0.21 -
A3	7 (0)	6 (0)	49 (1)	39 (2)	1.4 (0.0)	8.0 (0.1)	17.3 (1.4)	0.4 (0.1)	247 (48)	2.4 (0.4)	1.3 -	25.1 -	9.5 -	64.0 -	0.34 -
A4	5 (0)	3 (0)	56 (2)	17 (1)	0.9 (0.1)	8.1 (0.2)	17.3 (1.3)	0.5 (0.1)	122 (19)	2.9 (0.4)	0.7 -	59.6 -	22.3 -	17.3 -	0.29 -
A5	10 (0.1)	3 (0)	61 (1)	32 (1)	1.0 (0.1)	8.3 (0.2)	17.4 (1.3)	0.5 (0.2)	157 (26)	2.9 (0.6)	3.7 -	37.9 -	31.4 -	27.0 -	0.13 -
A6	11 (0)	10 (0)	111 (1)	101 (4)	5.3 (0.1)	8.2 (0.2)	17.1 (1.3)	0.5 (0.1)	61 (11)	2.7 (0.4)	7.5 -	38.2 -	4.0 -	50.2 -	0.25 -
B1	6 (0)	3 (0)	53 (1)	17 (1)	0.8 (0.0)	7.7 (0.1)	15.7 (1.3)	0.6 (0.1)	13 (2)	1.7 (0.3)	3.5 -	54.5 -	34.5 -	7.6 -	0.27 -
B2	5 (0)	3 (0)	40 (3)	13 (1)	0.6 (0.1)	7.7 (0.2)	15.9 (1.3)	0.6 (0.1)	23 (3)	1.8 (0.4)	1.0 -	49.1 -	46.0 -	3.9 -	0.37 -
B3	5 (0)	5 (0)	37 (2)	25 (2)	1.0 (0.1)	7.8 (0.2)	16.6 (1.3)	0.4 (0.1)	91 (16)	2.1 (0.3)	0.6 -	35.8 -	40.4 -	23.3 -	0.20 -
B4	12 (0)	3 (0)	98 (1)	40 (2)	1.6 (0.1)	7.8 (0.2)	16.7 (1.3)	0.6 (0.2)	45 (8)	1.8 (0.3)	3.3 -	20.5 -	59.3 -	16.0 -	0.25 -
B5	8 (0)	5 (0)	40 (1)	43 (2)	1.1 (0.0)	7.8 (0.2)	16.7 (1.2)	0.6 (0.1)	19 (3)	2.3 (0.4)	1.4 -	37.4 -	56.5 -	4.8 -	0.36 -
B6	11 (0)	5 (0)	72 (2)	51 (1)	1.7 (0.1)	7.8 (0.2)	16.7 (1.2)	0.4 (0.1)	31 (11)	2.2 (0.4)	3.9 -	43.4 -	44.6 -	8.2 -	0.24 -
Logger Branch Average	8 (0)	5 (0)	65 (3)	46 (4)	1.9 (0.2)	8.1 (0.1)	16.9 (0.5)	0.5 (0.1)	145 (14)	2.8 (0.2)	7.0 (2.5)	41.0 (6.2)	18.4 (4.1)	33.6 (8.5)	0.21 (0.05)
Unnamed Trib. Average	8 (0)	4 (0)	57 (3)	32 (2)	1.1 (0.1)	7.8 (0.1)	16.4 (0.5)	0.5 (0.0)	37 (5)	2.0 (0.1)	2.3 (0.6)	40.1 (4.9)	46.9 (3.9)	10.6 (3.1)	0.28 (0.03)
Grand Average	8 (1)	5 (1)	61 (8)	39 (8)	1.5 (0.4)	7.9 (0.2)	16.7 (1.2)	0.5 (0.1)	91 (30)	2.4 (0.4)	4.6 (1.4)	40.6 (3.8)	32.6 (5.1)	22.1 (5.5)	0.24 (0.03)

The pH of pool water was generally alkaline. On most sampling occasions the pH in Unnamed Tributary was lower than the pH in Logger Branch, however, both streams displayed the same temporal trends. There was a seasonal pattern of pH fluctuation with a peak in winter when recorded values were more alkaline, and troughs in summer where values were closer to neutral (Table 3.5 and Figure 3.4F).

The turbidity of pool water was low with only minor differences between individual pools and streams. Temporal fluctuations in the two streams showed similar patterns that appeared to be loosely associated with antecedent rainfall patterns (Table 3.5 and Figure 3.3G).

Logger Branch was slightly warmer on average than Unnamed Tributary, and there were small differences between individual pools on each sampling occasion. Temporal fluctuation in water temperature showed a strongly seasonal pattern, which closely matched that of photoperiod (Table 3.5 and Figures 3.2D and E).

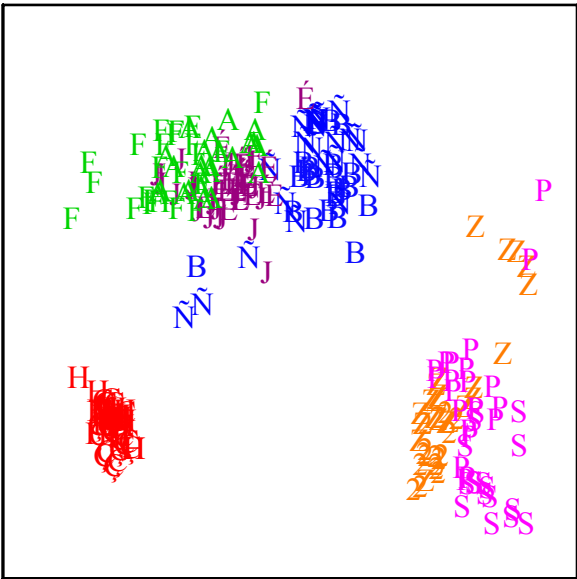
Logger Branch consistently had much higher levels of CPOM in pools than Unnamed Tributary, although individual pools were variable over time without any obvious seasonal pattern. Cobble epilithon mass was also higher in Logger Branch pools than in Unnamed Tributary pools. Again, there was considerable spatial and temporal variability within streams. The two streams displayed similar patterns of temporal change in mean cobble epilithon mass. This change appeared to be aseasonal and was not obviously linked to discharge or rainfall patterns (Table 3.5 and Figure 3.3H and I).

3.3.2 Faunal Differences Between Habitat Types

The habitat types sampled displayed consistent faunal differences and the magnitude of these differences was greater than the spatial or temporal variation that was recorded within habitat types (Figure 3.3). There was some overlap in the faunal composition of gravel and litter samples and of boulder and bedrock samples but each habitat type was significantly different from all others (ANOSIM, $p < 0.05$).

The fauna of the various habitat types sampled appears to be influenced by a gradient of substrate particle size from coarse (bedrock and boulder) to fine (gravel). This is evident from the ordination plot showing the composition of the fauna from all habitat types (Figure 3.5). Boulder and bedrock samples were distinct from other habitat types and yet discernibly different from each other. Cobble and litter samples had distinctive faunas, with gravel samples showing overlap with both, especially the latter. Of these three habitat types, cobble fauna was most similar to boulder and bedrock faunas. The fauna of sweep samples was distinct from that of all other habitat types.

Figure 3.5. Ordination plot indicating the faunal composition of all samples from Logger Branch and Unnamed Tributary on the four occasions when all habitats were sampled (see Table 3.1). The samples are coded to indicate habitat type and stream. Pneuston samples were excluded as they were outliers on the ordination. Ordination based on proportional abundance of fauna in each sample to account for differences in total abundance between different sampling techniques. Stress = 0.18.



	Logger Branch	Unnamed Trib.
Cobble	B	G
Sweep	H	C
Gravel	J	E
Litter	F	A
Boulder	Z	2
Bedrock	P	S

3.3.3 Sweep Samples¹

a) Fauna

A total of 37 taxa were collected from 132 sweep samples. The average richness of samples was 5.2 species (s.e. = 0.02) and the average abundance was 41 individuals per sample (s.e. = 2.5). This equates to a mean density of 8.2 individuals m⁻² (SE = 0.5). *Paratya australiensis*, Notonectidae and *Episynlestes albicauda* were the most commonly collected taxa (Table 3.6.)

b) Spatial and temporal patterns in fauna

There were differences in the fauna collected in sweep samples from individual pools on every occasion samples were collected. The magnitudes of differences were generally large (Table 3.7), with mean Bray-Curtis values consistently greater than the 0.35 threshold recommended by Humphrey *et al.* (1997) as a maximum value at which the fauna of two samples can be considered comparable and on some occasions greater than the 0.5 threshold at which they considered the fauna of two samples to represent different assemblages. Differences fluctuated over time (Table 3.7), but this fluctuation was not significantly correlated with measured environmental variation. The nature of the faunal differences between pools were inconsistent over time and no consistent patterns are evident from ordination plots showing the distribution of pools based on their fauna (Figure 3.6).

The abundances of *Episynlestes albicauda* and Notonectidae sp.B were strongly and significantly correlated with faunal differences between pools in most months and the abundance of *Paratya australiensis* in many months (Figure 3.6). Other taxa were strongly correlated only at certain times.

¹ In order to avoid unnecessary repetition, expanded results of all analyses are only presented for sweep samples and more concise versions for the other habitat types. The extra detail of the expanded version aids comprehension of the methodologies employed but all salient results are presented in the condensed form. This does not imply sweep samples are considered more significant than samples from the other habitats.

Table 3.6. Predominant taxa collected in each type of sample with the proportion of samples in which the taxon was present (%) and the mean abundance per sample (expressed as abundance m⁻²), with the standard error of the mean in brackets. For a listing of all taxa collected during the study refer to Appendix II.

Taxon	cobble		gravel		litter		boulder		bedrock		sweep		pneuston		composite	
	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.
Oligochaeta			90	3474 (705)	77	1158 (263)									96	281 (85)
<i>Ferissia</i> sp.					75	632 (147)	8	0 (0)	11	5 (2)					90	15 (4)
Hydrobiidae sp.A															27	1 (0)
<i>Pisidium</i> (<i>Pisidium</i>) sp.A			31	105 (32)											40	6 (3)
Copepoda			48	105 (21)	63	316 (84)									75	9 (4)
<i>Paratya australiensis</i>											97	4 (0)			98	7 (2)
<i>Bungona narilla</i>	100	3615 (355)	83	1789 (347)	54	526 (200)									100	345 (57)
<i>Tasmanocoenis queenslandica</i>			90	1368 (232)	44	211 (53)									92	50 (14)
<i>Atalophlebia</i> sp.AV13	66	136 (14)	98	1895 (284)	94	1053 (116)									100	110 (25)
<i>Tillyardophlebia</i> sp.AV6	70	205 (20)	33	105 (53)											79	39 (16)
<i>Koornonga</i> sp.AV1			54	421 (105)	94	1263 (211)									98	33 (11)
<i>Ulmerophlebia</i> sp.AV3			81	737 (158)	44	211 (63)									85	74 (26)
<i>Episynlestes albicauda</i>			25	105 (21)	38	105 (21)					70	1 (0)			85	3 (1)
Zygoptera juveniles															35	3 (2)
<i>Austrogomphus anphiclitus</i>			52	105 (32)	25	32 (11)									65	6 (2)
<i>Eusynthemis nigra</i>			56	105 (32)											60	6 (2)
<i>Orthotrichia</i> sp.															29	3 (1)
<i>Hellyethyra simplex</i>	23	34 (7)	69	421 (147)					9	5 (3)					81	19 (7)
<i>Paranyctiophylax</i> sp.AV5	44	68 (14)	29	105 (42)											56	11 (3)
<i>Tasiagma ciliata</i>							89	167 (8)	77	117 (13)					90	31 (6)
<i>Tasimia palpata</i> ?							55	67 (0)	40	33 (8)					60	9 (3)
<i>Helicopsyche Ptychopteryx</i>							7	0 (0)	12	5 (2)					25	4 (2)
<i>Anisocentropus</i> sp.					67	421 (105)									77	11 (4)
Leptoceridae juveniles															58	7 (2)
<i>Triplectides elongatus</i>					33	105 (21)									38	2 (1)

Table 3.6 *continued*.

Taxon	cobble		gravel		litter		boulder		bedrock		sweep		pneuston		composite	
	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.	%	Abund.
Notonectidae sp.A															35	1 (0)
Notonectidae sp.B															75	2 (0)
Notonectidae sp.C															60	0 (0)
<i>Sclerocyphon minimus</i>	42	68 (7)	40	105 (32)			17	17 (0)	16	17 (3)					77	13 (2)
<i>Austrolimnius (Limnelmis) sp.A (l)</i>			27	105 (63)											31	2 (1)
<i>Austrolimnius (Austrolimnius) sp.C (l)</i>			81	842 (147)	42	105 (11)									85	51 (22)
Gyrinidae (a)													69	0.4 (0.1)	69	0 (0)
Ceratopogonid sp.A															60	11 (4)
Ceratopogonid sp.D															29	15 (7)
Chironominae sp.B					38	105 (42)									71	3 (1)
Chironominae sp.D			96	2947 (642)											96	161 (50)
Tanypodinae sp.A			58	211 (53)	63	211 (53)									77	12 (4)
Tanypodinae sp.E			58	947 (232)	58	421 (105)									79	72 (26)
Tanypodinae sp.G			81	632 (126)											98	34 (10)

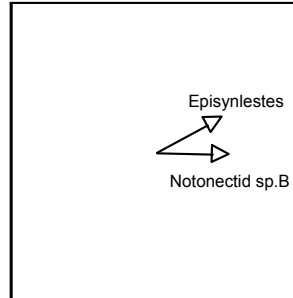
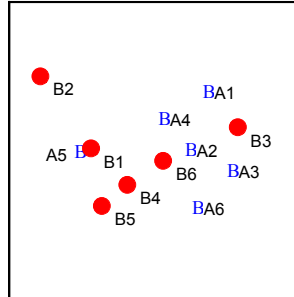
Table 3.7. Mean difference in sweep sample fauna between pools on each sampling occasion and over all occasions. This difference is expressed as the mean Bray Curtis dissimilarity between all pairs of pools. The s.e. = of the mean (s.e.) indicates the variability of the difference.

Time	Mean Bray-Curtis	s.e.
9209	0.40	0.02
9210	0.41	0.02
9212	0.53	0.02
9301	0.38	0.02
9302	0.45	0.02
9303	0.49	0.02
9305	0.45	0.02
9306	0.40	0.02
9308	0.41	0.02
9309	0.58	0.03
9312	0.54	0.03
Overall	0.46	0.02

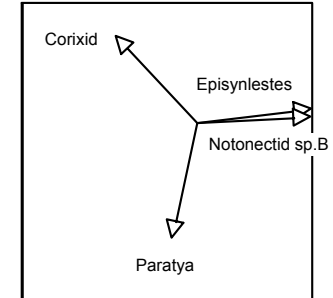
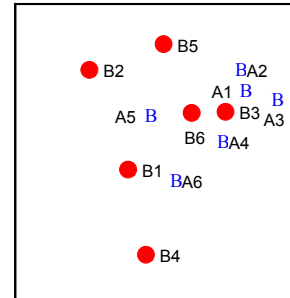
Figure 3.6 (over page). Plots of two-dimensional SSH MDS ordinations of pools based on differences in sweep sample fauna ($\log_{10}(x+1)$ abundance, following removal of rare taxa). Independent ordinations were performed for each sampling occasion and these are presented. All ordinations were rotated to match the structure of the 9209 ordination. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.8 or greater. Abbreviated taxon names are explained in Appendix III. Pool numbers (A1, A2,..., B1, B2,...) as per Figure 2.5.

Stress values for the ordinations in order of sampling occasion were: 0.12, 0.13, 0.15, 0.14, 0.10, 0.13, 0.11, 0.09, 0.13, 0.10, 0.10.

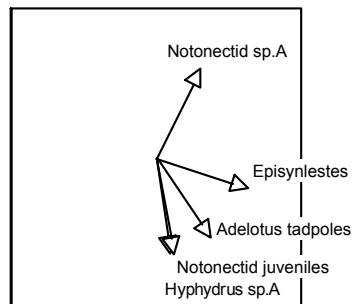
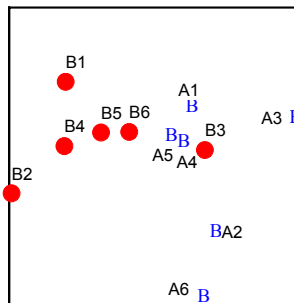
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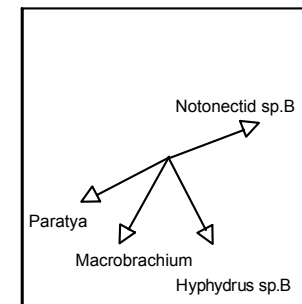
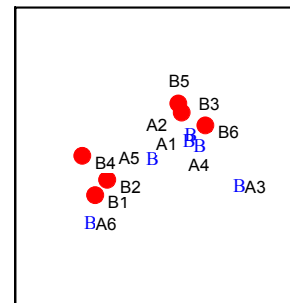
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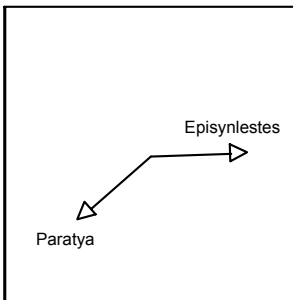
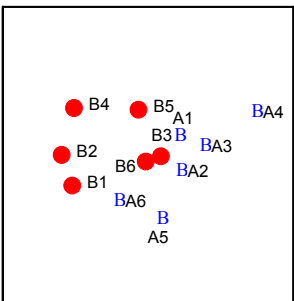
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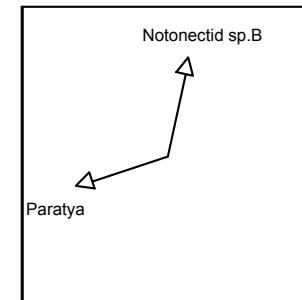
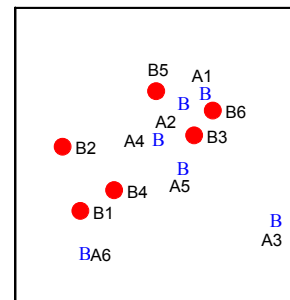
9302



9212

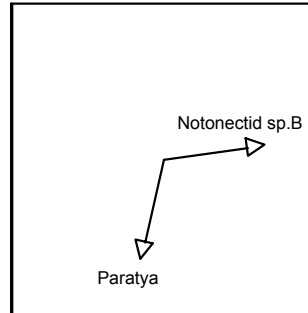
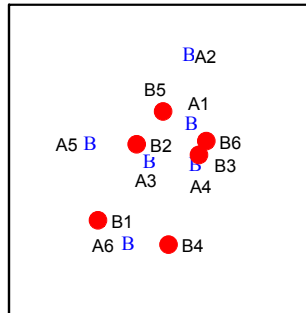


9303

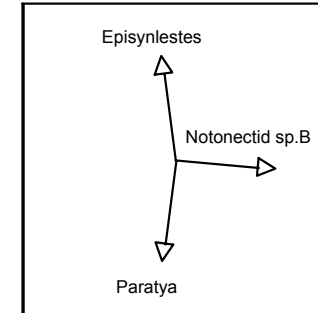
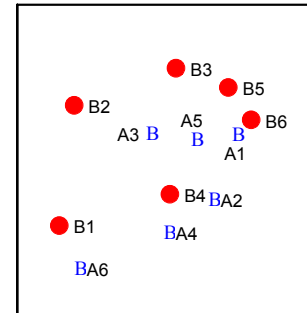


Sweep samples – sites within times

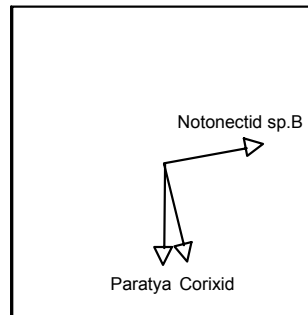
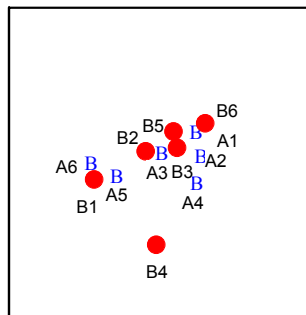
9305



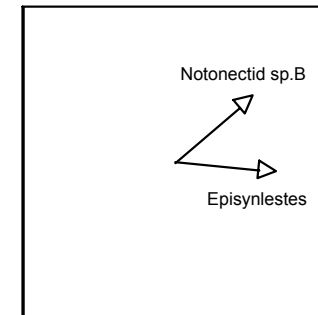
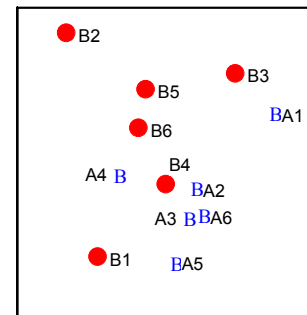
9309



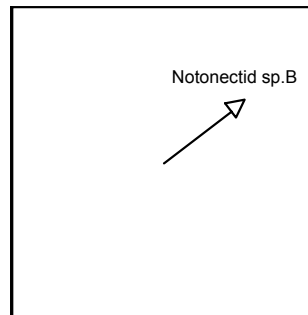
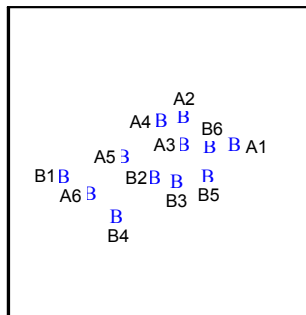
9306



9312



9308



Sweep sample fauna changed over time in each of the twelve pools. The magnitude of temporal change varied from pool to pool (Table 3.8), but this variation was not significantly correlated with measured environmental variation. The mean temporal Bray Curtis difference between faunal samples in each pool ranged between 0.35 and 0.57. The magnitude of the mean spatial Bray Curtis difference between samples at each time recorded a very similar range of 0.38 to 0.58. The overall temporal and spatial mean difference between samples were both 0.46 with small and equivalent standard errors (Tables 3.7 and 3.8). The measured variation in sweep sample fauna was thus equally partitioned between its spatial and temporal components during the course of the study. The magnitudes of these differences were generally large (Tables 3.7 and 3.8), with mean Bray-Curtis values consistently greater than the 0.35 threshold recommended by Humphrey *et al.* (1997) as a maximum value at which the fauna of two samples can be considered comparable and on some occasions greater than the 0.5 threshold at which they considered the fauna of two samples to represent different assemblages.

The nature of the temporal change in pool fauna in many pools followed a similar trajectory from 9209 until about 9301/9302 after which changes were inconsistent between pools (Figure 3.7). The reasonably consistent period of change was generally associated with changes in the abundance of *Episynlestes albicauda* and Notonectidae.

On three of the sampling occasions, (9210, 9212 and 9312), there was a significant difference between the faunal assemblages of the two streams (Table 3.9 and Figure 3.6). *Episynlestes albicauda*, *Paratya australiensis* and species of Notonectidae were important contributors to the difference between the streams on all three occasions although the differences in their mean abundance between the streams were often small (Table 3.10).

The magnitude of the difference in fauna between the two streams (*i.e.* ANOSIM R) was significantly correlated with the difference in discharge between the streams the preceding month ($r = 0.93$, $n = 11$, $p < 0.001$) but was not significantly correlated with the difference between discharges at the time the samples were collected or with any

other environmental variables. Taxa tended too have higher abundances in the stream with higher discharge the previous month (Table 3.10).

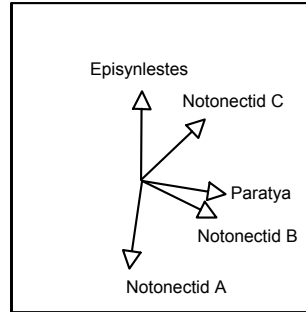
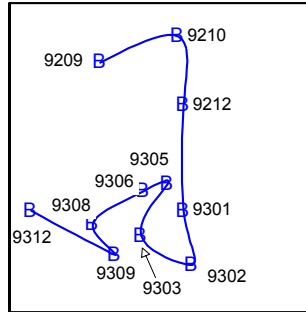
Table 3.8. Mean difference in sweep sample fauna between sampling times in each pool and overall. This difference is expressed as the mean Bray Curtis dissimilarity between all pairs of times. The standard error of the mean (s.e.) indicates the variability of the difference.

Pool	Mean Bray-Curtis	s.e.
A1	0.45	0.02
A2	0.46	0.02
A3	0.55	0.02
A4	0.54	0.02
A5	0.47	0.02
A6	0.45	0.02
B1	0.35	0.02
B2	0.57	0.03
B3	0.43	0.02
B4	0.35	0.02
B5	0.55	0.02
B6	0.36	0.02
Overall	0.46	0.02

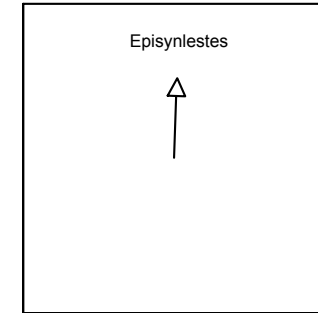
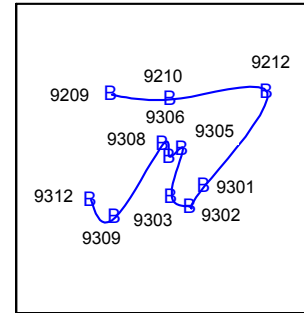
Figure 3.7 (over page). Plots of two-dimensional SSH MDS ordinations of sampling times based on differences in sweep sample fauna ($\log_{10}(x+1)$ abundance, following removal of rare taxa). Independent ordinations were performed for each pool and plots of these are presented. All ordinations were rotated to match the structure of the pool A1 ordination. Consecutive sampling times are connected by lines on the plots to indicate the temporal trajectory of faunal change in each pool. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.8 or greater. Abbreviated taxon names are explained in Appendix II.

Stress values for the ordinations in order of pools were: 0.11, 0.18, 0.13, 0.13, 0.12, 0.18, 0.16, 0.07, 0.14, 0.13, 0.09, 0.16.

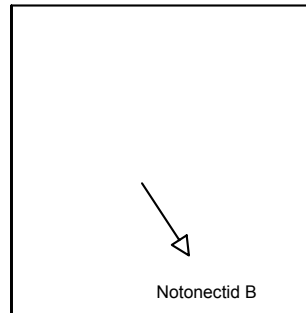
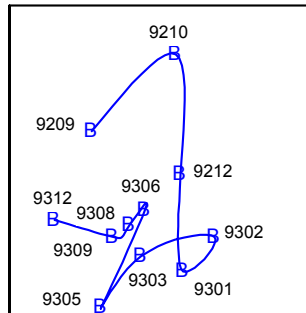
A1



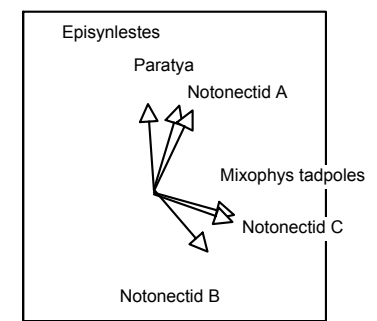
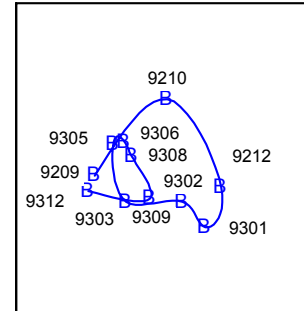
A4



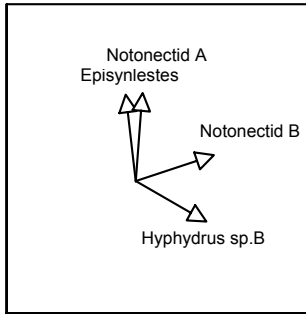
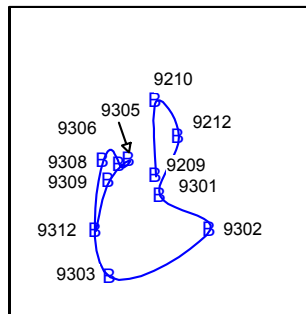
A2



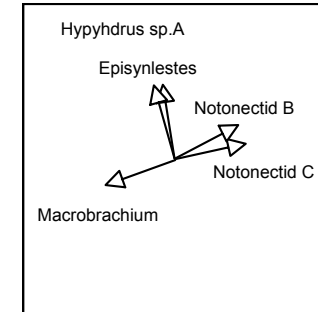
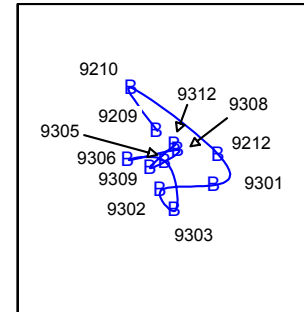
A5



A3

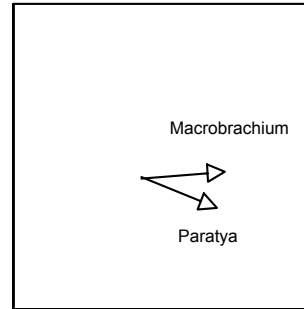
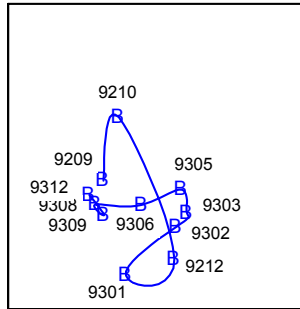


A6

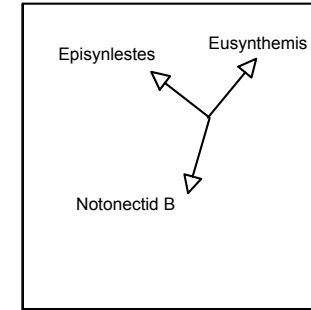
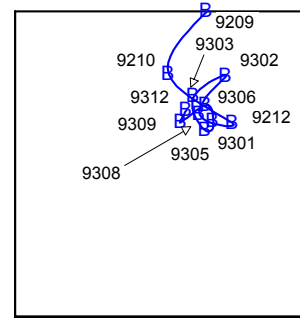


Sweep samples – times within pools

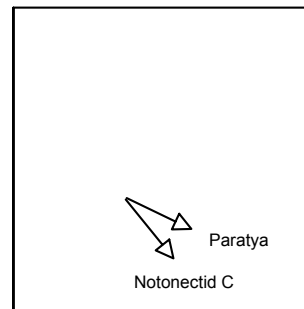
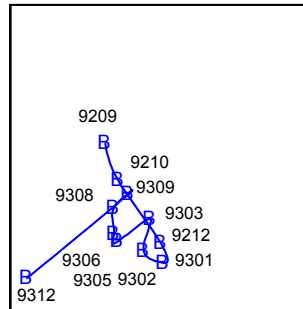
B1



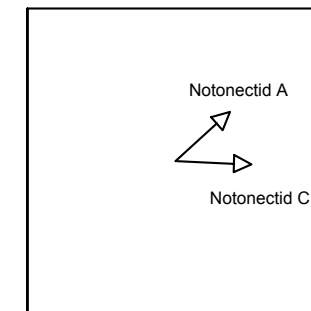
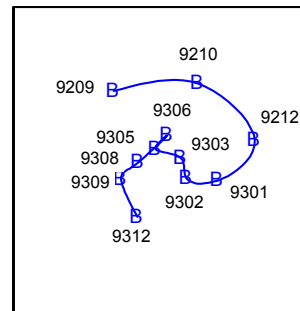
B4



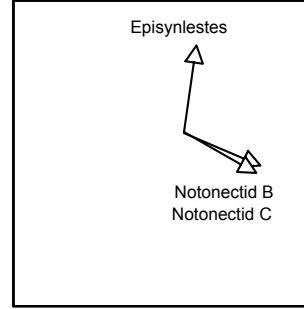
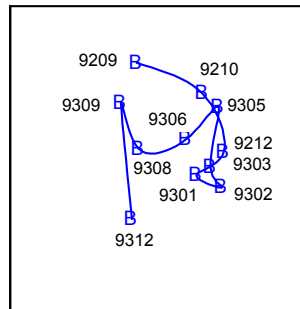
B2



B5



B3



B6

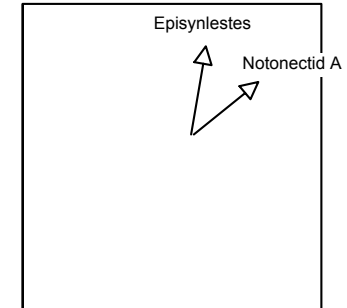
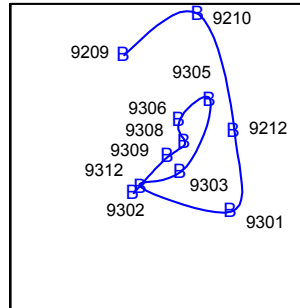


Table 3.9. The magnitude (R) and significance (p) of differences in sweep sample fauna between the two streams (ANOSIM). Shaded rows highlight those sampling occasions where a significant stream difference was identified ($p < 0.05$).

Time	R	p
9209	0.089	0.19
9210	0.376	0.01
9212	0.267	0.03
9301	0.057	0.27
9302	0.023	0.32
9303	-0.026	0.51
9305	-0.130	0.92
9306	-0.054	0.59
9308	-0.054	0.63
9309	-0.096	0.78
9312	0.250	0.03

Table 3.10. Contribution of important taxa to the difference in sweep sample fauna between streams (A = Logger Branch, B = Unnamed Tributary) at sampling occasions when the difference was significant (SIMPER). Numbers in brackets indicate the stream discharge 1 month prior to sampling ($\text{m}^3 \text{ day}^{-1}$).

Time / Taxon	Average Abundance		% contribution to difference
	Stream A	Stream B	
9210	(1555)	(518)	
<i>Episynlestes albicauda</i>	30.3	5.5	24.4
Notonectid sp.A	27.0	15.3	13.4
<i>Paratya australiensis</i>	12.5	15.5	11.8
9212	(950)	(346)	
Notonectid sp.B	15.7	9.5	13.7
<i>Episynlestes albicauda</i>	7.7	0.3	13.2
Notonectid sp.A	10.8	3.5	11.3
<i>Paratya australiensis</i>	17.2	22	10.9
9312	(1210)	(432)	
<i>Paratya australiensis</i>	8.8	6.7	27.7
Notonectid sp.B	5.5	5.2	23.4
<i>Mixophyes</i> tadpoles	1.3	0	12.2
<i>Adelotus</i> tadpoles	0.8	0	11.6
<i>Episynlestes albicauda</i>	1.2	0.3	10.9

c) Environmental variation associated with samples

PCA on environmental variables associated with pool sweep samples resulted in eight factors with eigenvalues greater than 1.0. All factors were clearly associated with one or more environmental variables. Together these eight factors explained 87% of total environmental variation with the first three factors explaining over 50% (Table 3.11).

Table 3.11. Sweep sample environmental PCA factors with eigenvalues greater than 1.0, the percentage of total variance they explained and associated environmental variables with factor loadings of 0.7 or greater (+ve) or -0.7 or less (-ve). Abbreviations are explained in Table 3.2.

PCA Factor	% Total Variance	High Loading Environmental Variables
1	27	(vol, area, x area, depth, length, width) +ve
2	16	(temp, phot, rain) +ve, (pH) -ve
3	13	(CPOM, %BR) +ve, (%B) -ve
4	9	(discharge, min flow) -ve
5	7	(%G) +ve, (substrate heterogeneity) -ve
6	6	(%C) +ve
7	5	(epilithon) +ve
8	4	(turbidity) +ve
Total	87	---

With the exception of factors 1 and 3, most PCA factors expressed their variation in only one spatial or temporal category. The division of the proportion of total variation explained by each factor into spatial and temporal categories (Table 3.12) resulted in 59.5% of total explained environmental variation considered spatial and 42% temporal. The sum of these proportions is not 100% because of the nested nature of variation expressed in factors 1 and 3 (Table 3.12, *see* section 3.2 for further explanation of this effect). Final figures partitioning spatial and temporal variation between PCA environmental factors (Table 3.13) indicate that spatial variation was accounted for by factors 1, 3, 5 and 6, in order of decreasing contribution. Temporal variation was accounted for by factors 2, 4, 1, 7, 8 and 3, again in order of decreasing contribution.

Table 3.12. The percentage of the total variation in measured environmental parameters that is explained by each PCA factor in each of the categories of spatial and temporal variation. In the last row of the table the proportions of the total variation in measured environmental parameters that is spatial and temporal is indicated. This does not add up to 100% because all PCA factors were not used in this analysis and because of the nested nature of variation in factors 1 and 3.

Factor	Environmental Variation				
	Spatial		Temporal		
	Streams	Pools	Seasonal All Pools	non-Seasonal All Pools	Within Pools
1		27%			5.4%
2			16%		
3	6.5%	13%			2.6%
4				9%	
5		7%			
6		6%			
7				5%	
8				4%	
Total	59.5%		42%		

Table 3.13. Spatial and temporal faunal and environmental variation explained by each environmental factor. Abbreviations are explained in Table 3.2.

Factor	Associated Variables	Spatial Variation		Temporal Variation	
		% Env ¹	% Faunal	% Env ¹	% Faunal
1	(vol, area, x area, depth, length, width) +ve	45.4	1.0	12.9	5.0
2	(temp, phot, rain) +ve, (pH) -ve	0	0	38.1	1.0
3	(CPOM, %BR) +ve, (%B) -ve	32.8	0	6.2	1.0
4	(discharge, min flow) -ve	0	0	21.4	4.0
5	(%G) +ve, (substrate heterogeneity) -ve	11.7	0	0	4.0
6	(%C) +ve	10.0	0	0	1.0
7	(epilithon) +ve	0	0	11.9	3.0
8	(turbidity) +ve	0	1.0	9.5	1.0
Total		100	2.0	100	20.0

¹ Values for environmental variation are expressed in terms of the total variation explained by the 8 PCA factors used (87%). The remaining 13% of total variation remains unattributed.

d) Links between environmental and faunal variation

Many of the correlation coefficients calculated between faunal and environmental difference matrices were near zero. Randomisation tests confirmed that in many cases there was no significant association between matrices, and thus no relationship between environmental factor scores and sweep sample fauna. Coefficients of determination in these cases were also zero (Tables 3.14 and 3.15).

PCA factors 3, 4 and 8 were the only individual environmental factors to explain some of the spatial variation in fauna. In all three cases these relationships were non-zero at only one of the eleven sampling times and only a small proportion of faunal variation was explained (4 - 10%). The overall proportion of faunal spatial variation explained by each individual factor, as indicated by the mean over all times, was zero or near zero for all factors (Table 3.14).

Table 3.14. Coefficients of determination (r^2) between sweep sample faunal difference matrices and difference matrices based on each environmental factor at each sampling time (BIOENV). The figures indicate the proportion of faunal spatial variation explained by each environmental factor at each time. The overall proportion of faunal spatial variation explained by each factor is indicated by the mean over all times.

	PCA Factor							
Time	1	2	3	4	5	6	7	8
9209	0	0	0	0	0	0	0	0.10
9210	0	0	0.07	0.04	0	0	0	0
9212	0	0	0	0	0	0	0	0
9301	0	0	0	0	0	0	0	0
9302	0	0	0	0	0	0	0	0
9303	0	0	0	0	0	0	0	0
9305	0	0	0	0	0	0	0	0
9306	0	0	0	0	0	0	0	0
9308	0	0	0	0	0	0	0	0
9309	0	0	0	0	0	0	0	0
9312	0	0	0	0	0	0	0	0
MEAN	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01
s.e.	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01

The maximum proportion of faunal spatial variation explained by measured multivariate environmental variation (Table 3.15) varied between sampling times, but was always low. The average proportion recorded was 0.07, meaning that, on average, 93% of

faunal spatial variation was unrelated to measured environmental variation. The environmental factors contributing to these maxima were inconsistent, and often included factors with insignificant spatial variation components. All factors, except factor five, explained some spatial faunal variation at one or more times.

Temporal variation in fauna was more frequently explained, at least to a limited extent, by individual environmental factors than was spatial variation. All eight factors were correlated with temporal faunal patterns in at least one of the twelve pools. Explained variation was most often zero but ranged as high as 31% for factor 5 in pool A3. There was however no consistency between replicate pools in the factors explaining faunal variation or in the strength of relationships. For example, in some pools temporal variation seemed related to PCA factor 1 (pools A4 and A5), whereas in other pools PCA factor 1 explained none of the temporal variation, and other PCA factors appeared important (PCA factor 7 in pools A6 and B4 for example). Despite moderately high values in some pools, the overall proportion of faunal temporal variation explained by each factor, as indicated by the mean over all times, was near zero for all factors (Table 3.16).

The maximum proportion of faunal temporal variation explained by measured multivariate environmental variation (Table 3.17) varied between sampling times and was generally low, but was frequently higher than was the case for spatial variation. The average proportion recorded was 0.24, meaning that, on average, 76% of faunal temporal variation was unrelated to measured environmental variation. The environmental factors contributing to these maxima were inconsistent, and often included factors with insignificant temporal variation components. All factors explained some temporal faunal variation in one or more pools.

Table 3.15. Maximum coefficients of determination (r^2_{\max}) and contributing PCA environmental factors (Factors $_{\max}$) from BIOENVs calculated for each sampling time. These figures indicate the maximum proportion of sweep sample faunal spatial variation explained by measured multivariate environmental variation.

Time	r^2_{\max}	Factors $_{\max}$
9209	0.12	7,8
9210	0.19	1,3,4,8
9212	0.03	2,6
9301	0.05	3,4,6
9302	0.05	1,2,3
9303	0.18	1,3,4,7,8
9305	0.02	1
9306	0.04	1,2,6
9308	0.02	1,6,8
9309	0.05	1,6,8
9312	0.03	2,7,8
MEAN	0.07	---
s.e.	0.02	---

Table 3.16. Coefficients of determination (r^2) between sweep sample faunal difference matrices and difference matrices based on each environmental factor in each pool (BIOENV). The figures indicate the proportion of faunal temporal variation explained by each environmental factor in each pool. The overall proportion of faunal temporal variation explained by each factor is indicated by the mean over all pools.

Pool	PCA Factor							
	1	2	3	4	5	6	7	8
A1	0.07	0	0	0.12	0	0	0	0
A2	0	0	0	0.09	0	0	0	0
A3	0	0	0	0	0.31	0.06	0	0
A4	0.17	0	0	0.14	0	0	0.02	0
A5	0.14	0.05	0.10	0	0.11	0.07	0	0.06
A6	0	0	0	0	0	0.04	0.12	0
B1	0	0	0	0	0.02	0	0	0
B2	0	0.07	0	0	0	0	0	0
B3	0.09	0	0	0.08	0	0	0	0
B4	0	0	0	0	0	0	0.17	0
B5	0	0	0	0	0	0	0	0
B6	0.10	0	0	0	0	0	0.04	0
MEAN	0.05	0.01	0.01	0.04	0.04	0.01	0.03	0.01
s.e.	0.02	0.01	0.01	0.02	0.03	0.01	0.02	0.01

Table 3.17. Maximum coefficients of determination (r^2_{\max}) and contributing PCA environmental factors (Factors_{max}) from BIOENVs calculated for each pool. These figures indicate the maximum proportion of sweep sample faunal temporal variation explained by measured multivariate environmental variation.

Pool	r^2_{\max}	Factors _{max}
A1	0.18	1,4,7
A2	0.11	1,2,4
A3	0.37	5,6,7
A4	0.34	1,4,5,8
A5	0.35	1,2,3,6
A6	0.15	6,7
B1	0.05	5,8
B2	0.35	1,2,4,5
B3	0.24	1,4,5,6,7
B4	0.26	6,7
B5	0.19	1,2,6,8
B6	0.29	1,2,3,5,7,8
MEAN	0.24	---
s.e.	0.03	---

Overall, there was, at most, a weak link between sweep sample faunal assemblage structure and measured environmental variation (Table 3.13). None of the environmental factors considered, and thus none of their associated environmental variables, explained the observed spatial and temporal variation in pool sweep sample fauna. Factors which when combined accounted for nearly 90% of measured environmental variation, explained in total only 20% of measured faunal variation.

None of the factors explained more than 1% of faunal spatial variation and combined all eight explained only 2%. Most factors explained none of the faunal variation.

Relationships between temporal variation in fauna and environmental factors were more evident than spatial associations, but were only very weakly expressed. None of the factors explained more than 5% of faunal temporal variation and combined all eight explained only 20%. The environmental factors displaying the most temporal variation, (factors 2 and 4, combined accounting for 60% of temporal environmental variation), explained only 1% and 4% of faunal variation respectively. Other factors which

displayed comparatively greater temporal stability (factors 5 and 6) explained equivalent proportions of faunal variation.

3.3.4 Cobble Samples

a) Fauna

A total of 46 taxa were collected from 132 cobble samples. The average richness of the samples was 5.5 species (s.e. = 0.2) and the average abundance was 65 individuals (s.e. = 5) per cobble. This equates to a mean density of 4434 individuals m^{-2} (SE = 341). Mayflies, notably *Bungona narilla* (Baetidae), were the most common taxa on cobbles (Table 3.6).

b) Spatial and temporal patterns in fauna

Cobble fauna varied in both space and time with no consistent pattern (Figures 3.7 and 3.8). Faunal variation was slightly greater between spatial replicates than temporal replicates, with mean Bray-Curtis differences of 0.41 (s.e.= 0.01) and 0.36 (s.e.= 0.02) respectively. These differences were large, as they are greater than the 0.35 threshold recommended by Humphrey *et al.* (1997) as a maximum value at which the fauna of two samples can be considered comparable.

In some months there was little variability among pools within a stream (*e.g.* 9210, Unnamed Tributary, Figure 3.8) compared with other months (*e.g.* 9309 Unnamed Tributary). None of the environmental variables measured could account for this pattern, as none were significantly correlated with the mean within stream Bray-Curtis difference between pools for each sampling occasion.

Faunal correlations with ordinations of temporal variation (Figure 3.9) varied considerably between replicate pools in both the taxa identified and in the orientation of vectors representing the same taxon.

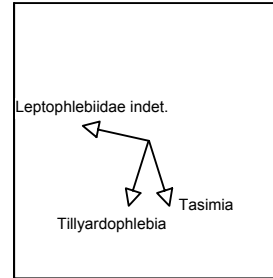
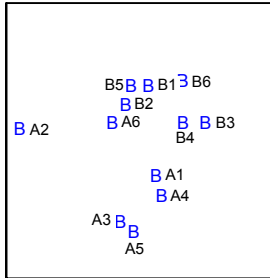
There was a significant difference between the cobble fauna of the two streams on every sampling occasion. These are evident on the ordination plots (Figure 3.8). The magnitude of the difference fluctuated, but this could not be related to any measured

environmental fluctuation. The difference was consistently explained by cobbles from Logger Branch pools having fewer *Bungona narilla* and more *Tillyardophlebia* sp.AV6 (Leptophlebiidae) individuals than cobbles from Unnamed Tributary pools (SIMPER). Correlation vectors for one or both of these species were significantly and highly correlated with ordinations of pools at all times. The orientations of the vectors further highlight the role of these species in separating cobble samples from the two streams (Figure 3.8).

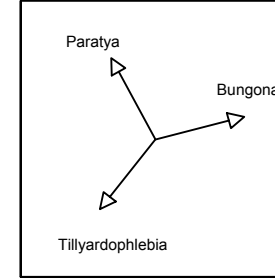
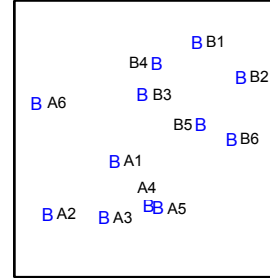
Figure 3.8 (over page). Plots of two-dimensional SSH MDS ordinations of pools based on differences in cobble fauna ($\log_{10}(x+1)$ abundance, following removal of rare taxa). Independent ordinations were performed for each sampling occasion and these are presented. All ordinations were rotated to match the structure of the sampling occasion 9209 ordination. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.8 or greater. Abbreviated taxon names are explained in Appendix II.

Stress values for the ordinations in order of sampling occasion were: 0.17, 0.15, 0.14, 0.15, 0.17, 0.19, 0.10, 0.11, 0.19, 0.16, 0.15.

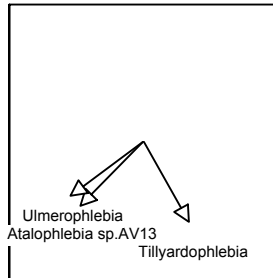
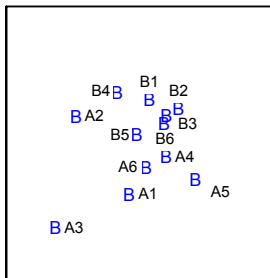
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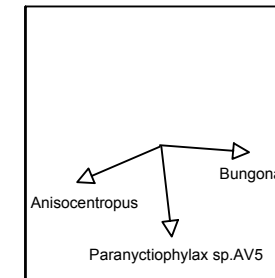
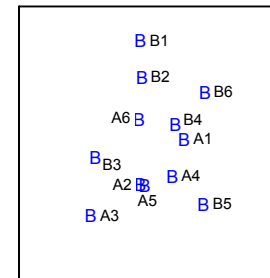
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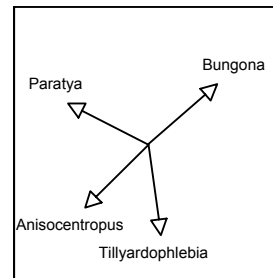
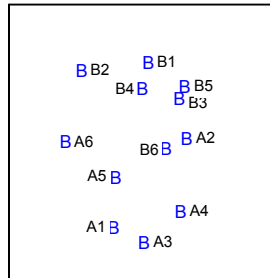
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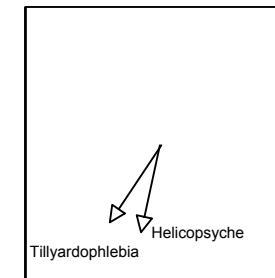
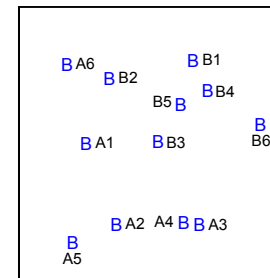
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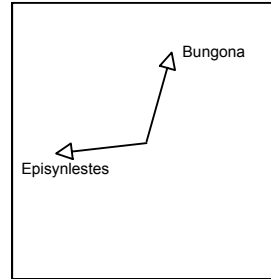
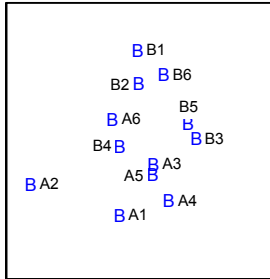
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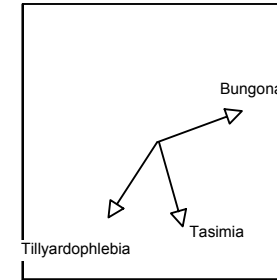
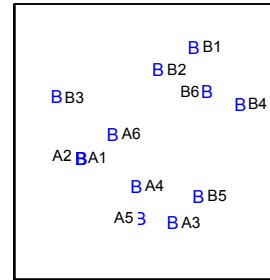
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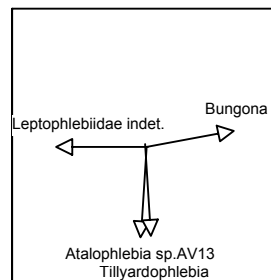
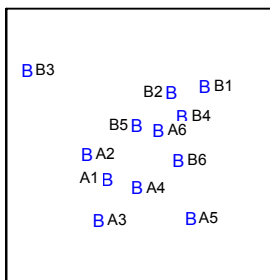
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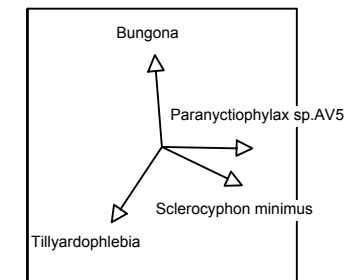
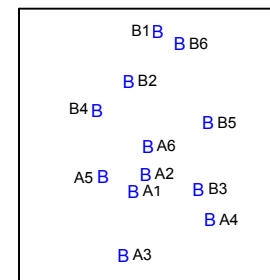
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9312



9308

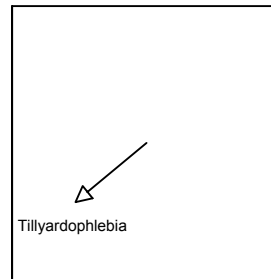
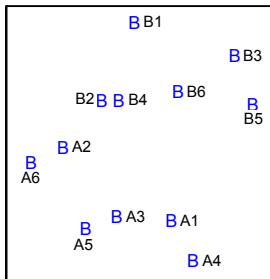
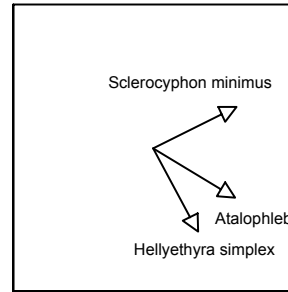
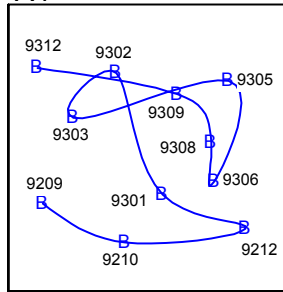


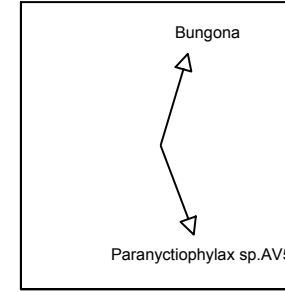
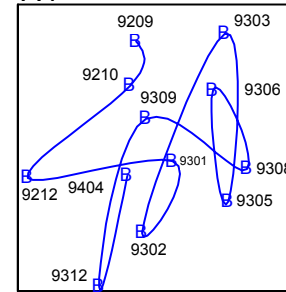
Figure 3.9 (over page). Plots of two-dimensional SSH MDS ordinations of sampling times based on differences in cobble fauna ($\log_{10} (x+1)$) abundance, following removal of rare taxa). Independent ordinations were performed for each pool and plots of these are presented. All ordinations were rotated to match the structure of the pool A1 ordination. Consecutive sampling times are connected by lines on the plots to indicate the temporal trajectory of faunal change in each pool. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.8 or greater. Abbreviated taxon names are explained in Appendix II.

Stress values for the ordinations in order of pools were: 0.16, 0.11, 0.17, 0.19, 0.17, 0.19, 0.12, 0.16, 0.15, 0.16, 0.15, 0.19.

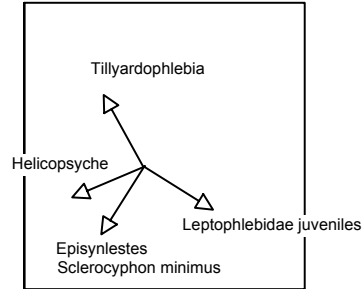
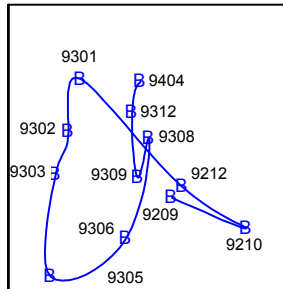
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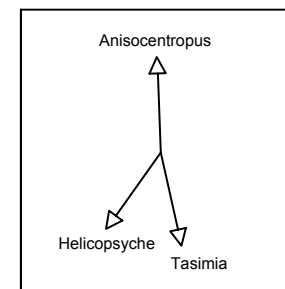
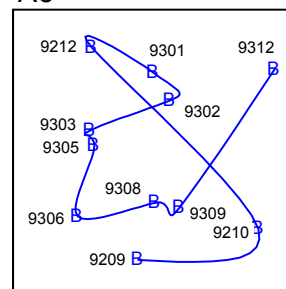
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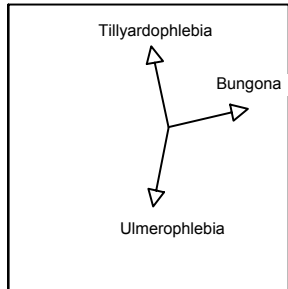
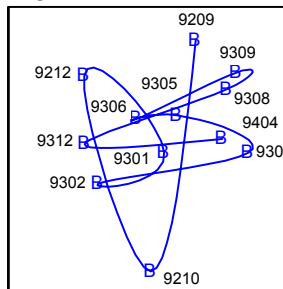
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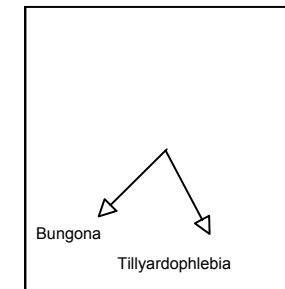
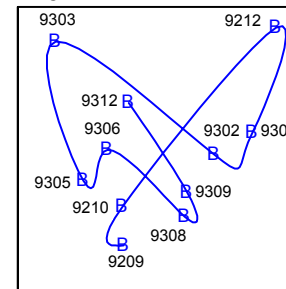
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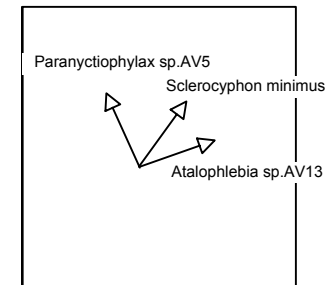
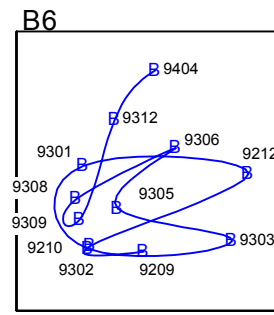
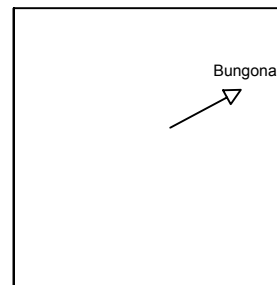
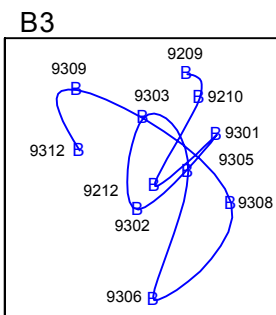
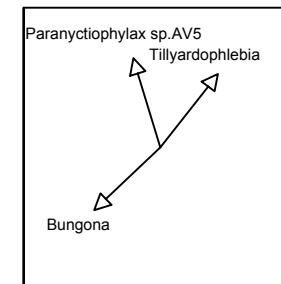
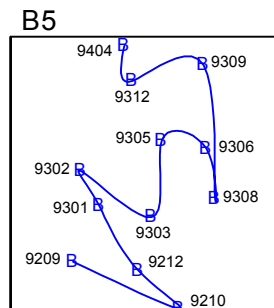
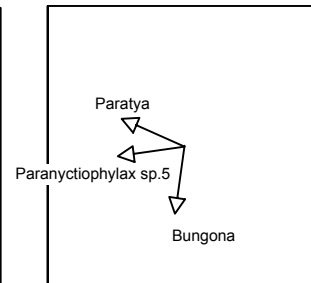
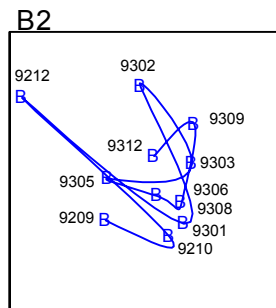
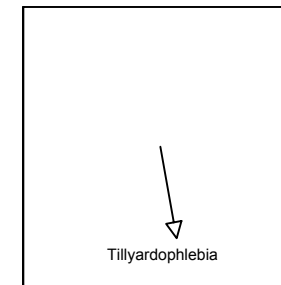
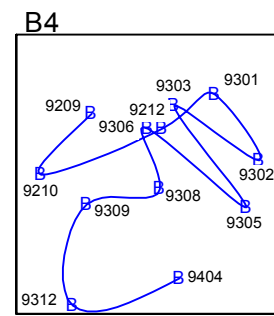
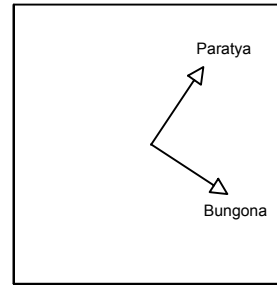
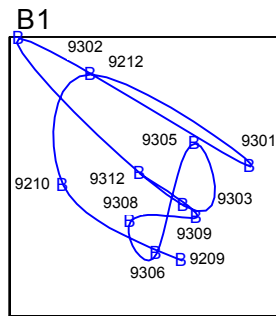


A3



A6





c) Environmental variation associated with samples

Seven PCA factors (Table 3.18) accounted for 83% of total variation in environmental variables measured in association with cobble samples. Of this 56% was associated with spatial variation and 40% with temporal variation. Most of the spatial variation was associated with the size and substrate composition of pools and most temporal variation with stream discharge, cobble epilithon mass, cobble area and seasonally fluctuating factors (temperature, pH and photoperiod).

d) Links between environmental and faunal variation

There was, at most, a very weak link between cobble fauna assemblage structure and measured environmental variation (Table 3.18). None of the environmental factors considered, and thus none of their associated environmental variables, explained the observed spatial and temporal variation in pool cobble sample fauna. Factors which when combined accounted for over 80% of measured environmental variation, explained in total less than 10% of measured faunal variation.

None of the factors explained more than 3% of faunal spatial variation and combined, all seven explained only 3.5%. Most factors explained none of the faunal variation.

Relationships between temporal variation in fauna and environmental factors were similarly very weak. None of the factors explained more than 3% of faunal temporal variation and combined all seven explained only 6%. The environmental factors displaying the most temporal variation, (factors 2 and 4, combined accounting for 60% of temporal environmental variation), explained only 3% of faunal variation.

Table 3.18. Spatial and temporal cobble faunal and environmental variation explained by each environmental factor. Abbreviations are explained in Table 3.2.

Factor	Associated Variables	Spatial Variation		Temporal Variation	
		% Env ¹	% Faunal	% Env ¹	% Faunal
1	(area, x area, depth, length) +ve	40.7	0	11.4	0.5
2	(epilithon) +ve, (discharge, min flow) -ve	0	3.0	43.0	0
3	(%BR) +ve, (%B) -ve	34.7	0	6.5	0.5
4	(temp, phot) +ve, (pH) -ve	0	0.4	24.4	3.0
5	(%G) +ve, (substrate heterogeneity) -ve	13.6	0	0	0
6	(%C) +ve	11.1	0	0	1.0
7	(cobble area) +ve	0	0	14.7	1.0
Total		100	3.5	100	6.0

¹ Values for environmental variation are expressed in terms of the total variation explained by the 7 PCA factors used (83%). The remaining 17% of total variation remains unattributed.

3.3.5 Gravel Samples

a) Fauna

A total of 105 taxa were collected from 48 gravel samples. The average richness of samples was 20 species (s.e. = 1) and the average abundance was 176 individuals per sample (s.e. = 17). This is equivalent to a mean density of 18 526 individuals m⁻² (SE = 1790). The most common taxa collected were *Atalophlebia* sp.AV13, Chironominae sp.D, *Tasmanocoenis queenslandica*, Oligochaeta, *Bungona narilla*, *Austrolimnius* (*Austrolimnius*) sp.C, Tanypodinae sp.G and *Ulmerophlebia* sp.AV3 which occurred in 80% or more of gravel samples (Table 3.6).

b) Spatial and temporal patterns in fauna

The composition of gravel fauna in pools showed no obvious multivariate patterns. The fauna was spatially variable but replicates showed little consistency in the nature of this variation (Figures 3.9). Some pools showed similar patterns of temporal change (e.g. pools A1, A5, B1, B2 and B5) (Figure 3.11) but there was no association between such patterns and environmental differences (based on analysis of the similarity of temporal patterns between pools using Mantels Tests and multivariate correlation of these

similarities with environmental factors). Faunal variation between spatial and temporal replicates was similar, with mean Bray-Curtis differences of 0.47 (s.e.= 0.01) and 0.44 (s.e.= 0.03) respectively.

On two of the sampling times (9212 and 9306) pool B1 was identified as an extreme outlier and was excluded from analyses of spatial patterns. Pool B1 was exceptional at these times because a depauperate fauna was collected in terms of both richness and abundance. No environmental explanation for this was apparent.

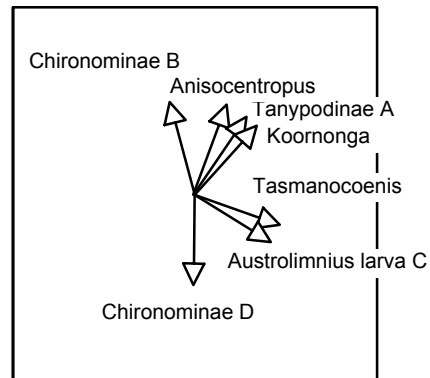
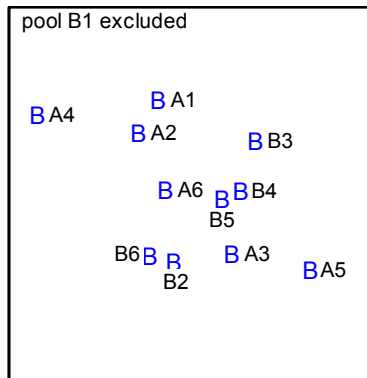
Faunal correlations with ordinations of both spatial and temporal variation (Figures 3.9, 3.10) varied considerably between replicates, again with variation in both the taxa identified and in the orientation of vectors representing the same taxon.

There was a significant difference between the gravel fauna of the two streams on two sampling occasions (9303 and 9309), especially on 9309. This is evident on the ordination plots (Figure 3.10). The magnitude of the difference in fauna between streams was significantly correlated with mean differences between the streams in the total mass of gravel and the masses of different size fractions of gravel in samples. The difference in ambient or antecedent discharge between the streams was not correlated with faunal differences. At the times when the fauna between the streams was significantly different, the difference was explained by small and inconsistent differences in many taxa rather than by large differences in a few (SIMPER). This is evident in the faunal correlation vectors on ordination plots as variation in both the taxa identified and in the orientation of vectors representing the same taxon (Figure 3.10).

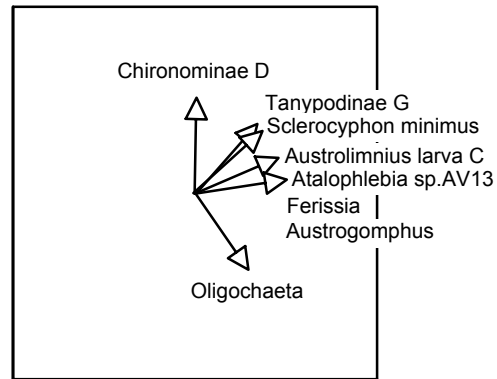
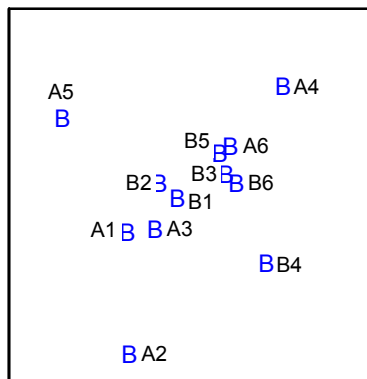
Figure 3.10 (over page). Plots of two-dimensional SSH MDS ordinations of pools based on differences in gravel fauna ($\log_{10}(x+1)$ abundance, following removal of rare taxa). Independent ordinations were performed for each sampling occasion and these are presented. All ordinations were rotated to match the structure of the sampling occasion 9212 ordination. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.75 or greater. Abbreviated taxon names are explained in Appendix II.

Stress values for the ordinations in order of sampling occasion were: 0.18, 0.14, 0.15, 0.16.

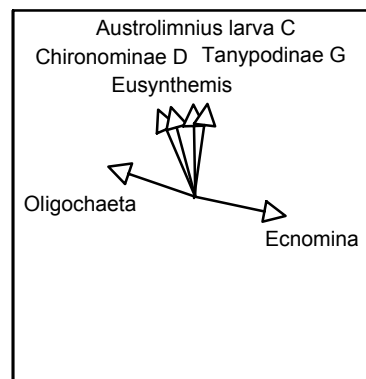
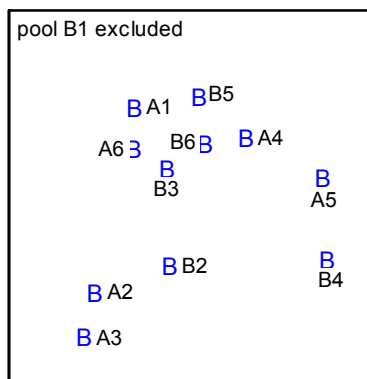
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9303



9306



9309

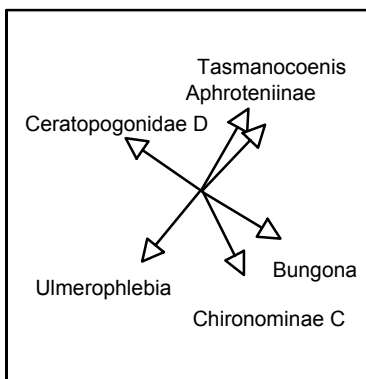
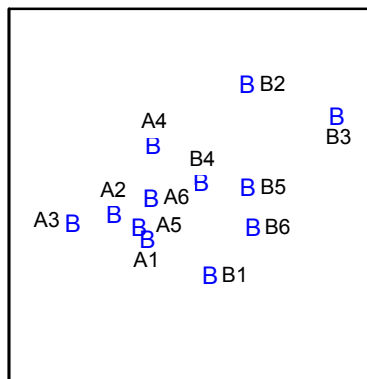
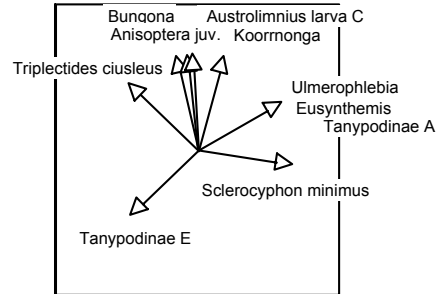
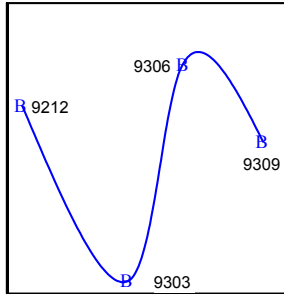


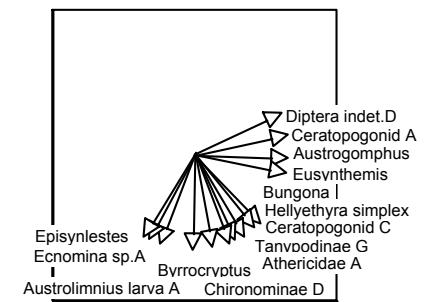
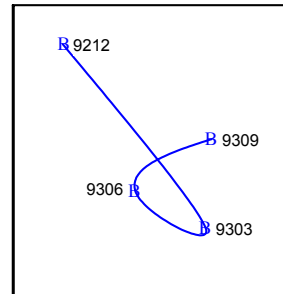
Figure 3.11 (over page). Plots of two-dimensional SSH MDS ordinations of sampling times based on differences in gravel fauna ($\log_{10} (x+1)$) abundance, following removal of rare taxa). Independent ordinations were performed for each pool and plots of these are presented. All ordinations were rotated to match the structure of the pool A1 ordination. Consecutive sampling times are connected by lines on the plots to indicate the temporal trajectory of faunal change in each pool. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.95 or greater. Abbreviated taxon names are explained in Appendix II.

Stress values for the ordinations in order of pools were: 0.12, 0.14, 0.04, 0.06, 0.12, 0.08, 0.05, 0.05, 0.07, 0.10, 0.10, 0.13.

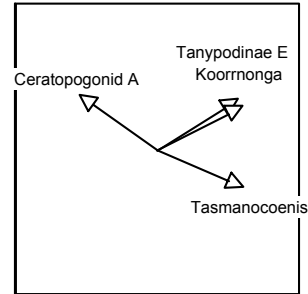
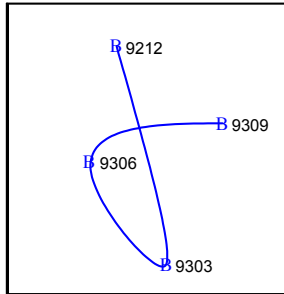
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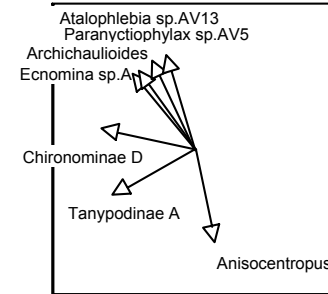
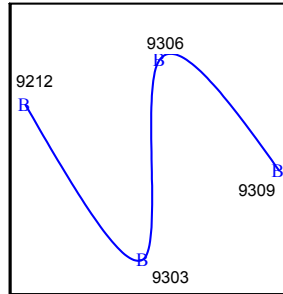
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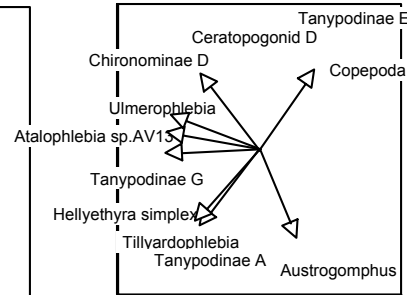
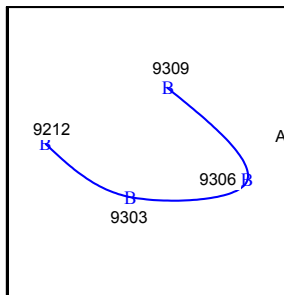
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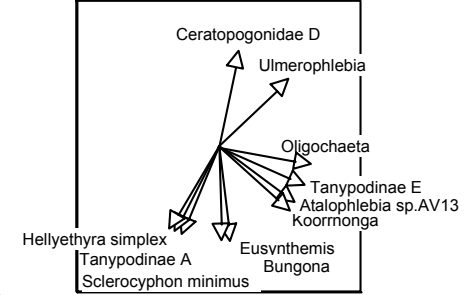
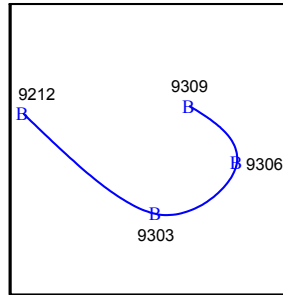
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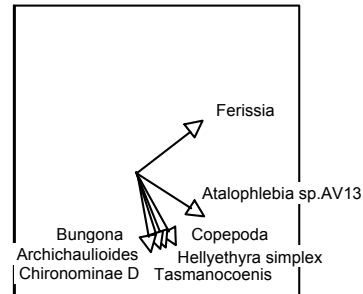
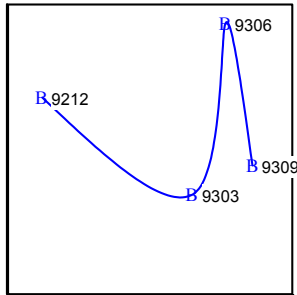
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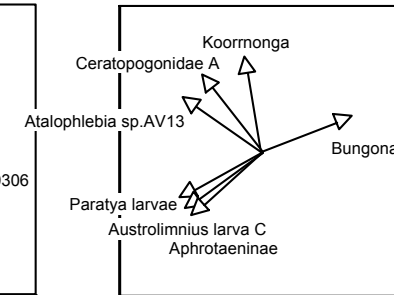
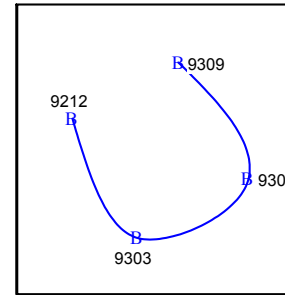
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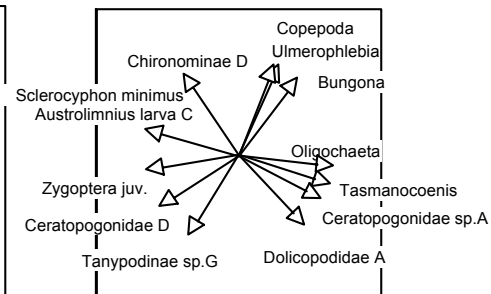
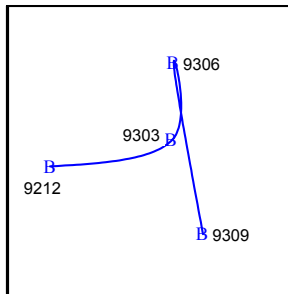
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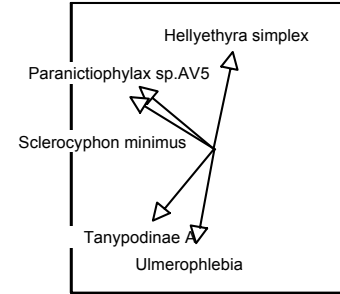
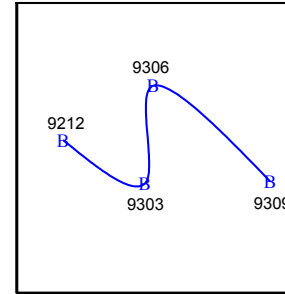
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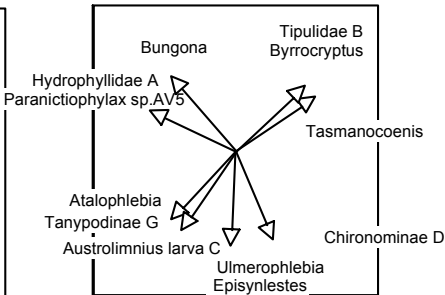
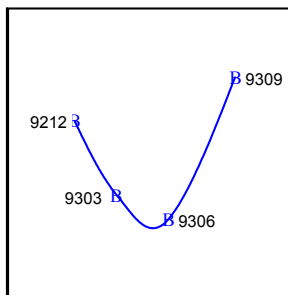
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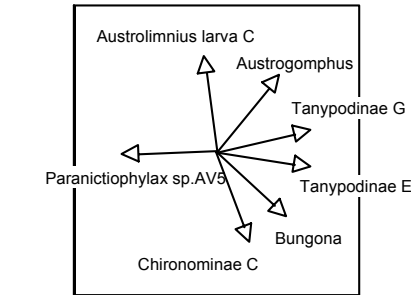
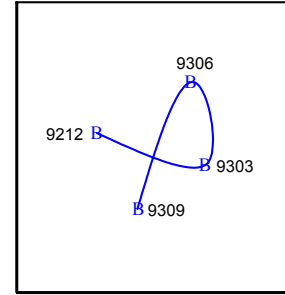
B5



B3



B6



c) Environmental variation associated with samples

Eight PCA factors (Table 3.19) accounted for 86% of total variation in environmental variables measured in association with gravel samples. Of this 50% was associated with spatial variation and 41% with temporal variation. Most of the spatial variation was associated with the size and substrate composition of pools and the organic matter content of gravel in samples. Most of the temporal variation was associated with the organic matter content and particle size composition of gravel in samples, stream discharge and seasonally fluctuating factors (temperature, pH and photoperiod).

Table 3.19. Spatial and temporal gravel faunal and environmental variation explained by each environmental factor. Abbreviations are explained in Table 3.2.

Factor	Associated Variables	Spatial Variation		Temporal Variation	
		% Env ¹	% Faunal	% Env ¹	% Faunal
1	(leaves, sticks, FPOMg, CPOMg, total org) +ve	34	0	28	0
2	(length, area, depth, x area) +ve	31	0	7	0
3	(temp, epilithon, phot) +ve	0	0	31	12
4	(%1 mm, %0.5 mm) +ve, (%4 mm, gravel het) -ve	6	0	21	0
5	(%G) +ve, (substrate heterogeneity) -ve	13	2	0	0
6	(discharge, min flow) +ve	0	2	14	0
7	(%C) +ve	9	0	0	0
8	(%B) -ve	7	0	0	0
Total	---	100	4	100	12

¹ Values for environmental variation are expressed in terms of the total variation explained by the 8 PCA factors used (86%). The remaining 14% of total variation remains unattributed

d) Links between environmental and faunal variation

There was, at most, a weak link between gravel fauna assemblage structure and measured environmental variation (Table 3.19). None of the environmental factors considered, and thus none of their associated environmental variables, explained the observed spatial variation in pool gravel sample fauna.

None of the factors explained more than 2% of faunal spatial variation and combined all eight explained only 4%. Most factors explained none of the faunal variation.

Relationships between temporal variation in fauna and environmental factors were stronger in individual replicate pools. However, there was a high degree of variation between replicate pools. Furthermore, the results of randomisation tests indicated that even some very high correlation coefficients (>0.8) were not significantly different from zero. These results suggest that the relationships found are likely to be influenced by chance to an unacceptable degree. This is because there were only four temporal replicates for each pool. The differences between these four samples based on fauna could be, and were, easily replicated by chance environmental factors and combinations of factors. This is akin to points on an ordination plot based on one set of attributes forming a very similar pattern based on a different set of attributes. With many objects (points) it is intuitively apparent that this is unlikely to occur by chance. However with only four objects this becomes very much more probable. If these strong relationships truly existed, the same factor(s) would be expected to be identified as important in many of the replicate pools. This was clearly not the case.

As a result of randomisation tests determining that most relationships were not significantly different from zero, the overall temporal variation in gravel fauna explained by environmental factors was zero for most factors (Table 3.19). Factor 3 explained an average of 12% of faunal variation. This relationship was however significantly different from zero in only two of the twelve replicate pools (A3 and A6). The variables strongly loaded on this factor (Table 3.19) varied seasonally indicating that, in some pools only, there was seasonal variation in gravel fauna.

3.3.6 Litter Samples

A total of 95 taxa were collected from 48 litter samples. The average richness of samples was 14 species (s.e. = 1) and the average abundance was 72 individuals (s.e. = 6). This equates to a mean density of 7 579 individuals m^{-2} (SE = 632). The most common taxa collected were *Koorrnonga* sp.AV1 and *Atalophlebia* sp.AV13 which occurred in 94% of samples (Table 3.6).

3.3.7 Boulder Samples

A total of 14 taxa were collected from 132 boulder samples. The average richness of samples was 2 species (s.e. = 0.1) and the average abundance was 15 individuals (s.e. = 0.6). This is equivalent to a mean density of 250 individuals m⁻² (SE = 1). The most common taxa collected were *Tasiagma ciliata* and *Tasimia palpata* ? (Table 3.6).

3.3.8 Bedrock Samples

A total of 16 taxa were collected from 132 bedrock samples. The average richness of samples was 2 species (s.e. = 0.1) and the average abundance was 13 individuals (s.e. = 1.5). This equates to a mean density of 217 individuals m⁻² (SE = 25). The most common taxa collected were *Tasiagma ciliata* and *Tasimia palpata* ? (Table 3.6).

3.3.9 Pneuston Samples

The only taxon recorded from pneuston samples was Gyrinidae adults. Other taxa were present (Veliidae, Mesoveliidae and Gerridae), but could not be accurately sampled by the observational method utilised. Adult Gyrinidae were recorded from 62% of the 132 samples. Their mean abundance was 15 individuals (s.e. = 3). This equates to a mean density of 0.4 individuals m⁻² (SE = 0.08).

3.3.10 Composite Samples

a) Fauna

Composite pool fauna, calculated by patch weighting the various habitat types in each pool, was numerically dominated by abundant taxa from gravel and litter habitats. A total of 132 taxa were collected from 48 composite pool samples. The average richness of samples was 35 species (s.e. = 1) and the average abundance was 18195 individuals (s.e. = 3048) per pool. This equates to a mean density of 455 individuals m⁻² (SE = 76). The most common taxa collected were *Bungona narilla*, *Atalophlebia* sp.AV13, Tanypodinae sp.G, *Koorrnonga* sp.AV1, *Paratya australiensis*, Oligochaeta, Chironominae sp.D, *Tasmanocoenis queenslandica*, *Tasiagma ciliata* and *Ferissia* sp. which occurred in 90% or more of samples (Table 3.6).

In terms of biomass, the most significant species of macroinvertebrates in these pools were the Atyid shrimp *Paratya australiensis*, naiads of the Synlestid damselfly *Episynlestes albicauda*, nymphs of the Baetid mayfly *Bungona narilla* and the Leptophlebiid mayflies *Atalophlebia* spAV13, *Tillyardophlebia* spAV6 and *Koornoonga* spAV1, and two species of Notonectidae.

b) Spatial and temporal patterns in fauna

As with the individual habitat types, the composition of composite pool fauna in pools was variable in both space and time. The magnitude of variation between spatial and temporal replicates was similar, with mean Bray-Curtis differences of 0.42 (s.e.= 0.02) and 0.37 (s.e.= 0.01) respectively. These mean differences can be considered to be large, as they are greater than the 0.35 threshold recommended by Humphrey *et al.* (1997) as a maximum value at which the fauna of two samples can be considered comparable. Spatial replicates showed little consistency in the nature of this variation (Figure 3.12). Half of the pools displayed similar temporal trajectories (pools A1, A2, A3, A5, B1 and B5 (Figure 3.13), but similarities between pools in temporal behaviour could not be explained by measured environmental factors.

Faunal correlations with ordinations of spatial and temporal variation (Figures 3.11 and 3.12) varied considerably between replicate pools, with variation in both the taxa identified and in the orientation of vectors representing the same taxon.

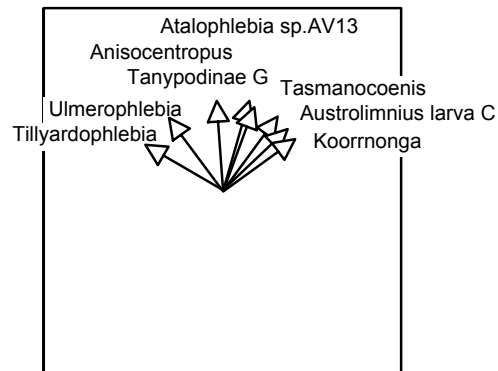
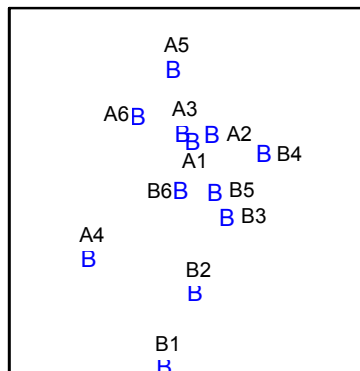
There was a significant difference between the composite pool fauna of the two streams on all sampling occasions, as is evident on the ordination plots (Figure 3.12). The magnitude of the difference in fauna between streams was significantly correlated with mean differences between the streams in the mass of CPOM in pools. The difference in ambient or antecedent discharge between the streams was not correlated with faunal differences. Once again, differences between streams were due to small and inconsistent differences in the abundance of many taxa rather than any large differences in particular species (SIMPER).

Figure 3.12 (over page). Plots of two-dimensional SSH MDS ordinations of pools based on differences in composite pool fauna ($\log_{10} (x+1)$ abundance, following

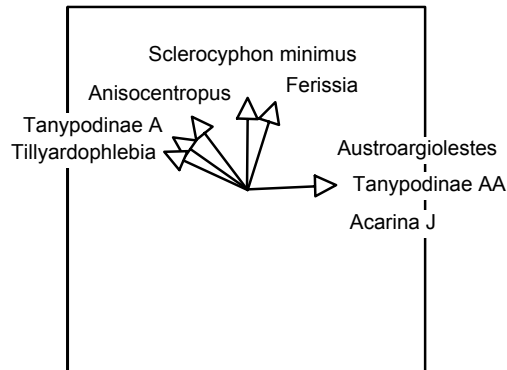
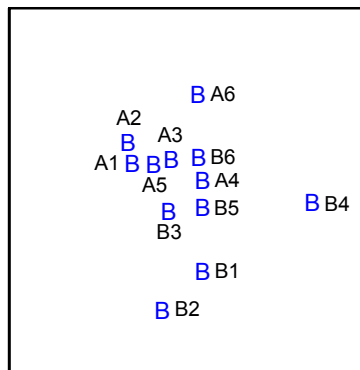
removal of rare taxa). Independent ordinations were performed for each sampling occasion and these are presented. All ordinations were rotated to match the structure of the sampling occasion 9212 ordination. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.8 or greater. Abbreviated taxon names are explained in Appendix II.

Stress values for the ordinations in order of sampling occasion were: 0.12, 0.16, 0.11, 0.18.

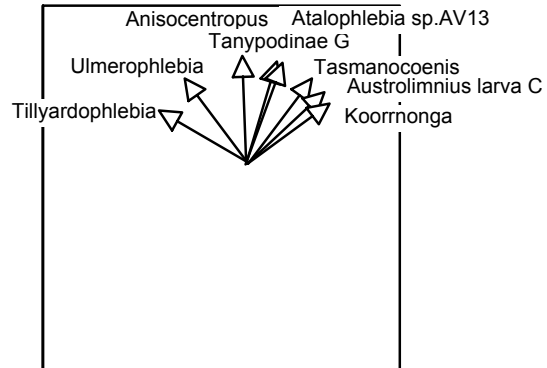
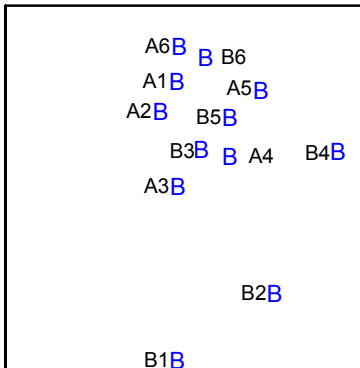
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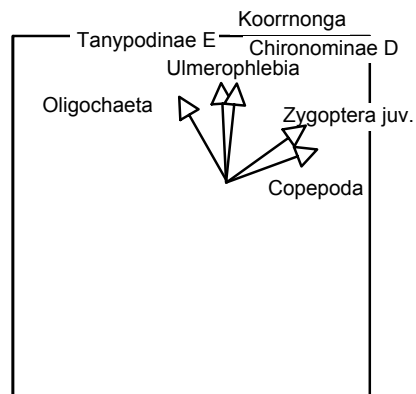
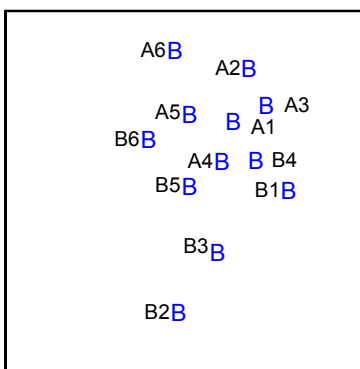
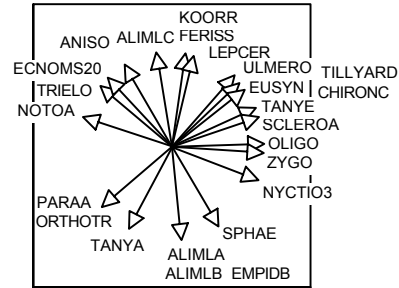
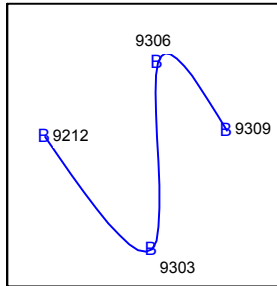


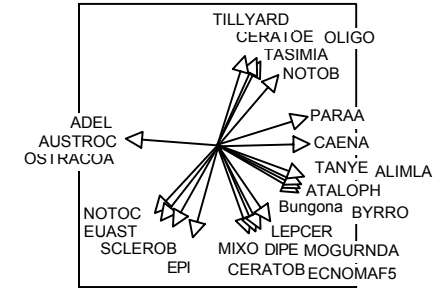
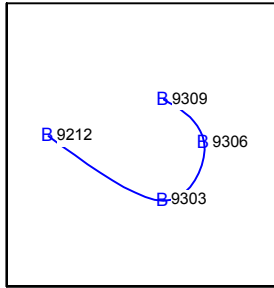
Figure 3.13 (over page). Plots of two-dimensional SSH MDS ordinations of sampling times based on differences in composite pool fauna ($\log_{10} (x+1)$ abundance, following removal of rare taxa). Independent ordinations were performed for each pool and plots of these are presented. All ordinations were rotated to match the structure of the pool A1 ordination. Consecutive sampling times are connected by lines on the plots to indicate the temporal trajectory of faunal change in each pool. Correlation vectors for taxa are presented for those with significant correlation coefficients of 0.95 or greater. Abbreviated taxon names are used to fit the large number involved into a small space and these are explained in Appendix II.

Stress values for the ordinations in order of pools were: 0.10, 0.10, 0.12, 0.13, 0.14, 0.10, 0.09, 0.11, 0.14, 0.13, 0.11, 0.14.

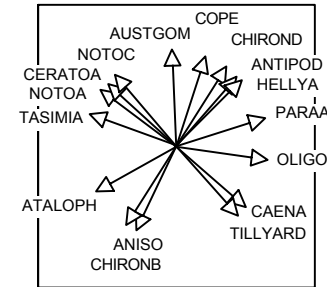
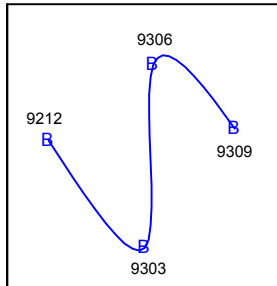
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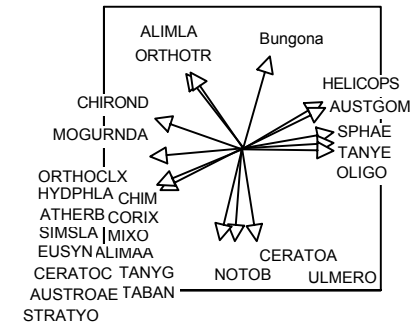
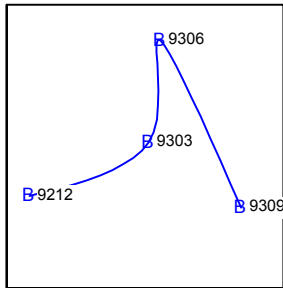
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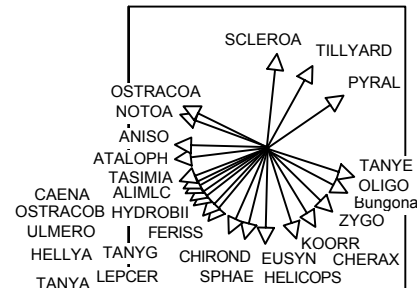
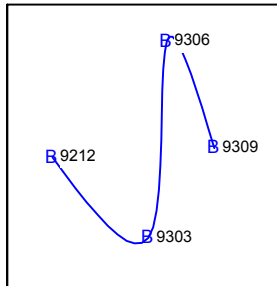
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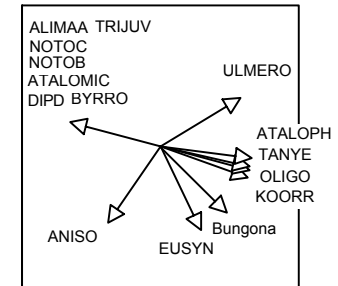
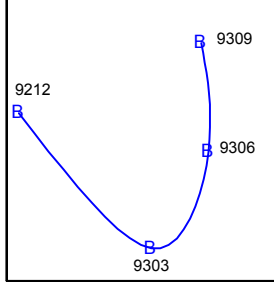
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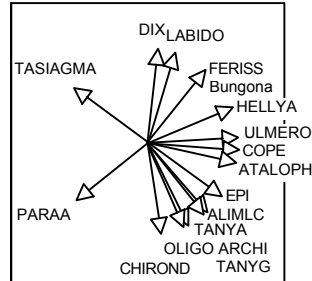
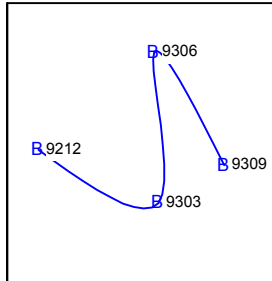
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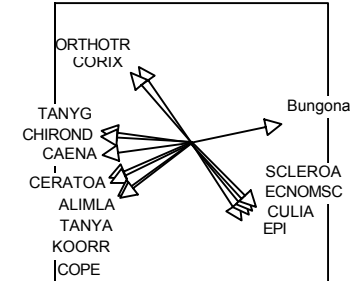
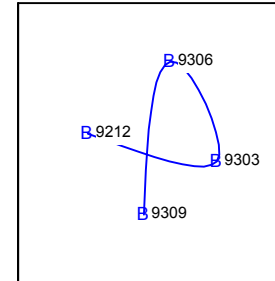
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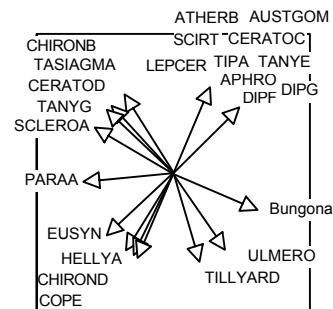
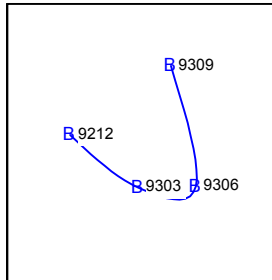
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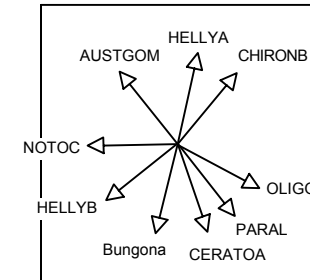
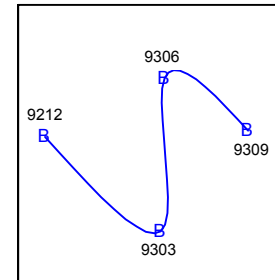
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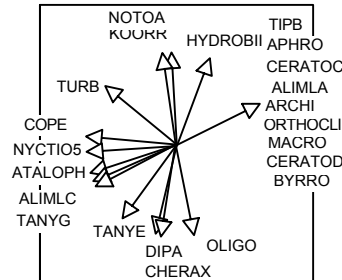
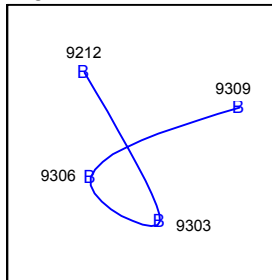
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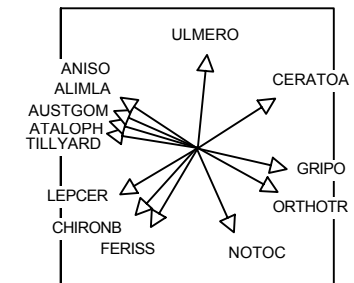
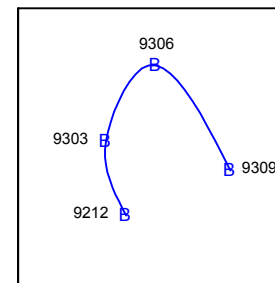
B5



B3



B6



c) Environmental variation associated with samples

Six PCA factors (Table 3.20) accounted for 85% of total variation in environmental variables calculated in association with composite samples. Of this 65% was associated with spatial variation and 38% with temporal variation. Most of the spatial variation was associated with the size and organic matter content of pools, the particle size composition of gravel samples and the organic matter content of litter samples. Most of the temporal variation was associated with the organic matter content and particle size composition of gravel samples, the organic matter content of litter samples, the size and organic matter content of pools, stream discharge and seasonally fluctuating factors (temperature, pH and photoperiod).

d) Links between environmental and faunal variation

Almost none of the variation in composite pool fauna could be related to measured environmental variation (Table 3.20). None of the environmental factors considered, and thus none of their associated environmental variables, explained any of the observed spatial variation in composite pool fauna. Relationships between temporal variation in fauna and environmental factors were also absent in most replicates. There was a high degree of variation between replicate pools. Furthermore, as was the case with temporal variation in gravel samples, the results of randomisation tests indicated that even some very high correlation coefficients (>0.8) were not significantly different from zero. Once again these results suggest that the relationships found are likely to be influenced by chance to an unacceptable degree. This is because there were only four temporal replicates for each pool. If these strong relationships truly existed, the same factor(s) would be expected to be identified as important in many of the replicate pools. This was clearly not the case.

As a result of randomisation tests determining that most relationships were not significantly different from zero, the overall temporal variation in pool fauna explained by environmental factors was zero for most factors (Table 3.20). Factor 4 explained an average of 6% of faunal variation. This relationship was however significantly different from zero in only one of the twelve replicate pools (A3). The variables strongly loaded

on this factor (Table 3.20) varied seasonally indicating that, in one pool only, there was seasonal variation in pool fauna.

Table 3.20. Spatial and temporal composite faunal and environmental variation explained by each environmental factor. Abbreviations are explained in Table 3.2.

Factor	Associated Variables	Spatial Variation		Temporal Variation	
		% Env ¹	% Faunal	% Env ¹	% Faunal
1	(width, depth, area x area, 4 mm, 1 mm, 0.5 mm, 0.25 mm, total gravel, C, BR) +ve	58	0	20	0
2	(litter organic total, litter CPOM, pool CPOM, litter sticks, litter FPOM, litter leaves) +ve	25	0	17	0
3	(gravel organic total, gravel CPOM, gravel FPOM, gravel leaves, gravel sticks) +ve	9	0	16	0
4	(temp, phot, rain) +ve, (pH) -ve	0	0	24	6
5	(discharge, min flow) +ve	0	0	16	0
6	(length, B) +ve	8	0	7	0
Total	---	100	0	100	6

¹ Values for environmental variation are expressed in terms of the total variation explained by the 6 PCA factors used (85%). The remaining 15% of total variation remains unattributed

3.4 Discussion

3.4.1 Pool Fauna

The macroinvertebrate fauna of the study streams was diverse, with 68 families recorded during this study. This is very high with respect to many streams in Queensland. The family-level richness of individual pool samples recorded from this study ranged from 17 to 38 with a median of 26 taxa. In comparison, the richness of pool samples collected from numerous other streams throughout Queensland ranges from 2 to 38 with a median of 15 taxa and the richness of pool samples from other streams in the Brisbane River catchment ranges from 4 to 31 with a median of 18 taxa (Queensland Department of Natural Resources, Freshwater Biological Monitoring Unit, *unpublished data*).

As well as displaying a high family-level diversity, the macroinvertebrate fauna of the study streams also included several taxa that have very limited distributions within Queensland. These include the Trichopteran families Antipodoecidae and Tasimiidae, the Chironomid sub-family Aphroteniinae and the Parastacid genus *Euastacus*. Several species of Leptophlebiidae are known only from the Conondale Range area including the study streams (John Dean, *pers comm*, 1999).

The pool of taxa available as potential colonists of the study streams consists of all species that pass through basin/watershed environmental filters for the region (Poff, 1997). As both study streams are in the same basin, they share key basin level attributes such as climate, vegetation geology, evolutionary history and zoogeography (*see* Chapter 2). It is reasonable to assume they thus share a common pool of potential taxa.

Many of the taxa recorded from this regional pool occur within south east Queensland typically only in undisturbed, heavily forested, upland streams with predominantly rocky beds (Queensland Department of Natural Resources, Freshwater Biological Monitoring Unit, *unpublished data*). Examples of such taxa include the Coleopteran families Psephenidae, Elmidae, Scirtidae and Ptylodactylidae; Plecoptera of the families Gripopterygidae and Eustheniidae; Odonata of the families Synlestidae, Diphlebiidae and some genera of Aeshnidae and Corduliidae; Megaloptera of the family Corydalidae; Trichoptera of the families Polycentropodidae and Helicopsychidae; Ephemeroptera of the family Ameletopsidae and most genera of Leptophlebiidae and Diptera of the families Dixidae, Stratiomyidae, Athericidae and Empididae.

Other macroinvertebrates commonly present in study stream pools are taxa that range widely throughout Queensland and occur in many streams. Examples of these include the Hemipteran families Corixiidae, Notonectidae and Veliidae; the Coleopteran family Dytiscidae; the Trichopteran family Ecnomidae and the Ephemeropteran families Baetidae and Caenidae.

3.4.2 Valley/Reach Level Environmental Filters

There were significant faunal differences between the two study streams for all of the habitat types examined on at least some sampling occasions. Differences between the

streams indicate that landscape filters had some influence on stream fauna at the valley/reach level. The magnitude of difference between streams was smaller than the differences between habitat types. Comparison of faunal composition with a nearby, but physically different stream (Branch Creek, dominated much more by bedrock and with far fewer small pools), indicates that the magnitude of faunal differences between streams is not directly linked to the perceived level of physical difference between the streams (*unpublished data*). Given the limited replication at this scale, it is difficult to isolate which environmental factors were acting as valley/reach filters. However many factors can be ruled out, as they were found to have no influence on fauna at the pool level. The magnitude of variation in these factors at the pool level was similar to or greater than that at the stream level. It is unlikely that environmental variation of equivalent magnitude could be responsible for the differences observed in fauna between the streams yet be irrelevant at the pool level. For example, differences between the streams in gravel fauna were correlated with differences between the streams in the mean mass of gravel collected but the mean mass of gravel collected explained none of the spatial or temporal variation in gravel fauna between pools. Differences between the streams in discharge one month before sampling were correlated with differences between the streams in sweep sample fauna. Once again, this variable explained none of the spatial or temporal variation in sweep sample fauna at the pool scale.

These results support the general observation of Hawkins *et al.* (2000) that within the hierarchy of environmental filters proposed by Poff (1997), larger scale environmental features (*i.e.* stream scale) account for substantially less biotic variation than local features (*i.e.* habitat type). However, stream scale features explained more faunal variation than pool scale features, which contradicts this generalisation.

3.4.3 Habitat Level Environmental Filters

There were significant differences in the faunal composition of the different within-pool habitat types examined. Of the three spatial scales examined, (stream, habitat and pool), habitat type had the greatest influence in determining assemblage structure.

What is portrayed as “habitat” differences here to some extent may be due to the different sampling methods employed. Habitat types were well defined as part of the stratified random sampling design utilised. Location within the pool, water depth and in some cases particle size ranges, were kept standard for all samples. This may have accentuated faunal differences between the habitat types. For instance, fauna inhabiting the gravel-pebble matrix surrounding cobbles may be intermediate between the defined cobble and gravel habitat types sampled. Furthermore, the logistical compromises of the sampling methodologies employed in order to minimise the destructive influence of sampling upon faunal assemblages, are likely to have further exaggerated faunal differences between the habitat types. The prime example of this is with the fauna collected by sweep samples. Many of the small and relatively cryptic taxa typical of cobble, gravel and leaf litter samples were also collected in sweep samples but were not identified or enumerated as part of the sample. Sweep samples concentrated on the larger and more mobile taxa. As a consequence of this, the fauna of sweep samples appears to be more different from the other habitats than it actually is. In a similar vein, the fauna of boulders and bedrock is actually more similar to that of cobbles than indicated from the samples. Areas of boulder and bedrock sample sometimes included mayflies of the families Baetidae and Leptophlebiidae that could not be collected by the hand picking procedure employed. These are taxa that were commonly recorded from cobbles. While the effects of sampling methodologies may have exaggerated the magnitude of faunal differences between habitat types, it is unlikely that they seriously altered the nature of the differences.

It appears that the attributes of habitat type acting as environmental filters at this level are largely related to the predominant size class of sediment forming the substrate. This is in accordance with the long established view that substrate is an important physical determinant of biota (*e.g.* Flecker and Allan, 1984). The presence of a surface film on the water is obviously an important environmental filter influencing pneustonic taxa. Substrate particle size may exert influence on the fauna in several ways. Available food resources in habitats dominated by coarse substrates are quite different from those dominated by fine substrates. On boulders and bedrock, epilithon is the primary source of food available to fauna and the taxa that inhabit these habitats are predominantly grazers (Negus, 1995). The predominant food resources available in gravel habitat are

both coarse and fine particulate organic matter and most taxa here are collectors and shredders. Some epilithon is undoubtedly present on the surface of the gravel but in quantities much smaller than the particulate organic matter. Cobbles can be considered intermediate in that epilithon is the primary resource available on the upper surface of the stones, while particulate organic matter (POM) is usually present either under the stones or in the area closely surrounding the stones. In fact, the presence of POM may be an important environmental filter *per se*, as it is absent from only pneuston, boulder and bedrock habitats and these are widely separated from the other types in terms of faunal composition.

Another factor correlated with substrate size is disturbance frequency. The size and frequency of flood events necessary to mobilise the substrate is much lower for gravel than for cobble and in turn boulders. Given the steep slopes of the study streams (1:12.6, 1:8.9, *see* Table 2.1) gravel substrates could be mobilised by depths of flow of only a few centimetres and leaf litter patches may be disturbed by even lower levels of flow (Lancaster and Hildrew, 1993a). Spates with this level of flow are likely to occur often following heavy rainfall events such as thunderstorms, a common feature of the climatic regime of the study area. However, many gravel patches, including those sampled, may be protected from small flood events in “dead spots” downstream of larger substrate elements (*see* Bond *et al.*, 2000). Additional gravel can be added to protected patches during these small flow events, and this too may act as a source of disturbance to the fauna (Matthaei *et al.*, 1999). At the other end of the substrate spectrum, crevices in bedrock are likely to act as faunal refugia during even the harshest of discharge events.

Species traits of taxa that favour different habitat types may reflect their susceptibility to disturbance. Many of the taxa living in gravel and litter patches for example, are small species with short life histories probably measured in days to weeks. This strategy may be required to persist in a habitat type subject to frequent disturbance (Townsend *et al.*, 1997). However the Trichopteran fauna typical of boulders and bedrock have longer life histories stretching to months, perhaps reflecting the more infrequent nature of disturbance in these habitat types (Bunn, *unpublished data*).

However, comparison of faunal samples collected shortly after a large and physically destructive spate in the study streams revealed no significant change in assemblage characteristics from samples described in this chapter and only minor abundance reductions in a few taxa (Marshall, *unpublished data*). This indicated that all common taxa were resistant to spates and persisted in pools despite the absence of specific resistance traits in some. At the scale of streams, the pools themselves appear to thus represent faunal refugia to disturbance from spates.

Another selective force associated with the faunal gradient between coarse and fine substrates is the level of available shelter from predation. Animals living on boulders and bedrock are confined to the rock surface where the only available shelter is in pits and crevices. The caddisflies common in these habitats have their own shelter in the form of cases. The fauna of cobbles are often able to shelter beneath the stone as well as in pits and crevices on its surface. Animals that populate gravel and leaf litter habitats live not only on the surface but also within the substrate, where they gain protection from predation.

3.4.4 Pool Level Environmental Filters

Whereas habitat level differences in fauna were strong and obvious, influences of pool level environmental attributes on faunal composition within habitat types and between pools were almost absent. Faunal differences between pools were inevitably recorded in both space and time and were large (*sensu* Humphrey *et al.*, 1997) in all habitat types analysed, but were apparently random with respect to measured environmental variation. Some factors were identified as important determinants of fauna in some pools and at certain times, but there was no consistency between spatial or temporal replicates. Overall, none of the environmental parameters measured adequately explained pool level variation. This finding is contrary to the concept that prevailing environmental conditions determine the composition of stream fauna (*e.g.* Diamond and Reice, 1985).

Wolda (1981) demonstrated that when random samples of fewer than 100 individuals were drawn from a simulated assemblage of 100 000 individuals representing 150 to 750 species, the Bray-Curtis similarity between samples was less than 1. The measure

was thus indicating that the samples were different from each other. Some other indices were less likely to demonstrate such a difference. This can be interpreted as the sample size must be large enough for the associations to be reliably estimated and consequently in this case constitutes a sampling error issue rather than a problem with the suitability of the Bray-Curtis index. If Wolda's random samples really were different from each other due to random sampling error, then the Bray-Curtis index was sensitive to such differences whereas some of the other measures were less sensitive. This property has been considered as a positive characteristic of the Bray-Curtis index (see Cao *et al.*, 1997).

The Bray-Curtis association measure was used for this study for a number of reasons. Faith *et al.* (1997) reported that the Bray Curtis association measure was one of a number of measures that gave the most robust and effective ordinations in reference to ecological data. It is a very commonly used measure in stream ecological research with numerous examples in the literature (Cao *et al.*, 1997). It has important characteristics that make it ecologically relevant and justify its widespread application. Firstly samples with shared absences for particular taxa are not considered as similarities and secondly, differences in small abundances of a taxon are weighted over differences in large abundances. For example two samples with 1 and 5 individuals of a taxon would be considered more different than samples with 1001 and 1005 of the taxon (Faith *et al.*, 1997; Belbin, 1995). Finally, it is sensitive to changes in sample taxon composition and relative abundance and shows a higher capacity to discriminate between samples than some other indices others have recommended (see Cao *et al.*, 1997). Importantly, these characteristics were relevant to the data investigated in this thesis.

The key issue raised by the work of Wolda (1981) and Cao *et al.* (1997) in relation to the results of this study can be interpreted as whether the samples collected were representative of the actual faunal assemblages in the pool habitats sampled or alternatively, did random sampling error mask the true assemblage structures? I suggest, for a number of reasons, that the samples collected were indeed representative of the actual faunal assemblages.

In Wolda's (1981) simulation experiment sample sizes of less than 100 individuals from a population of 100 000 were identified as problematical due to sampling error. This equates to sample sizes of 0.1% of the total number of individuals in the actual assemblage. In this study, samples from two habitat types (cobble and general pool) consistently contained fewer than 100 individuals. However, when estimates are made of the total assemblage sizes by patch weighting for these habitat types (see Section 3.2.3), in almost every case samples represent far in excess of 0.1% of the total assemblage size (mean values were 0.5% for cobble habitat and 12% for general pool habitat). Wolda (1981) also observed that the effect of sample error with less than 0.1% of the assemblage total number of individuals was reduced where diversity is low. The diversity of cobble and general pool habitats recorded here was 46 and 37 taxa respectively. This is substantially lower diversity than the 150 to 750 taxa Wolda utilized in his simulations which suggests that the effect of small sample sizes would also be lower.

The data pre-treatment protocol applied in this study was specifically designed to minimise the consequences of sampling error of the type discussed by Wolda (1981) (see Section 3.2.4). Firstly, rare taxa were removed from the dataset before analysis. It is these taxa that are most susceptible to sampling error and their presence or absence in a sample can be the result of this error. Secondly, log transformation of the taxon abundances in samples down-weights the influence of abundance upon the association measure, once again reducing the influence of sampling error. Thus the data pre-treatment procedure reduced the influence of sampling error on both composition and abundance, making comparisons between samples better reflect comparisons between the sampled assemblages.

Therefore, the observed lack of spatial and temporal patterns is unlikely to be a consequence of random sampling error.

There is potential that environmental variables other than those recorded were responsible for the spatial and temporal patterns in the fauna. However, it should be noted that the variables that were recorded include those reported as being the most important habitat determinants of stream faunal assemblages, including substrate

composition, stream discharge and flow velocity and primary food resource levels (*e.g.* Cummins and Lauff, 1969; Hynes, 1970; Minshall and Minshall, 1977; Minshall, 1984; Marchant, 1988; Richardson and Neill, 1991; Dudgeon, 1992, Wright and Symes, 1999; Kay *et al.*, 1999; Turak *et al.*, 1999; Smith *et al.*, 1999; Rempel *et al.*, 2000). Some variables known to influence stream fauna are not of relevance to the study because they were consistent between pools (*e.g.* water chemistry, pollution and other anthropogenic impacts, *see* Chapter 2). Other variables with potential to influence the fauna correlate with the variables recorded [*e.g.* shear stress (Wetmore *et al.*, 1990; Bouckeart and Davis, 1998), incident solar radiation (Cummins, 1973; Bunn *et al.*, 1998)]. Siltation of pools can alter the composition of faunal assemblages (Richardson, 1985; Campbell and Doeg, 1989; Pringle *et al.*, 1993, Wood and Armitage, 1997; Wood and Petts, 1999) but siltation rates in the study streams are very low and siltation has no effect pool fauna (*see* Chapter 4). The surface structure of stones in terms of pits, cracks and texture has been shown to influence the structure of faunal assemblages living on them (Downes *et al.*, 1998a; Downes *et al.*, 2000). This was not measured, as an appropriate methodology for quantifying the surface characteristics of stones was first developed by Sanson *et al.* (1995) (Downes *et al.*, 1998a), after the data for this study was collected. It is unlikely however, that the texture of cobbles, boulder and bedrock varied greatly between pools, as all had the same base geology (*see* Chapter 2). Furthermore, this variable could not be responsible for the equivalent faunal patterns observed in gravel and sweep samples.

It is therefore considered very unlikely that any additional environmental factors could adequately explain the observed highly variable spatial and temporal faunal patterns. Almost all of the observed spatial and temporal variation in fauna at the scale of within-pool habitats was apparently independent of environmental variation. As a consequence of this apparent random spatial and temporal variation in faunal assemblages within habitat types there is no capacity to predict faunal composition from the physical nature of habitat in these pools. Patterns such as this can occur as a result of biological processes over-riding habitat-biota relationships (Bunn and Davies, 2000).

When environmental conditions are benign, resources of space and food may become limited and biotic interactions may play an important role in structuring faunal

assemblages (e.g. Lake and Barmuta, 1986; Dodson, 1987; Hildrew and Townsend, 1987; Power *et al.*, 1988, Poff and Ward, 1989). The environmental conditions prevalent during this study may be considered benign, as there were no major disturbances in the form of floods or drought. Conditions may therefore have been ideal for the development of strong biological interactions. However, no strong negative correlations in the abundances of species with similar resource requirements were identified in any of the habitat types. There was thus no evidence that competitive dominance for resources was important. Negative associations between some taxa occurred in most spatial and temporal replicates but there were no consistent patterns detected. Furthermore, there is no evidence that resources of either space or food were limited, as both algal and detrital sources were present in all pools at all times and faunal patterns were not associated with fluctuations on availability. Primary food resource levels and habitat size were not significantly associated with faunal composition in any of the habitat types. There is little evidence that competition was an important force influencing the composition of pool fauna in this study or in streams in general (Hildrew and Townsend, 1987; Dudgeon, 1992; Bunn and Davies, 2000).

Predation may have played some role in structuring faunal assemblages. Experimental manipulations of the density of the fish, *Mogurnda adspersa*, the top-level predator in the study pools, indicated that predation does have some influence upon the faunal composition of pools (Chapter 5). The effects of this predation are unpredictable, possibly stemming from the observation that fish are patchy in their occurrence and individual fish have different preferences for prey taxa. Evidence suggests that predation by *M. adspersa* increases faunal variation between pools and thus potentially lessens any apparent influence of abiotic factors upon faunal composition (Chapter 5). However, preliminary analyses of data from pools in which *M. adspersa* were naturally absent failed to identify a stronger link between abiotic factors and faunal composition than was observed in pools as reported here (see Section 3.2.7).

Strong biotic interactions, when they are present, are often distinctive and lead to predictable outcomes (e.g. Power *et al.*, 1985; Power, 1990; Hart, 1992; Closs and Lake, 1994). The presence or absence of high abundances of key species triggers the development of one community type or another. No such effects were noted in this

study. The taxa correlated with spatial and temporal patterns in faunal composition in this study were inconsistent and provided little evidence that biotic interactions were responsible for the observed patterns.

These results suggest that within a habitat type, as defined by the sampling protocol used for this study, the magnitude of spatial and temporal environmental variation was insufficient to exert a controlling influence upon faunal composition. Thus environmental filters at the level of pool could not be detected. However, evidence from other components of the study demonstrates that pool level filters can influence the abundances of some taxa (*Mogurnda adspersa* and *Paratya australiensis*, see Chapters 5 and 6). The pool level of environmental filter must therefore exist, but in comparison with the other levels is of minor importance in determining the composition of fauna at a place and time.

Even though some of the apparent differences between habitat types may be due to the different sampling methods applied (see Section 3.4.3), it is pertinent to further consider the finding that between habitat differences were large and consistent whereas there was little evidence for spatial or temporal within habitat differences. Differences between the habitat types can be considered large and fundamental. For instance cobble habitat is different from gravel habitat in every pool and at all times. The particle size of cobbles is always orders of magnitude greater than particles of gravel. It is apparent that this is the scale at which biota in the study pools perceive their world. In contrast, differences between pools and/or times in one habitat type are much smaller. The cobbles in one pool are not very different from the cobbles in all the other pools and results suggest that fauna do not perceive or at least do not respond to this scale of difference. To them it appears that a cobble is a cobble, a patch of gravel is a patch of gravel and indeed a pool is a pool. What this means in terms of the biology of the pool fauna is that as long as sufficient of the habitat type they require to feed, shelter and sustain their other life functions is present they are capable of existing in any of the study pools without discriminating between them. As all of the study pools contained all of the habitat types sampled, all pools were equally suitable as habitat. Clearly something other than the physical attributes of the pools themselves governed the faunal assemblages present in them at any time.

This is at least true of pools within each of the study streams. If however, additional pools were sampled that were not so very similar in habitat character it is likely that within-habitat faunal differences linked to habitat attributes would be apparent. Indeed, this was observed between the two streams for some habitat types even though it is not clear what attributes of habitat differed (Section 3.4.2) suggesting that quite subtle within-habitat differences can manifest a response in fauna. It is important to note that most studies in which within habitat type difference in biota between sites in response to gradients of habitat attributes have been reported involved sites that were not as similar to each other as the pools within streams used in this study.

3.4.5 *Random Recruitment*

The results of this study agree with those of previous studies that have concluded that large differences between stream biotic assemblages can occur at the scale of location relative to those at larger spatial units such as whole rivers (Downes *et al.*, 2000; Hawkins *et al.*, 2000; Li *et al.*, 2001). Evidence suggests that bio/ecoregion, (which is the equivalent of basin/watershed in Poff's (1997) landscape hierarchy), explains most of the spatial variability in assemblages of stream biota on a regional scale, but unexplained local variation is a close second (Li *et al.*, 2001). Bio/ecoregion was not considered in this study, but the fauna of the study streams is known to be distinctly different from near-by non-rainforest streams so it is likely to be important (Queensland Department of Natural Resources, Freshwater Biological Monitoring Unit, *unpublished data, see also* Section 3.4.1). Within the spatial scales considered in this study, unexplained local variation certainly had the greatest influence upon faunal spatial variability, and as we have seen this was unrelated to environmental fluctuations and could not readily be attributed to the effects of biotic interactions. Temporal variations in assemblages of stream biota at a location have generally been considered to occur as a consequence of environmental change, be it either gradual (*e.g.* drought) or catastrophic (*e.g.* cyclone or fire) (*e.g.* Bunn *et al.*, 1986; Pusey *et al.*, 1993; Humphrey *et al.*, 1997; Townsend *et al.*, 1997; Extence *et al.*, 1999; Linke *et al.*, 1999), but in this study temporal variation in fauna was large and apparently unrelated to environmental change. The mechanisms governing spatial and temporal patterns in fauna in these streams thus appear largely divorced from the abiotic and biotic drivers conventionally

considered important. The fact that the study pools were very similar in physical attributes is likely to be an important contributor to this phenomenon (*see* Section 3.4.4).

The stochastic influence of random recruitment on faunal composition offers a plausible explanation for both the spatial and temporal patterns observed in this study and evidence from population genetics studies in the area provide some support.

Stochastic processes have previously been implicated in the control of stream fish communities by Grossman *et al.* (1982). This conclusion was subsequently heavily criticised on a number of procedural grounds including sampling methodology, site selection and analytical approach (Herbold, 1984; Rahel *et al.*, 1984; Yant *et al.*, 1984). These criticisms are not directly relevant to the current study; however further conceptual criticism by Yant *et al.* (1984) of the use of the term “stochastic” and other terminology by Grossman *et al.* (1982) warrants consideration.

Grossman *et al.* defined a ‘stochastic’ assemblage as one which is not at equilibrium or which changes over time. According to this definition, all non-successional assemblages with variable structure are ‘stochastic’ assemblages. In the case of the fish assemblages that they concluded were ‘stochastic’, these changes were postulated to be in response to environmental conditions such as floods and droughts. As discussed by Yant *et al.* (1984) this use of ‘stochastic’ is contrary to its conventional accepted usage. A true stochastic process has an ultimately unpredictable outcome within a set of possible outcomes (*e.g.* the roll of a dice). Knowledge of conditions will never allow accurate prediction of the outcome. This is in contrast to a true deterministic process (as opposed to Grossman *et al.*’s (1982) use of ‘deterministic’ as the opposite of their ‘stochastic’, *i.e.* at equilibrium), where the outcome is ultimately predictable given appropriate knowledge of current or antecedent conditions (Yant *et al.*, 1984). A deterministic process may include parameters with stochastic characteristics, but this does not make it a stochastic process, as the outcomes of the process are still predictable given appropriate knowledge (Yant *et al.*, 1984). For example floods have stochastic characteristics in streams, in that aspects of their timing, magnitude and duration are unpredictable. However, the response of biota to the timing, magnitude and duration of

floods could be predictable and thus the process deterministic. The model proposed here for control of assemblage structure by random processes of recruitment, represents a true stochastic process *sensu* Yant *et al.* (1984), as the outcomes, in terms of faunal assemblage composition in a pool at any single time, were found to be unpredictable within a set of possible outcomes. This fits the stochastic 'roll of a dice' analogy.

Supply of recruits can influence the composition of assemblages and the species present at a location at any one time may be a consequence of the stochastic effects of recruitment (Underwood and Fairweather, 1989; Sale, 1990). Most stream insects have life histories involving a winged adult phase that is responsible for widespread aerial dispersal. Populations of aquatic insects have been shown to be panmictic over spatial scales of catchments, indicating that adult dispersal is indeed widespread. However, there can be a high level of genetic differentiation at the smaller spatial scale of stream reaches (Schmidt *et al.*, 1995; Bunn and Hughes, 1997; Hughes *et al.*, 1998). This has been interpreted as indicating that all individuals of a species at a particular location may be the offspring of very few adult females. Implications of such patterns are that recruitment can be very limited and at random from the aerial pool of adults, and that in-stream movement can be very limited. The stochastic nature of this low level of recruitment may explain much of spatial and temporal faunal variation in some streams (Bunn and Hughes, 1997; Bunn and Davies, 2000). Consequences of such patterns of recruitment would be random patterns of assemblage composition in space and time, similar to those observed in this system (Underwood and Fairweather, 1989; Bunn and Davies, 2000). Where this occurs, there may be very little or even no capacity to predict faunal composition from the physical nature of habitat or from the nature of biotic interactions.

Some of the taxa inhabiting pools in this study are not insects and do not disperse via aerial adults. The shrimp *Paratya australiensis* has planktonic larvae but most recruitment occurs from within a pool (Hancock and Hughes, 1999). Spates during the larval stage minimise recruitment and the impact of spates is inversely related to the size of pool in which the larvae are living (Hancock, 1995). This may account for differences between streams and pools in population densities of shrimp. The recruitment mechanisms of other non-insect taxa are not as well understood, but it is

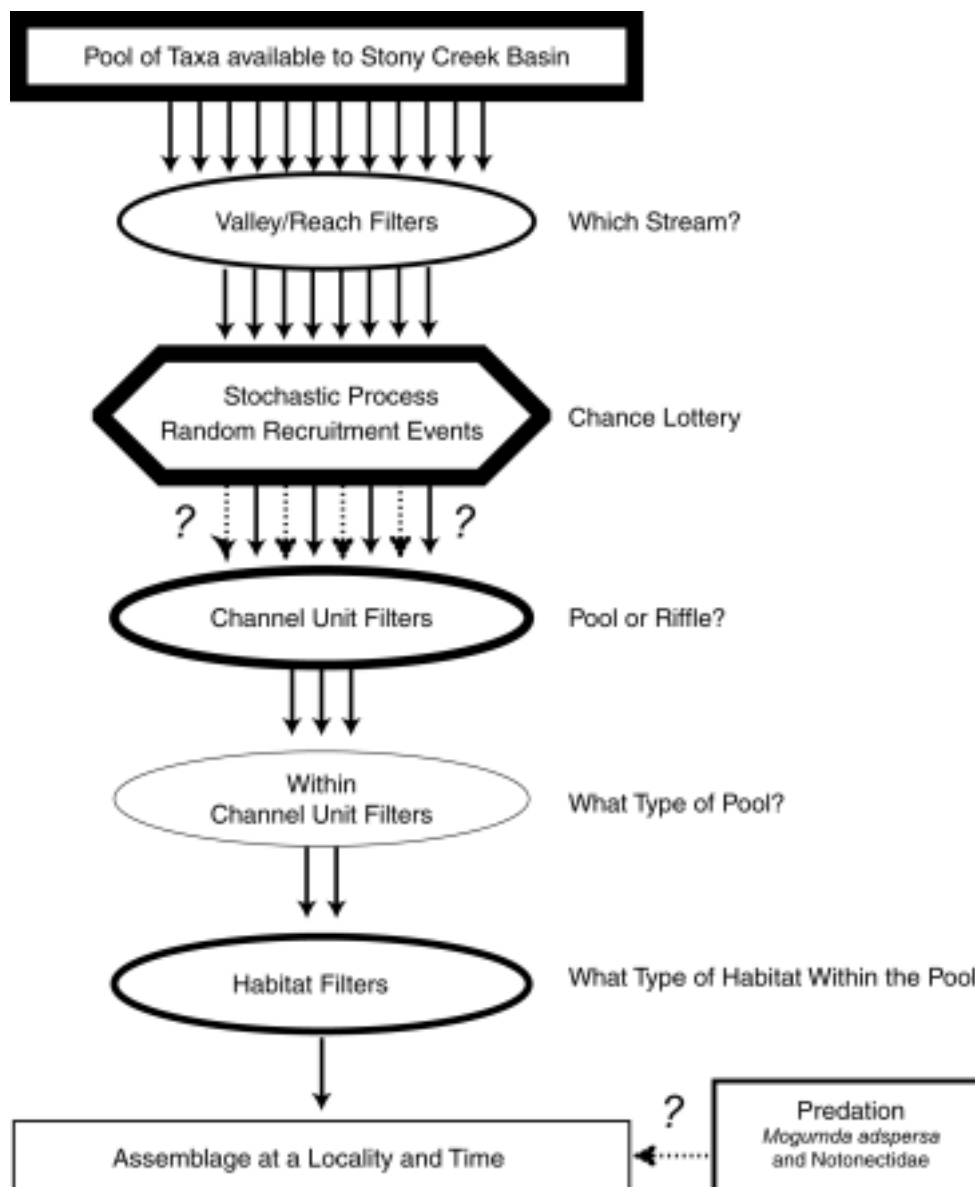
reasonable to assume that the majority of recruitment also occurs from within pools and may be influenced by spates. It may be that the recruitment success of these taxa is strongly influenced by the random timing and magnitude of disturbance by spates (see Chapter 2). However, wind or other animals may also aerially disperse the propagules of some taxa such as Acarina and Oligochaeta (*e.g.* Smith and Pearson, 1987). Further research is required to better understand recruitment processes for these animals.

The effects of random recruitment would not result in the observed patterns if there were widespread in-stream movement, as this would homogenise the fauna between locations. There are several lines of evidence to suggest that indeed in-stream movement is very limited in these streams, at least during base-flow periods. Firstly population genetic studies conducted in the study area indicate that in-stream movement is negligible in Conondale Range streams (Kingston, 1993; Schmidt *et al.*, 1995; Bunn and Hughes, 1997; Hughes *et al.*, 1995; Hughes *et al.* 1998). As a caveat to this however, it should be noted that these studies have been conducted at times of low flows. Hughes *et al.* (2000) have demonstrated that there is less genetic differentiation among populations of *Bungona narilla* after periods of higher flows compared with times of low flows, possibly implying greater in-stream movement at such times. Secondly, direct measurement of the in-stream movement of *Paratya australiensis* in the study area (Hancock, 1995; Hancock and Hughes, 1999) showed that significant movement only occurred during spates and even then was restricted to few individuals. Thirdly, stream drift rates in the study area are exceptionally low during base-flow periods (Kerby, 1991; Kerby *et al.*, 1995). The implication from this body of evidence is that movement is low during base-flow, but may be higher during high flow periods. If this were so, the fauna of replicate pools should display more homogeneity following high flow events, but this was not the case shortly after a large spate, suggesting that even when flows are elevated, in-stream movement may be minimal.

A conceptual model can be proposed as a possible explanation for the results of this study. In this model there is a pool of taxa potentially available to each habitat type. These can successfully pass through the basin, valley/reach, channel-unit type, within channel-unit, and habitat type environmental filters. All of the taxa within a habitat type pool are capable of living within the particular habitat type. Random presence of

potential taxa in the pool plus stochastic recruitment from this pool and perhaps, to a limited extent, the effects of predation, determine the composition of the assemblage at a particular location and time (Figure 3.14). Further research targeting recruitment and movement of key species at the spatial and temporal scales utilised in this study is required to confirm the role of stochastic mechanisms proposed in this model. Until such work is conducted stochastic recruitment represents only a plausible explanation for the lack of predictable biological pattern observed in this study.

Figure 3.14. Model of hierarchical landscape filters determining the composition of fauna in a habitat type within pools in Logger Branch and Unnamed Tributary (after Poff, 1997). The number of arrows represents the taxa with suitable traits at each level of the hierarchy. Taxa that lack traits suitable for passing through a large-scale filter have limited abundances at all lower levels. Stochastic processes of chance occurrence limit taxa available for recruitment to a sub-set of those with suitable traits. The final assemblage of taxa present at a particular locality and time is the consequence of these filters and the chance occurrence of potential taxa, plus the stochastic process of random recruitment from this pool of taxa. The effects of predation may modify the assemblage following recruitment but the effects of this may not be predictable. The thickness of the borders of filters indicate their relative influence in the study streams based on the results of this study except for the influence of the regional pool of taxa, which is after Li *et al.* (2001).



**CHAPTER 4: THE INFLUENCE OF THE
SHRIMP *PARATYA AUSTRALIENSIS* ON
SEDIMENT ACCUMULATION, ALGAL
GROWTH AND FAUNAL COMPOSITION
IN POOLS**

4.1 Introduction

4.1.1 *Functional importance and keystone species*

Within assemblages of organisms, certain species can be instrumental in maintaining the structural and functional organisation of the entire ecosystem, without necessarily having direct trophic effects on other species. These organisms have been termed “keystone species” or “ecosystem engineers” (Paine, 1969; Jones *et al.*, 1994). Paine’s (1969) use of the keystone of an arch as a metaphor for species that are important in structuring ecosystems has been widely applied without any precise definition, and in reality there is likely to be a continuum of species importance rather than a dichotomy between keystone and non-keystone species (Hurlbert, 1971, 1997).

Hurlbert (1971, 1997) defined the functional importance of a species as the change in productivity that would occur if it were removed from a community. The influence of species with high functional importance (commonly referred to elsewhere as keystone species, *e.g.* Mills *et al.*, 1993) can be manifest in several ways. Firstly, the effects of a species at one trophic level can influence predation and/or competition at lower levels. These effects can modify entire ecosystems and have been termed “trophic cascades” (Paine, 1980; Carpenter *et al.*, 1985). For example, the abundance of large predatory fish in pools can govern algal biomass (Power, 1990). These fish eat smaller predators, which feed on chironomid larvae, which eat algae. In the presence of large fish, the abundance of smaller predators is reduced, chironomids flourish and algal biomass is depleted. If fish are excluded, small predators proliferate, eat most of the chironomids and algae grows into dense tufts (Power, 1990). Similar cascades have also been demonstrated in systems with fewer trophic levels (*e.g.* Power *et al.*, 1985; Power, 1987).

A second means by which the activities of stream fauna can influence entire ecosystems is by indirectly providing food and nutrients to lower trophic levels (*e.g.* Cummins, 1973; McCormick and Stevenson, 1989; McCormick, 1990; Power, 1991; Richardson and Neill, 1991; *see also* Section 1.2.1).

The activities of some species can influence ecosystems by altering the physical environment (“ecosystem engineers” *sensu* Jones *et al.*, 1994; *see also* Section 1.2.4). In lakes and rivers for example, the feeding behaviour of benthivorous fish can alter the composition and abundance of phytoplankton. Resuspension of fine bed sediments by these fish increases the availability of nutrients to phytoplankton and increases turbidity. This in turn reduces the depth of light penetration, which favours species (such as certain cyanobacteria with gas vacuoles) that occur near the surface of the water (Breukelaar *et al.*, 1994; Gehrke and Harris, 1994; King *et al.*, 1997). Such changes to the quantity and quality of algal resources can influence higher trophic levels via “bottom-up” processes (McCauley and Kaliff, 1981; Mills and Schiavone, 1982; Canfield and Watkins, 1984). Habitat availability and thus the distribution and abundance of other species is also affected by these fish as their foraging behaviour can uproot macrophytes and alter the occurrence of macrophyte beds (Fletcher *et al.*, 1985).

4.1.2 The role of Atyid shrimp in tropical streams

Atyid shrimp have been found to play an influential role in tropical montane streams in Central America, where they are a dominant component of the fauna (Pringle *et al.*, 1993; 1995; Pringle and Blake, 1994; Buzby, 1995; Hemphill *et al.*, 1995; Pringle, 1996; Pringle *et al.*, 1999). These shrimp feed on fine deposited sediment by sweeping rocky substrata with the spines and setae on their chelae. This foraging behaviour has both direct and indirect effects on the ecosystem. Direct effects of feeding and foraging behaviour on other organisms include a reduction in the bio-volume of algae associated with the sediment and the physical removal of sessile Chironomidae larvae. Indirect effects of shrimp feeding stem from modifications to the environmental properties of patches with reduced quantities of fine deposited sediment and modified algal assemblages, which they create by feeding. Consequences of removing sediment include an increased biomass of epilithic algae as a result of more light reaching the substrate, and altered distribution and abundance of mobile grazers, Simuliidae and some Trichopteran larvae because of habitat modification (Pringle *et al.*, 1993; Pringle and Blake, 1994). In addition, the activity of shrimps strongly affects inter-stream differences in sediment and algal cover (Pringle *et al.*, 1995; Pringle, 1996) and they are important in retaining energy within a stream reach (Buzby, 1995).

4.1.3 *Paratya australiensis* in the study streams

The fauna of pools in the study streams are dominated in terms of biomass by an atyid shrimp *Paratya australiensis* Kemp (Decapoda: Atyidae) (Hughes *et al.* 1995, see Chapter 3) (Figure 4.1). This chapter investigates the role these shrimp play in influencing instream processes and community structure.

Figure 4.1. Photograph of adult *Paratya australiensis* with 5 mm scale bar.
(photo by Jon Marshall)



P. australiensis feed by scraping food from the substratum using the various spines and setae of the chelipeds, and by filter feeding by creating currents using the maxillae and trapping small suspended food particles in the maxillipeds. The chelae are also used to break up larger food particles and to hold pieces of food to be broken up by the mandibles (Gemmell, 1979a; 1979b). *Paratya*'s diet consists primarily of sediment with some algae, microorganisms and vascular plant tissue (Walker, 1972; Gemmell, 1979a). However, organic sediment of terrestrial origin is the only food type identified from the gut contents of individuals collected from the study streams (unpublished data) and is their primary carbon source in the study streams identified by stable isotope analysis (S. Bunn, *pers comm*). As most algae in these streams grow in adnate epilithic assemblages (Mosisch, 1995), the absence of algal cells from gut contents is in accordance with the observation of Gemmell (1979a) that *P. australiensis* does not remove firmly attached algae from rocks.

The feeding ecology of *P. australiensis* is thus similar to that of the Atyidae known to play a key ecological role in Central American streams. They are, however, smaller than the Central American shrimp, which were dominated by two co-occurring species *Atya lanipes*, (typically 80 – 100 mm long and occurring at a density of 5 – 15 m⁻²), and *Xiphocaris elongata*, (typically 30 – 40 mm long and occurring at a density of 10 – 20 m⁻²) (Pringle *et al.*, 1993). *P. australiensis* in the study pools was typically 15 – 25 mm long. In large pools in Conondale Range streams (150 m² or more) densities of *P. australiensis* approaching 250 m⁻² have been recorded (Hancock, 1995), but in the smaller study pools natural densities ranged from 5 – 20 m⁻².

4.1.4 Aims

This chapter explores the hypothesis that *P. australiensis* plays a key functional role in headwater streams in southeastern Queensland. A manipulative experiment was conducted on a whole pool scale to investigate the effects of removing *P. australiensis* on sediment cover, epilithic algal growth, faunal assemblage structure and the dispersion of grazing caddisfly larvae.

The results of Chapter 3 indicate that faunal assemblages in these pools are not obviously influenced by within-habitat environmental variation. Shrimp effects may need to be strong to over-ride confounding influences such as stochastic recruitment processes and no-response may be a likely outcome. However, only an experimental manipulation could help to resolve this issue.

The aim of this study was to test the following hypotheses:

Removal of *P. australiensis* from pools would result in:

1. Increase in the fine sediment cover on rocky substrates.
2. Decrease in the biomass of epilithic algae because of increased shading by sediment as a consequence of hypothesis 1.

In addition the following questions were addressed:

- *Does removing shrimp modify faunal assemblage structure in pools?* This may occur as a consequence of hypotheses 1 and 2 and the removal of direct physical foraging disturbance by the shrimp.
- *Does removing shrimp modify the distribution of grazers in pools?* This may also occur as a consequence of hypotheses 1 and 2 and the removal of direct physical foraging disturbance by the shrimp. Grazers may move to areas of high algal biomass and/or low sediment cover, the distribution of which may be altered by shrimp exclusion.
- *Does removing shrimp alter the composition of fauna emigrating from pools?* This may also occur as a consequence of hypotheses 1 and 2 and the removal of direct physical foraging disturbance by the shrimp which may reduce the numbers of highly mobile taxa such as *Bungona narilla* leaving pools. This species readily enters the water column when disturbed and is a strong swimmer so may leave a pool as a consequence of physical disturbance by shrimp.

4.2 Methods

4.2.1 Pool Selection

Pools to be used in the experiment were selected with intent to minimise physical variation and thus reduce potential variation in sediment deposition and removal and periphyton growth. More pools than were required were surveyed for a variety of physical attributes and multivariate analyses performed to identify the eight pools in each of the two study streams that had the least variation in this respect.

Ten pools upstream of pool A1 in Logger Branch and nine pools downstream of the waterfall in Unnamed Tributary were surveyed (*see* Figures 2.5 and 2.6) between 25 April and 6 May 1994 for the following variables (*as per* Chapter 3) Pool Length, Pool Maximum Depth, Pool Area, Pool Volume, Pool Substrate Composition, Length of Emergent Boulder and Length of Emergent Bedrock. An additional variable, termed Incident Solar Radiation Index (ISRI), was also recorded. To calculate ISRI channel width (measured as bankfull width in the middle of the pool) and compass orientation were plotted to scale on graph paper and a line was drawn across the channel in an east-

west orientation representing the approximate path of the sun. The length of this line within the channel represents the time that the channel is exposed to direct sunlight. This length was multiplied by the proportion of the channel not covered by foliage (estimated with the aid of a densiometer over the length of the channel containing the pool) to produce the ISRI.

Multivariate analyses of the data were performed for each stream using the PATN (Belbin, 1995) software package considering the above variables as pool attributes. Variables were range standardised so that all values fell between zero and one by subtracting the minimum value from each value and dividing by the range (Belbin, 1995). In order to select eight pools from each stream the two most atypical pools from Logger Branch and the single most atypical pool from Unnamed Tributary were eliminated based on a Euclidean Distance matrix calculated between all pools.

4.2.2 Experimental Design

A hierarchical nested block design was used. The first level of the hierarchy contained all 16 pools. The second level was nested within the first and consisted of two groups of eight pools. These groups were separated on the basis of stream, as it has already been shown (Chapter 3) that differences existed between these two streams.

The eight pools of each stream were divided into four blocks of two pools. Pairs of pools in each block were chosen to be as similar as possible based on physical attributes in an attempt to minimise within-block variation in sediment deposition and removal and epilithon growth. Pairs of pools were chosen based on the Euclidean Distance matrix calculated above.

One of each pair of pools was randomly assigned as an experimental treatment pool and the other as a control pool on the toss of a coin.

4.2.3 Manipulation of P. australiensis density in pools

P. australiensis were removed from pools by electro-shocking using a Smith Root Type VII backpack electrofisher while simultaneously sweeping the water with a “D” frame

net. This has been demonstrated to be an efficient and non-biased method of collecting freshwater shrimp (Penczak and Rodriguez, 1990). Pre-experimental trials indicated that this was an effective means of removing *P. australiensis* from pools and that it did not increase the mortality of *P. australiensis* or a range of other pool fauna, over a period of several hours in the field, or over a period of seven days under laboratory conditions. Trials also indicated that best results were obtained when the shocker unit was set on 200 v with a frequency of 60 Hz and a pulse width of 6 ms. These settings were used during the experiment.

The experimental treatment was carried out on the 12 and 13 September 1994 (experiment day 0). All pools (treatment and control) were electro-shocked. The order in which the streams were treated was decided by the toss of a coin and within streams, the order in which pools were shocked was randomised.

Each pass of a pool began at the down-stream end and moved to the upstream end, electro-shocking all the way. A 500 μ m mesh net attached to the anode of the electro-shocker and two 500 μ m mesh “D” frame nets were swept from side to side to catch *P. australiensis* disturbed by the shocking. *P. australiensis* and other animals caught in the nets were frequently emptied into plastic tubs filled with clean stream water where they were kept until they could be processed. Pools were shocked repeatedly, with intervals of five minutes or more between passes, until no *P. australiensis* were caught in a pass. The number of shocker units used (shocking time) to achieve this was recorded. This provided an indication of sampling effort.

P. australiensis from treatment pools were separated from other fauna, preserved in 70% aqueous ethanol and later counted. The other animals were released into the pool from which they were collected. *P. australiensis* from control pools were counted, a few at a time in a small aquarium net, and released, together with other fauna, into the pool from which they were collected. Leaf litter removed with the treatment was also returned to all pools.

Additional animals were collected to assess the effects of the electroshocking procedure upon common pool fauna. Two additional pools were sampled in Logger Branch, one

by the methods used to remove *P. australiensis* for the experimental treatment, and one by sweep sampling without electroshocking. *P. australiensis* and other common pool fauna collected by both methods were kept in a plastic tubs filled with clean stream water for several hours, after which they were assessed for abnormal behaviour and mortality. Examples of *P. australiensis* and other fauna collected using both methods were returned to aquaria in the laboratory and observed over a week. Mortality was noted during this period.

On the day following the completion of the treatment (experiment day 1), each pool was observed for five minutes in order to confirm the presence of *P. australiensis* in control pools and their absence from treatment pools.

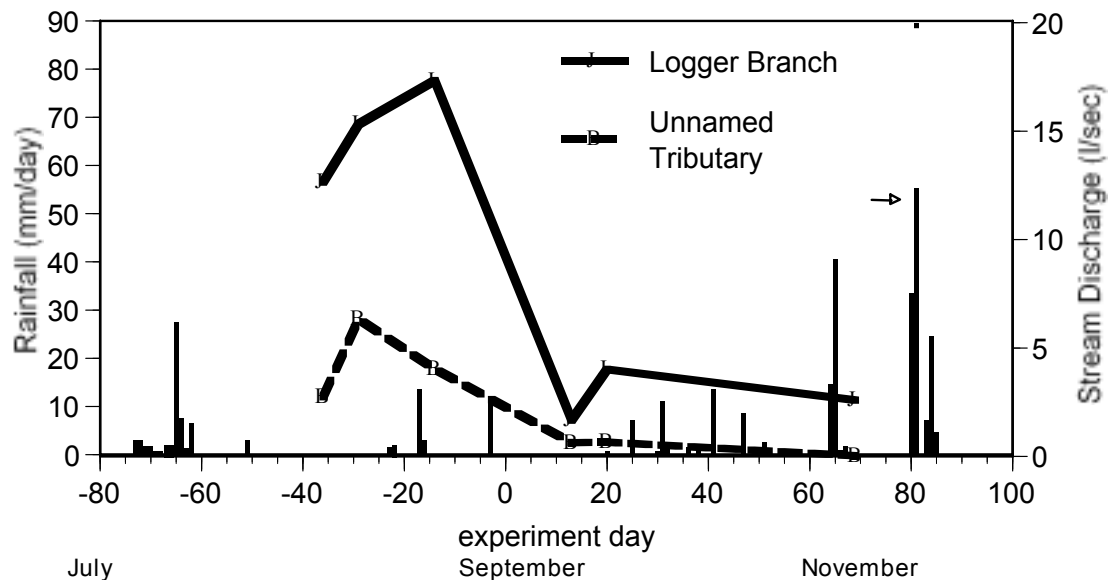
4.2.4 Effectiveness of the experimental removal of shrimp

The procedure utilised to manipulate *P. australiensis* density in pools did not result in high mortality of common pool fauna. *P. australiensis* and other common fauna removed from the pools by electroshocking during the experimental manipulation did not behave differently from fauna removed by netting and did not display increased mortality over a period of several hours in the field. *P. australiensis* and other fauna caught by the electroshocking procedure had very low levels of mortality when returned to the laboratory and kept in aquaria for one week. Mortality rates were similar to those of fauna caught by netting.

Observations made several days after the treatment confirmed that *P. australiensis* were present in all control pools but could not be detected in treatment pools and that other common taxa were present in all pools.

It was intended to re-survey all pools using the electro-shocking procedure at the completion of the experiment to quantify the number of *P. australiensis* present and confirm the effectiveness of the initial treatment. Unfortunately a sustained period of heavy rainfall after the collection of the last sample increased discharge to such an extent that small boulders and cobbles within the streams were mobilised (Figure 4.2). It is very likely that *P. australiensis* moved between pools in response to, (or were moved between pools by) this spate (Hancock and Hughes, 1999).

Figure 4.2. Rainfall recorded at Bellthorpe during the experiment (bars) and stream discharge recorded on each sampling occasion (lines). An arrow indicates the rainfall event that resulted in discharges that were likely to have triggered the movement of *P. australiensis* between experimental pools. This event prematurely terminated the experiment.



4.2.5 Sampling

Six pool samples were collected from each pool, three before and three following the experimental treatment. A single drift sample was also collected before and after treatment in each pool (Table 4.1). For reasons of practicality, samples were collected from pools in the two streams on consecutive days. The order in which the two streams were visited was determined by the toss of a coin on each occasion. Within each stream, the order in which pools were sampled was determined by their position and was thus the same on all occasions. The pool furthest down stream was sampled first, then the next upstream and so on until all eight pools were sampled. This mode of sampling was adopted so that disturbance to pools during sampling did not affect other pools before they themselves were sampled.

Table 4.1. Important dates in relation to the experiment. Experiment day 0 was the day treatment was conducted. Days before this are negative and days after positive experiment days.

Sample	Date	Experiment Day
Tile incubation	1 July	-95
Tiles into pools	22 July	-74
Tiles brushed & Sediment traps set	4 August	-39
Sample 1	8-9 August	-35
Sample 2	15-16 August	-28
Drift 1	18-19 August	-25
Sample 3	30-31 August	-13
Treatment	12 - 13 September	0
Sample 4	26-27 September	14
Sample 5	3-4 October	21
Drift 2	10-11 October	28
Sample 6	21-22 November	70

The following data were collected on each pool sampling occasion:

a) Tiles

Vitrified silicon tiles (Ariostea Mono (Italy) Vitrostone P358 “Torea” 300 mm x 300 mm floor tiles) were selected to resemble the colour of stream rocks as closely as possible. They were shot-blasted so that their texture also resembled stream rocks and cut into quarters so that each resulting tile measured 150 mm x 150 mm (surface area 22500 mm²). They were scrubbed to remove remnants of shot and immersed in running water in the laboratory for seven days to leach out potentially toxic soluble compounds. On experiment day -95, one hundred tiles were placed into a pool in Unnamed Tributary, which was not being used in the experiment, to incubate periphyton. On experiment day -74 the tiles were removed from the incubation pool, rinsed in stream water to remove any sediment which may have accumulated and picked clean of fauna. They were stored in plastic tubs filled with stream water while this procedure was carried out to prevent them from drying and desiccating. Six tiles were randomly selected and transported in plastic bags with a little stream water to each of the experimental pools. Tiles were placed horizontally, directly onto the bed of the pools at spots that were 250 mm to 350 mm deep and at least 2 m downstream of the pool inflow and 1 m upstream of the pool outflow. On experiment day -39 tiles were brushed *in situ* with a soft bristled paint brush, to remove any sediment which may have accumulated

on their surfaces. This set the accumulated sediment cover to zero before the collection of the first samples.

On each sampling occasion, a single tile was randomly selected from each pool. Tiles were lifted into submerged, open “zip-lock” plastic bags containing a little stream water and no air. This was done very carefully with the tiles kept horizontal to ensure none of the sediment settled onto the tiles was disturbed until they were inside the plastic bags. Once inside, the bags were sealed and lifted out of the water. Sediment was washed off the tiles by rinsing the water in the bags back and forth over their surface ten times. Tiles were then removed from the bags and any fauna on them was picked off using forceps and preserved in 70% aqueous ethanol in labelled vials. The water and agitated sediment left in the bags was poured through a 250 µm mesh sieve into labelled plastic bottles. The bags were rinsed several times with stream water to ensure that no sediment remained in them and the rinse water poured through the sieve into the bottle. Any animals trapped on the sieve were added to those picked from the tiles. Sediment which may have been trapped on the sieve was rinsed back into the bags with a little more stream water and then poured into the bottles. Tiles were then labelled and sealed into plastic bags with enough stream water to keep them moist. Bottles and tiles were kept cool and in the dark until they were processed in the laboratory.

b) Sediment Traps

Sediment traps consisted of straight-sided glass vials 75 mm high with an internal diameter of 24 mm (area of mouth 452.4 mm²). Vials were attached, using rubber bands, to 300 mm lengths of rigid galvanised wire. One of these sediment traps was set in each experimental pool on experiment day -39 by forcing the wire into the streambed so that the vials were orientated vertically with their bases resting on the bed. They were positioned using the same criteria as tiles. On each sampling occasion sediment traps were removed from the pools after carefully inserting “pop top” caps into the vials *in situ* and new traps were set .

Removed traps containing sediment samples were labelled and kept cool until they were processed in the laboratory.

c) Cobbles

On each sampling occasion, 3 cobbles from each pool were randomly selected and processed using the methods described in Chapter 3. Fauna and epilithon were sampled, and cobbles returned to the stream.

d) Drift Samples

A drift net with 250 μm mesh and a glass vial as a cod-end was set downstream and as close as possible to the outflow of each pool on two occasions (Table 4.1). The bottoms of the nets were in contact with the stream substratum and the tops above the surface of the water, so that they would collect not only animals drifting in the water column, but also animals moving downstream along the surface of the stream bed. The samples collected were therefore not drift samples *sensu stricto*, but will be referred to as such for the purposes of this study.

The nets were set for approximately 24 hours on both occasions. The cross-sectional area of the submerged portion of the opening of the nets was calculated and the flow velocity of water entering the nets was estimated by averaging five readings of the time taken for a coloured liquid (milk) released into the water in front of the net, to travel a known distance. Cross sectional area and velocity were used to calculate the volume of water passing through the nets in a given time. This was multiplied by the time the nets were in position, resulting in calculation of the volume of water that passed through the nets during the sample (Table 4.2).

At the completion of the sample, nets were lifted from the water and several buckets of stream water, which had been filtered through a 250 μm sieve, were poured into the openings to wash all of the contents of the nets into the cod-ends. The contents of the cod-ends, including the samples of fauna, were poured into a 250 μm sieve and transferred with a spatula into labelled vials of 70% aqueous ethanol. Drifting fauna were identified and counted in the laboratory. The abundance data of fauna collected by the nets were divided by the volume of water that the nets had sampled. Abundances of

fauna were expressed as number of animals per 100 m³ volume of water to standardise between nets.

Table 4.2. The velocity of water flowing into each drift net when set and the total volume of water flowing through each net during the period it was set for samples before and after the shrimp manipulation. Abundances of the fauna collected in the nets were standardised and expressed as number of animals per 100 m³ volume of water. Pools with a “L” prefix were in Logger Branch and those without in Unnamed Tributary.

pool	experiment day -25		experiment day 28	
	velocity m sec ⁻¹	Volume m ³	velocity m sec ⁻¹	Volume m ³
15	0.18	458.30	0.11	142.82
14	0.17	298.03	0.02	26.37
1	0.01	51.00	0.04	62.25
3	0.50	491.83	0.30	385.12
4	0.03	146.89	0.18	179.84
5	0.03	168.18	0.06	146.99
6	0.07	173.38	0.25	697.32
7	0.12	294.60	0.02	23.40
L2	0.02	46.92	0.01	5.11
L11	0.02	37.53	0.17	265.87
L3	0.06	156.04	0.09	66.66
L5	0.02	104.32	0.25	177.02
L6	0.07	175.22	0.09	232.92
L7	0.01	21.00	0.06	57.58
L9	0.01	35.51	0.09	207.22
L10	---	---	0.03	53.02

e) Grazer Distribution

Maps of each pool were drawn based on the surveys conducted during pool selection. These indicated the locations of boulders, bedrock and patches of other habitat types. On each sampling occasion the distribution of Tasimiidae grazers (*Tasiagma ciliata* and *Tasimia palpata*?) in the pools was marked onto these maps. Both of these species spend some time out of the water (Negus, 1995), so colour codes were used to indicate whether the grazers were in the water, on the water line or out of the water.

Changes in the patterns of grazer distribution over time were assessed by comparing maps from the sampling runs. Particular attention was paid to any patterns of change in response to *P. australiensis* manipulation. In addition an index of grazer dispersion on a

linear scale ranging from 1 – 10 was calculated from each map index based on the percentage of the pool in which grazers were recorded to occur.

f) Discharge

Discharge was measured from one location in each stream on each sampling occasion using the methods described in Chapter 3.

4.2.6 Laboratory Methods

a) Tiles

On return to the laboratory, tiles were processed for chlorophyll *a* and epilithon mass. The surface and sides of the tiles were scrubbed thoroughly with a stiff, nylon-bristled brush (“Namco” Dishwashing Brush) and rinsed with 100 ml of distilled water over a plastic tray. The brush was rinsed with a second 100 ml of distilled water and this was added to the scrubblings. The scrubblings were poured into a screw-top plastic jar, homogenised by vigorous shaking and 100 ml was immediately decanted off into a beaker. This divided the sample from each tile into two equal portions. One of these was used for chlorophyll *a* mass determination and the other for measuring epilithon mass.

The procedure used to calculate the mass of chlorophyll *a* on tiles is based on that of Mosisch (1995). Samples were vacuum filtered using a Sartorius 250 ml filter apparatus (SM 16510) onto 47 mm Sartorius glass-fibre pre-filters. The filter papers were rolled with the samples on the inside and inserted using fine forceps into labelled 10ml screw-capped polyethylene centrifuge tubes containing 10 ml of 90% aqueous acetone. Samples were left overnight to extract in a dark box in a refrigerator at approximately 4 °C. They were then sonicated for five minutes in a water bath (Branson B-32 ultrasonic bath) to rupture algal cells and returned to the dark box in the refrigerator for one hour. Extraction was then considered complete. Before measuring chlorophyll *a*, samples were centrifuged at 3000 rpm for five minutes (Clements GS 150 centrifuge) to settle suspended matter which would otherwise affect absorbance readings. Supernatant was transferred from the tubes into 10 mm path length optical glass cuvettes (“Lovibond”, Tintometer Ltd.) using a clean Pasteur pipette for each

sample. Absorbance was recorded at 665 nm and 750 nm using a “Varian series 634” spectrophotometer with 90% aqueous acetone in an identical cuvette as a reference standard. The readings at 750 nm enable the chlorophyll *a* absorbance at 665 nm to be corrected for background turbidity (Lorenzen, 1967; Mosisch, 1995). Samples were acidified with two drops of 2M HCl from a clean Pasteur pipette and absorbance re-measured at the same wavelengths. Acidification degrades chlorophyll *a* into phaeophyton *a* which has a low absorbance at 665 nm. Absorbance of chlorophyll *b* and *c* at 665 nm are not changed by acidification. Thus the difference between the absorbance readings of a sample at 665 nm (corrected for background turbidity), before and after acidification indicates the amount of chlorophyll *a* in the sample (Lorenzen 1967; Mosisch, 1995). Cuvettes were rinsed several times with aqueous 90% acetone before introducing a new sample in order to ensure previous samples did not contaminate the next analysis. Calibration of the unit was checked every four samples and adjusted as necessary.

Chlorophyll *a* mass was calculated using the method adapted by Mosisch (1995) from that devised by Lorenzen (1967). It was modified here to give values in $\mu\text{g cm}^{-2}$ (Equation 4.1):

$$\text{Equation 4.1} \quad \text{Chl } a (\mu\text{g cm}^{-2}) = (26.7 [(665_a - 750_a) - (665_b - 750_b)] \times V \times 2) / A$$

where

- 665 = absorbance reading at 665 nm
- 750 = absorbance reading at 750 nm
- a = absorbance reading before acidification
- b = absorbance reading after acidification
- V = volume of acetone extract (10 ml)
- A = area of tile, 225 cm^2

The results were multiplied by two to compensate for the fact that only half of the tile scrubblings were used for the determination of chlorophyll *a* mass.

Epilithon samples were similarly filtered onto 47 mm Sartorius glass-fibre pre-filters. However, for this and all other mass determinations, the filter papers were pre-ashed at 460 °C for four hours and individually pre-weighed using a Mettler AE240 analytical balance, which was accurate to 0.01 mg.

Filter papers containing the samples were oven dried at 60 °C for 24 hours. The dry filter papers were allowed to cool to room temperature in a vacuum desiccation chamber and weighed. Samples were ashed in a muffle furnace (“Ceramic Engineering”) at 460 °C for four hours. They were allowed to cool to room temperature in the desiccation chamber and reweighed. This was the ash free mass of the samples.

The results were multiplied by two to compensate for the fact that only half of the tile scrubblings were used for the mass determinations, and divided by the area of tiles to express mass as mg cm^{-2} .

b) Tile Sediment

Samples of tile sediment were made up to a standard volume of one litre with distilled water and homogenised by vigorous shaking. A 50 ml sub-sample was immediately decanted from each and used for the determination of organic, inorganic and total mass of tile sediment. It was necessary to sub-sample in this way as the total quantity of sediment in most samples was far in excess of that which could practically be filtered and processed using available resources. Sub-samples were filtered onto pre-ashed filter papers and masses were calculated in the same way as they were for tile epilithon. The final results were divided by 1/20 the area of the tiles to calculate the mass in mg cm^{-2} .

c) Sediment Traps

The contents of sediment traps were filtered onto pre-ashed papers and organic, inorganic and total mass was calculated in the same way as they were for tile epilithon.

Sediment accumulation rates were calculated as sediment mass from the traps divided by the number of days traps were set per unit area. This information was used to

calculate the mass of sediment that could potentially occur on tiles in the absence of sediment removal, by multiplying sediment accumulation rate by time.

d) Cobble Epilithon

Epilithon samples from cobbles contained small fragments of rock which had been scraped from the surfaces of the cobbles as the samples were collected. It was not possible to distinguish the inorganic mass of epilithon from the mass of these fragments. Thus, only the organic mass of cobble epilithon samples was calculated. For this reason it was not necessary to use pre-ashed filter papers. The samples were filtered and organic mass was calculated in the same manner as it was for tile epilithon.

4.2.7 Rainfall and Discharge

There was little rainfall during the experiment and stream discharge showed an overall pattern of reduction over time in both streams (Figure 4.2). The magnitude of change in discharge was greater in Logger Branch than Unnamed Tributary.

Heavy rainfall on experiment day 81 after the completion of the final samples elevated streamflow to an extent likely to be sufficient to trigger *P. australiensis* movement between pools (Hancock, 1995). There was evidence that stream bed material at least as large as cobbles were mobilised and remaining experimental tiles were displaced and broken in both streams.

4.2.8 Data Analysis

a) ANOVA

Changes in the values of variables in response to the manipulation of *P. australiensis* density in pools were assessed by split plot Analysis of Variance (ANOVA). Statistical units were pools and factors were stream, experimental block, experimental treatment and time. The pairs of treatment and control pools were treated as blocks and nested within stream. The analysis was split into sampling times. The error term for the main plot was treatment by block within stream and for the split plot was time by treatment by block within stream. As the focus of the experiment was on the effects of *P.*

australiensis removal on differences between treatment and control pools over time, the main interest in the analysis was the time by treatment and time by treatment by stream interactions. Significant sources of variation in the analyses were considered to be those factors and interactions with $p < 0.05$. Analyses tested the null hypothesis that manipulation of *P. australiensis* density had no effect on the difference between control and treatment pools.

In analyses where either of the interactions of primary concern were identified as significant sources of variation, *post-hoc* t-tests were employed to identify at which times the differences between treatment and control pools were significant.

Separate analyses were performed for the different variables measured as part of the experiment. Variables were $\log_{10}(x+1)$ transformed prior to analysis if there was a significant correlation between their mean and variance (Zar, 1984). The following variables were considered: the rate of organic and inorganic and total rate of sediment deposition; the mass of organic, inorganic and total sediment accumulated on tiles; the mass of chlorophyll *a* on tiles; the biomass of epilithon on tiles; the biomass of epilithon on cobbles and grazer dispersal index.

Mean values and standard errors of the means of the variables subjected to ANOVA were calculated for each sampling occasion. The organic proportion of both deposited and accumulated sediment from each sample was calculated and similarly treated. These values were calculated separately for the two study streams for variables where ANOVA results indicated significant stream differences. Values were plotted to illustrate temporal change in variable values, particularly those in response to the *P. australiensis* manipulation. This aided the interpretation of the results of ANOVAs and *post-hoc* t-tests.

b) Multivariate Analysis of Faunal Patterns

For each of the habitat types sampled, rare taxa were removed and abundances of remaining taxa $\log_{10}(x+1)$ transformed as described in Chapter 3. Bray-Curtis dissimilarity measures were calculated between all pairs of samples. The matrix of dissimilarities was subjected to analysis of similarity (ANOSIM). Two-way crossed

ANOSIMs were calculated between treatment and control pools on each sampling occasion with stream as the crossed factor. Each of these analyses tested the null hypothesis that there were no significant differences between the fauna of treatment and control pools allowing for differences between streams. Where significant differences were identified, similarity percentages (SIMPER) were calculated to identify the taxa making major contributions to the differences.

For each habitat type, the mean abundance of each taxon in control and treatment pools in each stream was calculated for each sampling time. Data were pre-processed as above and ordinated in two dimensions using semi-strong hybrid multidimensional scaling (SSH MDS). Ordinations were rotated so that all were in the same orientation and plotted to indicate temporal change in mean fauna in treatment and control pools. Ordination plots illustrated the results of the ANOSIMs.

4.3 Results

4.3.1 *P. australiensis* Density in Pools

The mean density of *P. australiensis* in experimental pools was 6.68 m⁻² (se = 1.08). There was no significant difference in the pre-manipulation density of *P. australiensis* in pools between streams ($t = 0.08$, $DF = 14$, $p > 0.05$) or between experimental treatments ($t = -1.13$, $DF = 14$, $p > 0.05$). There was a strong and significant correlation between pool maximum depth and *P. australiensis* density ($r = 0.70$, $p = 0.003$), but there was not a significant correlation between density and pool area or volume when all pools were considered (area: $r = 0.24$, $p < 0.05$, volume $r = 0.32$, $p < 0.05$). However, pool L6 recorded a high density (Table 4.3) and when it was excluded there was a significant positive relationship between *P. australiensis* density and both pool area and volume (area: $r = 0.51$, $p = 0.05$, volume: $r = 0.53$, $p = 0.04$).

Table 4.3. Pool attributes and the density of *P. australiensis* recorded in each experimental pool. Pools with an “L” prefix are in Logger Branch and those without in Unnamed Tributary.

Pool	Pool Max Depth (m)	Pool Area (m ²)	Pool Volume (m ³)	<i>P. australiensis</i> Density (number m ⁻²)
1	0.70	24.3	8.71	5.78
3	0.61	38.1	12.63	1.81
4	0.80	26.6	11.51	4.7
5	1.10	28.4	13.47	9.79
6	0.80	50.4	20.00	5.75
7	0.70	33.8	12.40	3.96
14	0.60	25.5	8.34	2.16
15	0.90	46.9	18.74	12.94
L2	0.85	48.9	16.04	6.81
L3	0.50	24.2	4.79	6.94
L5	0.75	29.5	9.89	3.86
L6	1.15	24.7	10.21	17.94
L7	0.85	21.5	11.34	5.35
L9	0.75	52.2	17.18	11.28
L10	0.80	15.8	5.57	3.1
L11	0.7	25.7	6.65	5.56

4.3.2 Sediment accumulation

a) Sediment deposition rate

The rate of sediment deposition was significantly higher in control pools than treatment pools. This difference was stable over time and was not significantly influenced by the manipulation of *P. australiensis* density (Table 4.4, Figure 4.3). This result is difficult to explain, as pools were consigned to treatment and control categories at random. The rate of sediment accumulation in all pools changed over time and there were significant differences between streams and experimental blocks. Results were similar whether organic content, inorganic content or total sediment accumulation rate were considered.

The organic content of deposited sediment showed a pattern of decrease over time in both streams. There was however an increase between experiment days 14 and 21 in both streams. This increase was not obviously linked to patterns of rainfall or discharge (Figure 4.4).

Table 4.4. Analysis of variance of the rate of organic, inorganic and total sediment deposition in pools. Sediment deposition rate was $\log_{10}(x+1)$ transformed. Statistical units are pools and factors are streams, experimental blocks, experimental treatment and time. The error term for the main plot is Treatment x Block (Stream) and for the split plot is Time x Treatment x Block (Stream). Significant interactions * $p < 0.05$, ** $p < 0.001$

		Organic	Inorganic	Total
Source of Variation	DF	F Values		
Main Plot				
Treatment	1	39.59**	38.43**	40.26**
Stream	1	40.48**	34.40**	37.92**
Block (Stream)	6	16.01**	22.14**	20.91**
Treatment x Stream	1	15.86**	11.14*	12.74**
Split Plot				
Time	5	9.99**	17.35**	15.16**
Time x Stream	5	1.15	1.75	1.48
Time x Block (Stream)	30	1.01	0.82	0.95
Time x Treatment	5	0.70	0.48	0.63
Time x Treatment x Stream	5	1.15	0.57	0.68

b) Sediment accumulation

The total mass of sediment accumulated on tiles showed a significant interaction term between time and treatment (Table 4.5). This indicates that the difference between control and treatment pools changed over time. However the change was not consistent with the prediction that the sediment cover in treatment pools would increase with respect to control pools (Figure 4.5). There was no significant difference between control and treatment pools at any individual time but differences were near significant on the occasions of the first and fifth sampling times. At these two times and over all times, control pools had a greater mass of accumulated sediment than treatment pools both before and after treatment. This possibly reflects the higher sediment accumulation rate recorded in control pools. There is no evidence that removing *P. australiensis* increased the accumulated sediment cover. Results for the organic and inorganic components of sediment accumulations were similar to those for total sediment however the time by treatment interaction terms were only near-significant at the 0.05 level (Table 4.5).

Figure 4.3. Mean rate of total sediment deposition in traps in control and treatment pools on each sampling occasion in a) Logger Branch and b) Unnamed Tributary. Bars indicate the standard error of the means. The rates of both the inorganic and organic components of sediment showed very similar temporal patterns.

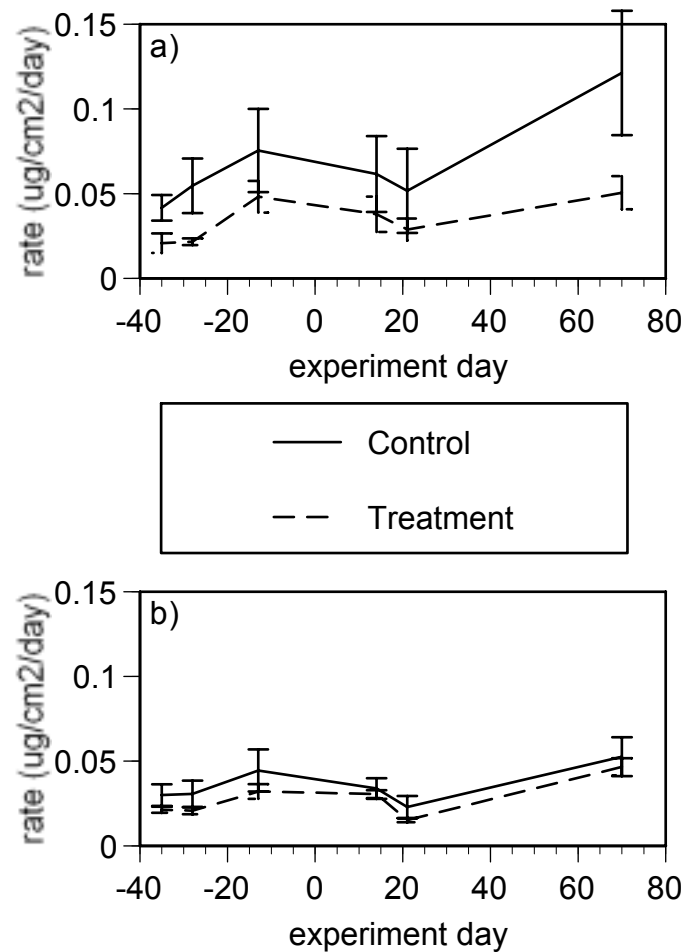


Figure 4.4. Mean organic proportion of sediment deposited in traps in control and treatment pools on each sampling occasion in a) Logger Branch and b) Unnamed Tributary. Bars indicate the standard error of the means.

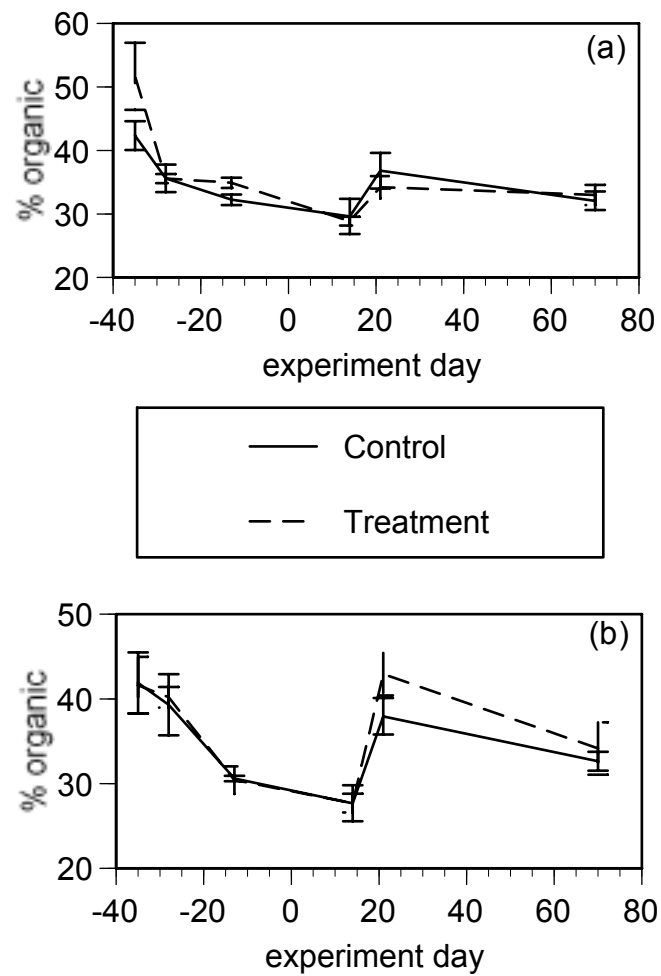


Table 4.5. Analysis of variance of the total mass of sediment accumulated on tiles in pools. Sediment mass was $\log_{10}(x+1)$ transformed. Statistical units are pools and factors are streams, experimental blocks, experimental treatment and time. The error term for the main plot is Treatment x Block (Stream) and for the split plot is Time x Treatment x Block (Stream). Significant interactions * $p < 0.05$, ** $p < 0.001$

		Total	Organic	Inorganic
Source of Variation	DF	F Value		
Main Plot				
Treatment	1	8.63*	8.39*	7.79*
Stream	1	0.07	0.03	0.07
Block (Stream)	6	5.42**	4.93*	5.47**
Treatment x Stream	1	8.72*	7.64*	9.32*

Split Plot				
Time	5	6.73**	12.57**	4.07**
Time x Stream	5	2.66*	2.24	2.72*
Time x Block (Stream)	30	1.84*	1.01	1.71
Time x Treatment	5	2.67*	2.4	2.35
Time x Treatment x Stream	5	0.82	1.76	0.73

The organic proportion of total accumulated sediment mass was more spatially and temporally variable than its counterpart in depositional sediment (Figure 4.6) but varied within a similar range of approximately 25% to 55% dry weight. This variation cannot readily be linked to patterns in rainfall or stream discharge. There is some evidence that the manipulation may have increased the organic proportion of sediment in both streams although this is more evident in treatment than control pools in Unnamed Tributary.

c) Observed vs. potential sediment accumulation

The predicted sediment cover on tiles (based on mean measured sediment accumulation rates in traps) was much higher than the observed cover in either treatment or control pools (Figure 4.7).

4.3.3 Epilithon

a) Tile chlorophyll *a*

There was no significant interaction between time and treatment for the mean mass of chlorophyll *a* on tiles (Table 4.6), indicating that removal of *P. australiensis* did not affect the mass of epilithic algae (Figure 4.8).

Figure 4.5. Mean total dry mass of sediment accumulated on tiles in control and treatment pools on each sampling occasion in a) Logger Branch and b) Unnamed Tributary. Bars indicate the standard error of the means. The dry masses of both the inorganic and organic components of sediment showed very similar temporal patterns.

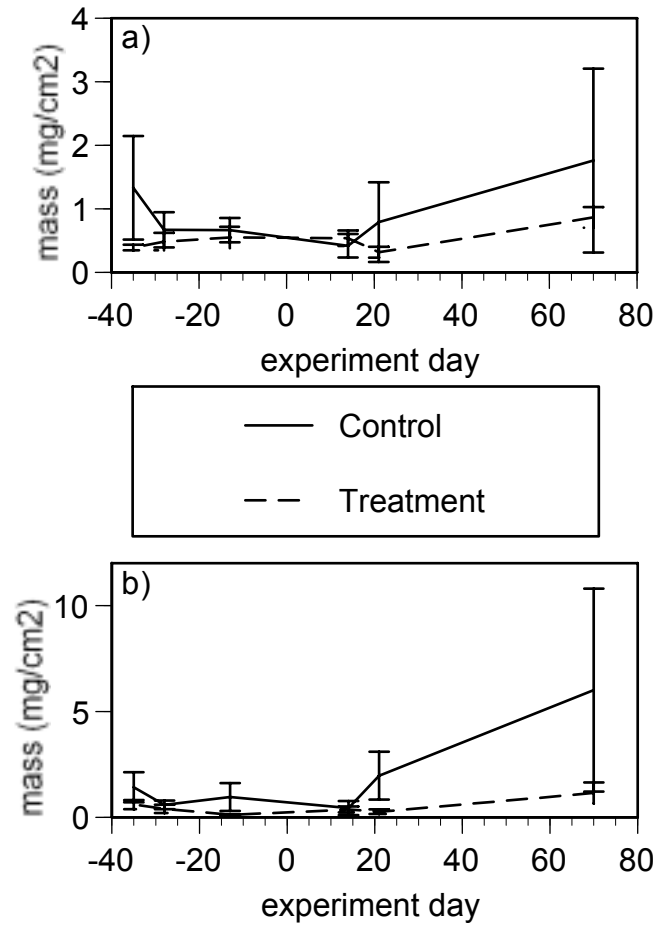


Figure 4.6. Mean organic proportion of sediment accumulated on tiles in control and treatment pools on each sampling occasion in a) Logger Branch and b) Unnamed Tributary. Bars indicate the standard error of the means.

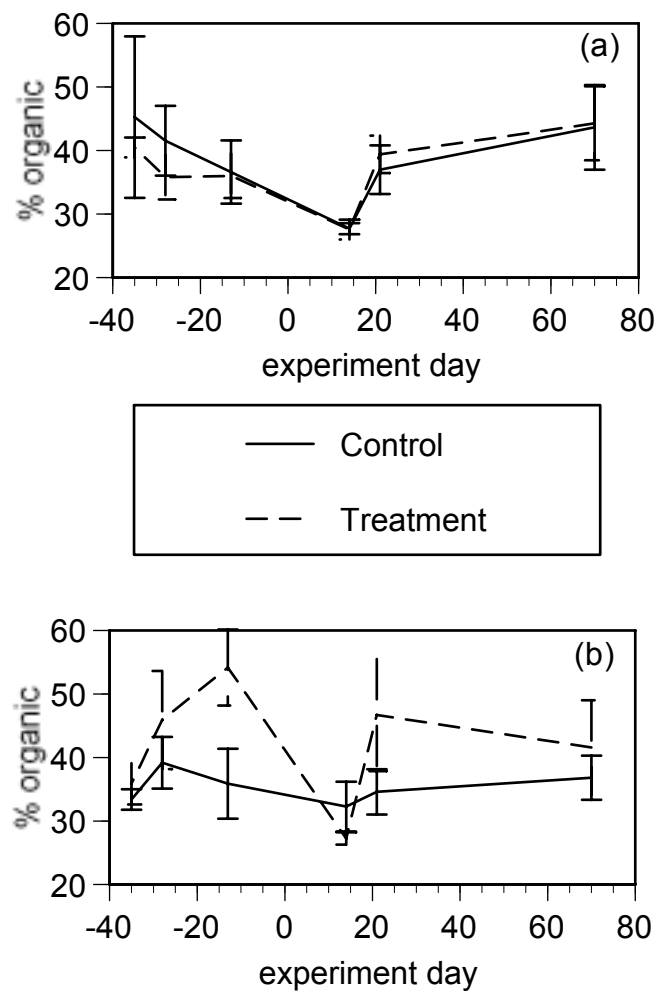


Figure 4.7. The potential sediment cover on tiles based on mean measured sediment accumulation rates and the mean observed cover in treatment and control pools. Bars represent the standard errors of the means.

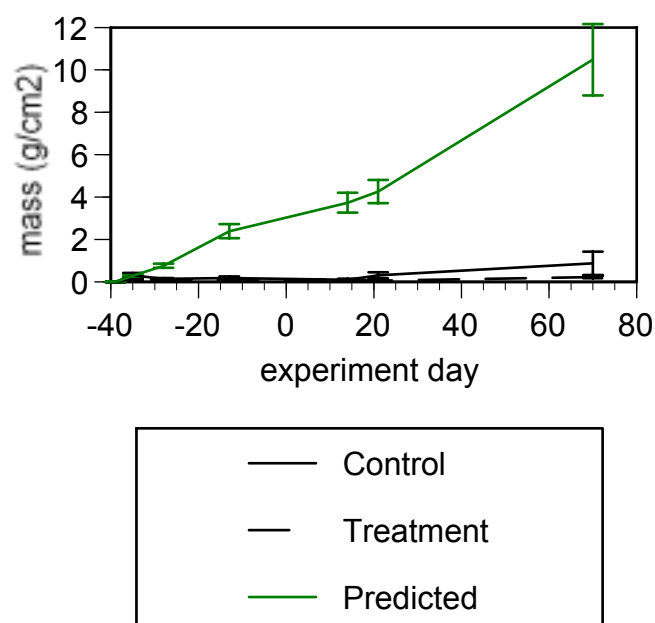
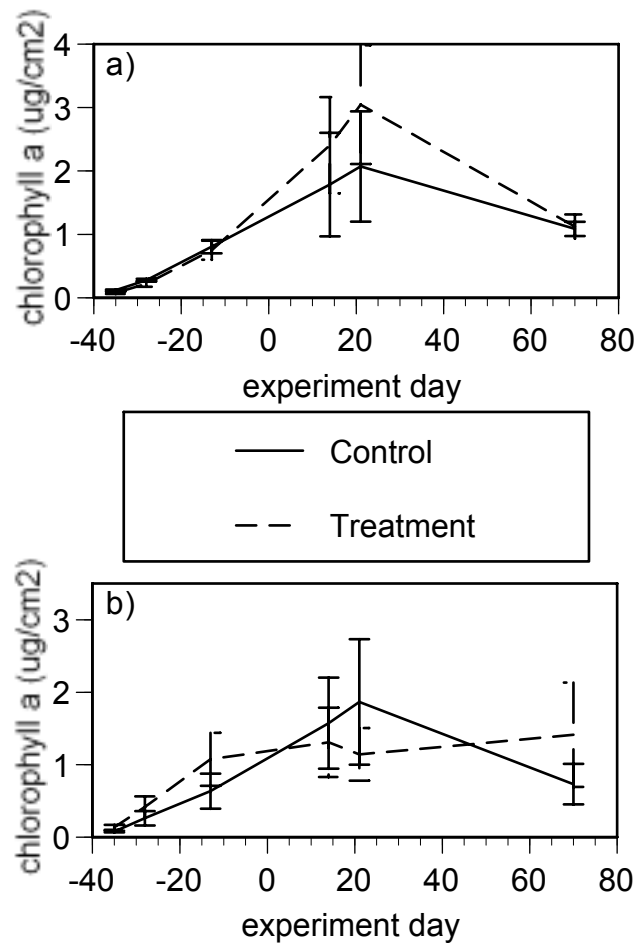


Table 4.6. Analysis of variance of the mass of chlorophyll *a* and epilithon biomass on tiles in pools. Mass was $\log_{10}(x+1)$ transformed. Statistical units are pools and factors are streams, experimental blocks, experimental treatment and time. The error term for the main plot is Treatment x Block (Stream) and for the split plot is Time x Treatment x Block (Stream). Significant interactions * $p < 0.05$, ** $p < 0.001$

		chl <i>a</i>	epilithon
Source of Variation	DF	F Value	
Main Plot			
Treatment	1	1.66	0.34
Stream	1	5.78*	0.07
Block (Stream)	6	2.88*	5.10**
Treatment x Stream	1	1.63	1.31

Split Plot			
Time	5	41.80**	31.29**
Time x Stream	5	0.73	2.23
Time x Block (Stream)	30	1.09	1.14
Time x Treatment	5	0.18	0.15
Time x Treatment x Stream	5	1.15	0.78

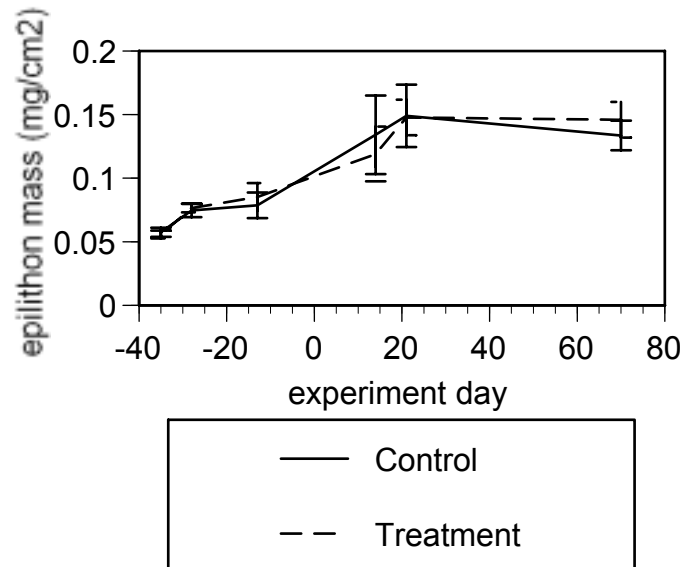
Figure 4.8. Mean mass of chlorophyll *a* on tiles in control and treatment pools on each sampling occasion in a) Logger Branch and b) Unnamed Tributary. Bars indicate the standard error of the means.



b) Tile epilithon biomass

The biomass of epilithon scraped from the upper surface of tiles changed over time but there was no significant difference between treatments (Table 4.6 and Figure 4.9). There is thus no evidence that manipulating the density of *P. australiensis* in pools altered the development of epilithon biomass.

Figure 4.9. Mean biomass of epilithon on the upper surface of tiles in control and treatment pools on each sampling occasion. Bars indicate the standard error of the means.



c) Cobble epilithon biomass

There were no significant differences between times, treatments or streams for the mean mass of epilithon scraped from the upper surfaces of cobbles in pools. There is thus no evidence that manipulating the density of *P. australiensis* in pools influenced cobble epilithon biomass (Table 4.7 and Figure 4.10).

4.3.4 Faunal Composition

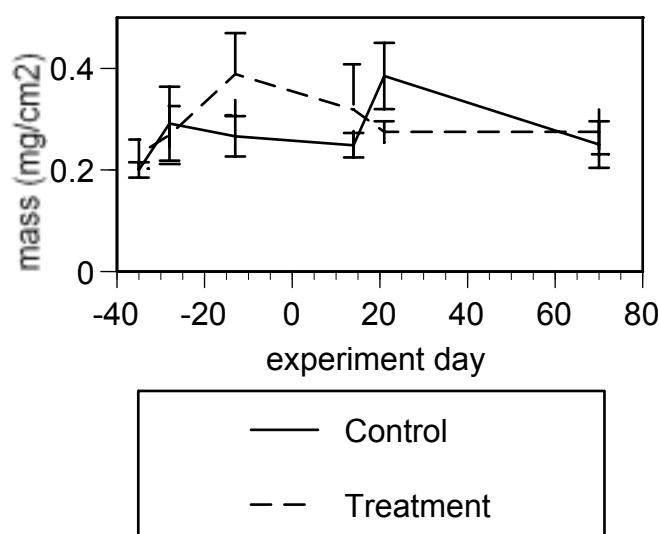
Twenty-seven taxa were collected from experimental tiles with an average of 4 taxa per tile (se = 0.2) and an average of 13 individuals (se = 1.6). However, 7 of the samples contained no fauna. Tile fauna was dominated by *Bungona narilla*, *Tasimia palpata?*, *Sclerocyphon minimus* and *Tillyardophlebia* sp AV6.

Thirty-two taxa were collected from cobbles with an average of 6 taxa per stone (se = 0.2) and an average of 28 individuals (se = 1.7). Cobble fauna was dominated by *Bungona narilla*, *Sclerocyphon minimus*, *Tasimia palpata?* and *Tillyardophlebia* sp AV6.

Table 4.7. Analysis of variance of the biomass of epilithon scrubbed from the upper surfaces of cobbles in pools. Statistical units are pools and factors are streams, experimental blocks, experimental treatment and time. The error term for the main plot is Treatment x Block (Stream) and for the split plot is Time x Treatment x Block (Stream). Significant interactions * $p < 0.05$, ** $p < 0.001$

Source of Variation	DF	F Value
Main Plot		
Treatment	1	0.54
Stream	1	0.26
Block (Stream)	6	2.34
Treatment x Stream	1	0.04
Split Plot		
Time	5	1.41
Time x Stream	5	1.49
Time x Block (Stream)	30	1.05
Time x Treatment	5	1.20
Time x Treatment x Stream	5	0.96

Figure 4.10. Mean biomass of epilithon on the upper surface of cobbles in control and treatment pools on each sampling occasion. Bars indicate the standard error of the means.

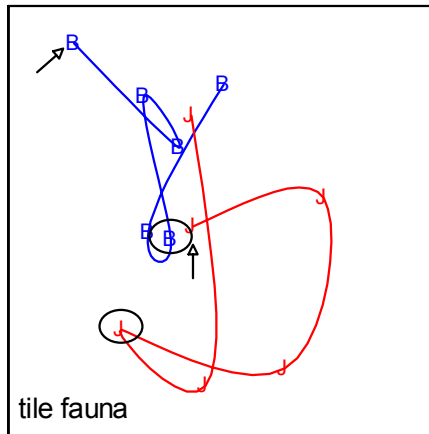


Forty-eight taxa were recorded in drift samples with an average of 9 taxa per sample (se = 0.8) and an average of 40 individuals per 100 m³ of water (se = 10). This fauna emigrating from pools was dominated by Chironomidae, Dixidae, Culicidae and *Bungona narilla*.

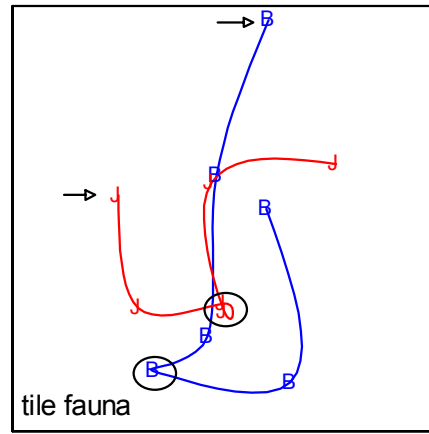
Before the experimental manipulation, there were no significant differences in the composition of fauna of treatment and control pools for any of the habitat types examined (Figure 4.11, Table 4.8). There was a significant difference in the fauna on tiles between treatment and control pools on experiment day 14. The difference was a result of higher abundances of *Bungona narilla* in treatment pools in both streams, higher abundances of *Tasimia palpata*? in treatment pools in Logger Branch, and lower abundances of *Tillyardophlebia* sp.AV6 in treatment pools in Unnamed Tributary (Table 4.9). This difference was not significant in subsequent post-manipulation samples. There were no significant post-manipulation differences in the fauna of cobbles or drift between treatment and control pools.

Figure 4.11. Ordination plots of mean fauna in control and treatment pools on each sampling occasion in Logger Branch and Unnamed Tributary. Lines join consecutive samples in each category. The first samples are indicated by arrows and the first post-treatment samples are circled.

Logger Branch



Unnamed Tributary



B control J treatment

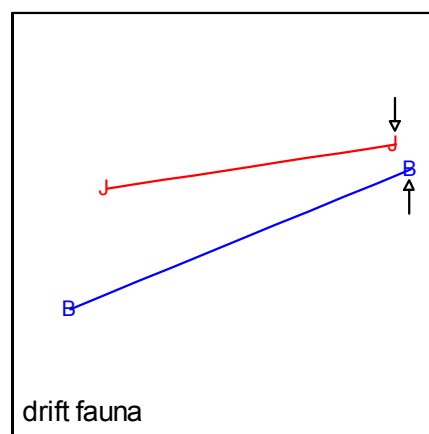
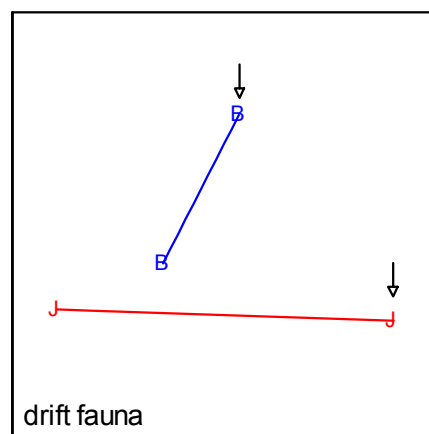
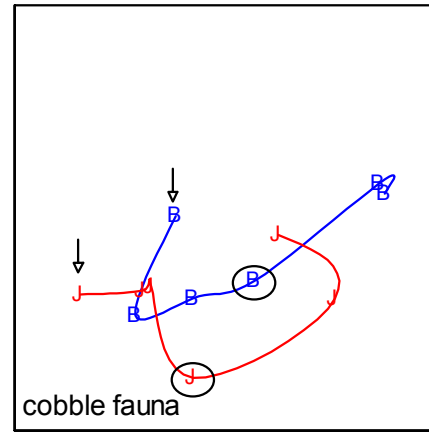
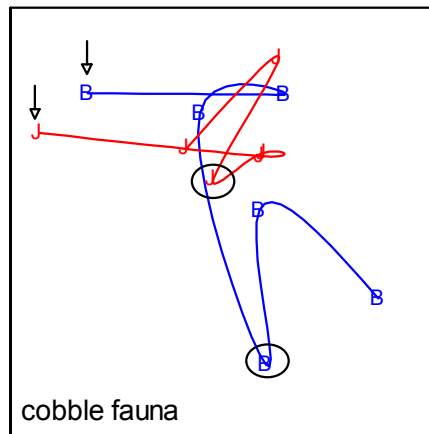


Table 4.8. Results of two-way ANOSIMs testing for differences between control and treatment pools allowing for differences between streams, on each sampling occasion both pre- and post- manipulation. Shading indicates significant differences.

	Sample	Tile Fauna		Cobble Fauna		Drift Fauna	
		R	p	R	p	R	p
pre-	1	0.07	0.38	-0.11	0.84	-0.24	0.98
	2	-0.15	0.81	0.04	0.35		
	3	0.12	0.21	0.05	0.34		
post-	4	0.35	0.04	-0.11	0.84	0.22	0.09
	5	-0.01	0.49	-0.06	0.69		
	6	-0.52	0.66	0.06	0.28		

Table 4.9. Taxa making a major contribution to the significant difference between treatment and control pools in tile fauna detected in samples from day 14 (SIMPER).

	Mean Abundance		% of Difference
	Treatment	Control	
Logger Branch			
<i>Bungona narilla</i>	13	2	23
<i>Tasimia palpata</i>	11	1	21
Unnamed Tributary			
<i>Tillardophlebia</i> sp. AV6	0	4	18
<i>Bungona narilla</i>	4	1	13

4.3.5 Grazer Distribution

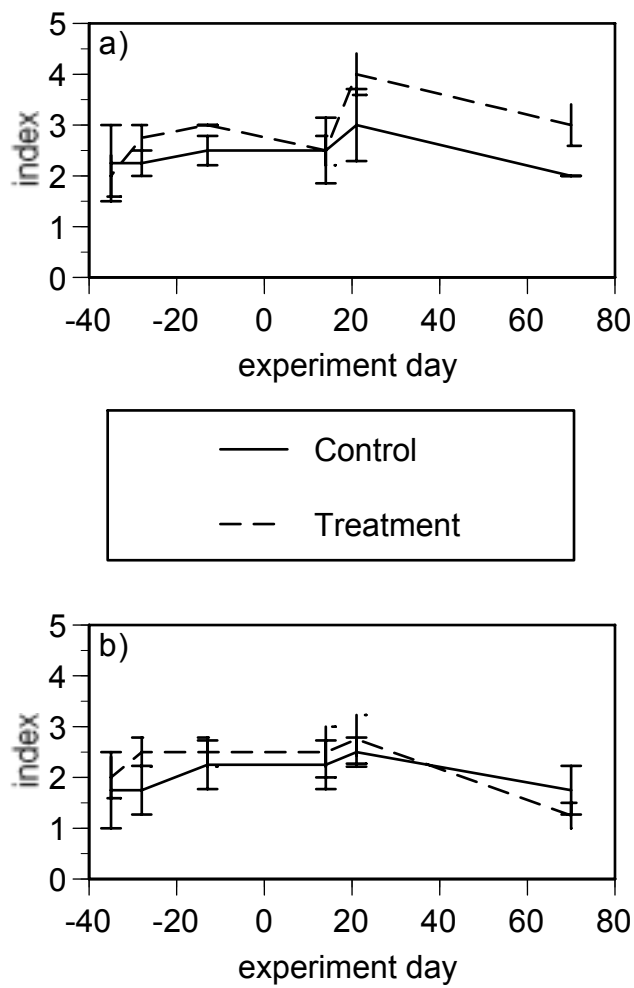
The index of dispersion of grazing Tasimiidae within pools was significantly different between experimental blocks and between streams, but the experimental manipulation of *P. australiensis* had no significant effect (Table 4.10 and Figure 4.12).

The distribution of these grazers within individual pools changed over time in all pools (see Appendix III). Removal of *P. australiensis* did not result in any consistent modification of these distribution patterns.

Table 4.10. Analysis of variance of grazer dispersion index. Statistical units are pools and factors are streams, experimental blocks, experimental treatment and time. The error term for the main plot is Treatment x Block (Stream) and for the split plot is Time x Treatment x Block (Stream). Significant interactions * $p < 0.05$, ** $p < 0.001$

Source of Variation	DF	F Value
Main Plot		
Treatment	1	4.00
Stream	1	42.25**
Block (Stream)	6	6.92*
Treatment x Stream	1	4.00
Split Plot		
Time	5	0.26
Time x Stream	5	0.67
Time x Block (Stream)	30	0.48
Time x Treatment	5	0.12
Time x Treatment x Stream	5	0.32

Figure 4.12. Mean grazer dispersal index in control and treatment pools on each sampling occasion in a) Logger Branch and b) Unnamed Tributary. Bars indicate the standard error of the means.



4.4 Discussion

4.4.1 Success of *Paratya* removal

The overall results of this study indicate that removal of *P. australiensis* had no effect on sediment cover or epilithic algal biomass and little effect on the biota in pools. These results are in stark contrast to the findings of Pringle *et al.* (1993) in Central America. Sediment cover on rocky substrates in the presence of Atyidae was similar in both studies, but sediment cover on the substrate when Atyidae were excluded was dramatically different. After only two days the sediment cover in Central America was 20 times that recorded in the study streams after 10, 20 or 65 days (Table 4.11).

Table 4.11. Sediment cover on hard substrates and deposition rates under base flow conditions recorded in this study and in Central American streams. The Central American rates are estimates calculated from data presented in Pringle *et al.* (1993).

	This Study	Central America
Mean sediment cover on substrate with shrimp	1.42 mg cm ⁻²	0.44 – 1.33 mg cm ⁻²
Mean sediment cover on substrate without shrimp	0.58 mg cm ⁻²	10 mg cm ⁻² in 2 days
Mean sediment accumulation rate	0.56 mg cm ⁻² day ⁻¹	5 mg cm ⁻² day ⁻¹ (at least)

One possible explanation for these results is that the manipulation was unsuccessful and that the experiment was thus confounded. There is however sufficient evidence to indicate that this is not the case. There is little doubt that the initial shrimp removal was successful as the densities of *P. australiensis* removed from pools were comparable with densities known to occur in the study area in small pools (Hancock, 1995) and observations made soon after the manipulation failed to locate any *P. australiensis* in treatment pools. It was also evident that electroshocking did not affect shrimp that were returned to control pools. There was not increased shrimp mortality as a result of electroshocking in test pools and they were observed to be present at normal densities in control pools shortly after the manipulation. Thus, at the very least, the lack of any observed effects of treatment in the first few days cannot be the result of failure to remove shrimp.

Uncertainty remains over the duration in which shrimp remained in their respective pools because a high discharge event, considered sufficient to trigger potential shrimp movement, occurred prior to the final census. Some assumptions can, however be made, based on existing in-stream movement data for *P. australiensis* in the study area (Hancock, 1995; Hancock and Hughes, 1999). These data show that during low flow periods, (such as those prevalent during the post manipulation period of this study), *P. australiensis* did not move upstream and showed very little tendency to move downstream. Over a 100 day low flow period, only two shrimp out of 16 000 tagged individuals moved downstream 10 m between pools. The two individuals were collected in a sample of 118 from a pool with a total population “in the order of a few thousand or less” (Hancock, 1995). It can therefore be assumed that the two sampled individuals represented approximately 40 tagged individuals in total present in the downstream pool. Thus 40 shrimps out of 16 000 moved downstream 10 m in 100 days, which is 0.1 m per day for each individual that moved. This equates to 0.25 mm per day per individual shrimp when all 16 000 shrimp are considered. Application of these figures to this study, with a mean number of shrimp per pool of 220 individuals (Table 4.3), results in an estimate that the most a shrimp in control pools would move would be 55 mm per day. If more than one shrimp were to move this figure would be divided by the number moving. These low estimates make it very clear that during low flow conditions, very few if any shrimp would have moved between experimental pools. This conclusion is further supported by the observation that no adult *Paratya* were collected in the drift samples collected before and after shrimp densities were manipulated.

During high flow events, movement is still very limited, but occurs more frequently and over longer distances, and tends to be in an upstream direction. For example, a rainfall event of 84 mm after a sustained dry period was sufficient to trigger such movement (Hancock, 1995; Hancock and Hughes, 1999). In the laboratory *P. australiensis* show random movement when there is no flow and are positively rheotactic at flow velocities of both 10 and 30 m s⁻¹. The velocity that instigates movement in the wild is unknown, but any event resulting in a rapid flow increase is a potential trigger (Marty Hancock, *pers comm.*). Furthermore, circumstantial evidence suggests that the prevalent behavioural response of *P. australiensis* is to remain in a pool given a choice of moving

during a high discharge event, or utilising flow refugia (if they are present) and remaining *in situ*. Hughes *et al.* (1995) found that Conondale Range populations of *P. australiensis* had large differences in genetic structure between streams. Even larger differences were found between headwater sites in different sub-catchments. They concluded this structure was the result of extremely limited movement of shrimp on a small spatial scale. Further evidence for very limited movement during even very high flow events, is provided by the findings that the abundance of *P. australiensis* in study pools was not reduced by a very large spate (see Chapter 3; Marshall, *unpublished data*), and that only a small proportion of tagged shrimp moved from pools over a 12 month period despite spates (Hancock, 1995; Hancock and Hughes 1999).

Observations indicate that in the study streams at low and medium flow levels, the velocity through pools was so low that a coloured liquid (milk) placed into a pool would sit for minutes with very little movement. Under such conditions it is very unlikely that shrimp would move. It is uncertain what magnitude discharge event would have triggered movement during this study. There was no substantial rainfall and thus no high discharge events to trigger shrimp movement between the experimental manipulation and days 14 and 21 when samples were collected (Figure 4.2). A small amount of rain (< 10 mm) fell several days before the second drift samples were collected on day 28, but this was almost certainly insufficient to trigger a flow event leading to shrimp movement, and no adult *Paratya* were collected in these samples (although larval *Paratya* formed a significant component of the samples). Thus, any observed effects of treatment in these samples must be the result of shrimp removal. There was a more substantial rainfall event of approximately 40 mm a week before samples were collected on day 70 (Figure 4.2) and it is possible that in response some shrimp may have moved between pools. There is therefore less certainty that the results obtained from this last set of samples reflected the consequences of shrimp removal.

If, however, shrimp did recolonise treatment pools, it is likely that this would occur at a different rate in each pool. This might be expected to increase the inter-pool variability of some response variables. There was no evidence of this occurring as variability of response variables was not noticeably altered in post-treatment “treatment” pools.

Therefore, both direct and indirect evidence lead to the conclusion that the manipulation of shrimp density was successful and that it remained effective for at least 28 days. Alternative explanations must therefore be considered to explain the lack of effect resulting from the experiment.

4.4.2 *Effects of Paratya on sedimentation*

Accumulation of fine sediment on the substrate of stream pools, must by reason, result from a discrepancy in the balance between the rate at which it is deposited and the rate at which it is removed. If deposited sediment were not removed at the same rate, pools would continue to accumulate sediment. This is illustrated by the potential sediment cover on tiles based on measured sediment accumulation rates in pools (Figure 4.7). It is possible (and perhaps likely) that deposition traps are far more effective at collecting and retaining sediment than the tiles. The measured deposition rates may therefore be exaggerated compared with those actually experienced by tiles and the substrate in general. Even if this were so, sediment would continue to accumulate if it were not removed at a rate similar to deposition. Such a build up of sediment did not occur in either Central America or in this study under base flow conditions when Atyid shrimp were present. This indicates that in both systems some factor or factors removed sediment at a rate at least similar to that at which it was deposited. In Central America, exclusion of Atyid shrimp resulted in a rapid cumulative increase in sediment cover while in this study it did not. It is evident that in Central America, the feeding and foraging activity of Atyidae was critical to the removal of sediment and prevention of its accumulation. This was once again not the case in this study. Despite this, *P. australiensis* are similar, all be it much smaller, shrimp to the Central American species, feed in a similar way (Gemmell, 1979a, 1979b; Pringle *et al.*, 1993) and are definitely capable of removing sediment from hard substrates. Preliminary trials using laboratory held *P. australiensis* in aquaria, demonstrated that the foraging activities of these shrimp removed deposited sediment from hard substrates. As the shrimp moved forward while foraging they left trails cleared of sediment. Observations suggested that the sediment cleared from these trails was ingested rather than re-suspended. Sediment that was not assimilated was compacted into faecal pellets occupying a much smaller surface area than before ingestion. Similar faecal pellets were commonly evident in pools. Thus

despite their small size, this species of shrimp does have the capacity to reduce sediment cover on hard substrates.

One possibility for the results here may be reduced shrimp activity during the cooler time of the year in which investigations were conducted. While there has not been a specific study of *Paratya* activity rates in relation water temperature in the study area, the work of Hancock (1995) provides indirect evidence that springtime activity rates are comparable to those during summer. Firstly growth rates of cohorts of shrimp were similar during spring and summer *in situ* and under spring and summer temperature regimes in the laboratory. Secondly larval drift rates were comparable in spring and summer.

The power of the experiment to detect a change in deposited sediment was not directly calculated due to the complexity of the ANOVA design, but variability was reasonably small, so failure to detect an effect is unlikely to be due to low power. It might be predicted that even if shrimp removal had no effect on the mean values of response variables, it may have changed the variability of some parameters. Once again, this does not appear to be the case.

The failure of *P. australiensis* removal to increase deposited sediment may relate to differences in the rates of sediment deposition in the study streams. It is possible that differences in results between this study and those in Central America were not due to differences in the activities of the shrimp, but rather were due to a substantial difference in sediment accumulation rates in the streams. The sediment accumulation rate under base flow conditions in Central America was at least ten times the rate recorded in the study streams (Table 4.11). It appears that the deposition rate in the study streams may have been so low that the combined effects of other factors capable of removing sediment, (be they physical or biological), maintained a balance between deposition and removal even when *P. australiensis* were absent. This is more plausible given the possible exaggerated accumulation rates derived from deposition traps in this study (discussed above). If the sediment accumulation rate were to increase for any reason, such as during storm events or following human interference in catchments, *P. australiensis* might then play an important role in removing deposited sediment.

Questions remain however, over the capacity of *P. australiensis* in these pools to remove sediment at rates comparable to those of the Central American atyids, which are much larger shrimp, so presumably more efficient at sediment removal, and also occur at higher densities. Further experimentation would be necessary to clarify this.

4.4.3 *Effects of Paratya on algal growth*

Predictions relating to reduction in the biomass of epilithic algae following *P. australiensis* manipulation were dependant upon an increase in sediment cover. As sediment cover was not influenced by the manipulation it is not surprising that epilithon mass and chlorophyll *a* mass were similarly unaffected. Note that as *Paratya* are not grazers (Walker, 1972; Gemmell, 1979a), their removal was not predicted to effect algal growth via a direct trophic mechanism (*sensu* McCormick, 1990).

4.4.4 *Biotic interactions*

It was predicted that several attributes of pool fauna may alter after removing shrimp and that this may occur as a consequence of either altering the distribution of habitat for mobile grazers by modifying sediment cover and epilithic algal biomass, or removing the direct effects of disturbance by foraging shrimp. As there was no effect on sediment cover or algal biomass, any faunal response to treatment must be due to removing the direct effects of disturbance by foraging shrimp.

Neither the dispersion and distribution of Tasimiid grazers in pools, nor the composition of fauna emigrating from pools were significantly altered by the manipulation. This indicates that direct disturbance by shrimp was not a significant influence upon these faunal attributes. This result, with regard to grazer distribution is also in contrast to the situation in Central America (Pringle *et al.*, 1993; Pringle and Blake, 1994), and may be a consequence of the much smaller size and lower density of *P. australiensis* compared with the Central American atyids.

The manipulation did however result in modifications to the mean fauna on experimental tiles. Significant increases in the mean abundances on tiles in experimental pools of *Bungona narilla* in both streams and *Tasimia palpata*? in Logger

Branch 14 days after the manipulation support this hypothesis. However, reduced mean abundances of *Tillyardophlebia* sp. AV6 in Unnamed Tributary removal pools cannot be explained by this mechanism. There was no significant change in fauna on experimental tiles with respect to control tiles evident on subsequent sampling occasions after the manipulation. Furthermore the effect was not repeated on the fauna of cobbles. The effect of *P. australiensis* removal on benthic pool fauna was thus short lived and inconsistent. If *P. australiensis* had a large influence upon the fauna in pools it would be expected that the relationship demonstrated between *P. australiensis* density and pool size would be reflected in other taxa mediated by the atyids. This is not the case as there was no significant relationship between pool size and faunal variation in these streams (Chapter 3). Even though the results of this experiment suggest that *P. australiensis* can influence some other taxa by direct disturbance, the stochastic processes influencing the abundance and distribution of other biota in both space and time (Chapter 3) may overwhelm any potential shrimp effect.

4.4.5 Functional importance, structural importance and *Paratya*

Overall, there is no evidence from this experiment to suggest that *P. australiensis* is instrumental in maintaining the structural or functional organisation of pool ecosystems in the study streams, either directly or indirectly. There is thus no justification to consider this a “keystone species” (*sensu* Paine, 1969) or to have high “structural importance”, as defined above. These shrimp can, however, still be considered to have a high “functional importance” (*sensu* Hurlbert, 1971; 1997), because they represent a large component of the in-stream animal biomass, they are likely to be responsible for a large percentage of carbon transfer in these streams, and thus their removal would be likely to result in a large change in system productivity. This implies that process and pattern were not linked, at least over the time frame of the manipulation.

**CHAPTER 5: THE EFFECTS OF
PREDATION BY THE FISH *MOGURNDA*
ADSPERSA ON POOL FAUNAL
ASSEMBLAGES**

5.1 Introduction

5.1.1 *Effects of fish predation on stream faunal assemblages*

Predation can be an important influence upon the structure and functional organisation of communities. The feeding activity of predators represents a form of disturbance, the consequences of which vary depending upon the attributes of the prey species as well as those of the predator (*e.g.* Darwin 1859; Paine, 1966; Lubchenko, 1978). Predation effects can be pronounced where predators are selective in favour of their prey and in some situations can result in dramatic consequences, such as “trophic cascades” (Paine, 1980; Carpenter *et al.*, 1985) that modify communities through multiple trophic levels (*see* Chapter 1).

Fish that prey upon macroinvertebrates are the primary predators in many small streams. Fish predation can result in a direct reduction of the abundance of invertebrate prey species in streams (*e.g.* Schofield *et al.*, 1988; Gilliam *et al.*, 1989; Morgan and Ringler, 1994), although this effect can be limited to a few prey species (Cooper, 1984a; 1988; Hemphill and Cooper 1984; Sih *et al.*, 1985; Closs, 1996). Predation by fish has also been demonstrated to be responsible for trophic cascades, in stream ecosystems. For example, the presence or absence of large predatory fish has been shown to dramatically influence algal biomass (Power, 1990; *see also* Sections 1.2.4 and 4.1.1).

Despite these potentially strong interactions between fish predators and their invertebrate prey, many studies have found no effects at all (*e.g.* Allan, 1978; 1982; Reice, 1983; 1991b; Flecker and Allan, 1984; Culp, 1986; Bechara *et al.*, 1992; 1993; Holomuzki and Stevenson, 1992).

Factors that may determine the importance of fish predation as an influence on stream macroinvertebrate assemblages include the ecological and behavioural attributes of both the fish and their prey, as well as attributes of their environment.

Fish that feed primarily on drift or at the surface of the water are thought to be less likely to influence macroinvertebrate communities than benthic feeders, as their prey is derived from upstream assemblages and much of it may in fact be of terrestrial origin

(Morgan and Ringler, 1992; Dahl and Greenberg, 1996; 1998; Pusey and Kennard, 1995).

The behaviour, size and conspicuousness of prey taxa render some species more vulnerable to fish predation than others and more vulnerable taxa are more likely to have their abundances reduced by fish. Most benthic feeding fish detect their prey visually; so invertebrate prey species can reduce their susceptibility to predation by minimising their visibility. The colour of stream invertebrates often matches the bottom and some species use bed material to build cryptic cases. Many other species stay under rocks or in interstitial spaces during the day and come to the surface to feed only at night when visual predators are inactive. There is evidence that insects can detect the presence of fish by chemical stimulæ (Cowan and Peckarsky, 1994) and modify their diel activity patterns accordingly, since nocturnal activity has no advantage in the absence of visual predators (McIntosh and Townsend, 1994). Air breathing nektonic species such as culicid larvae, adult coleoptera and hemiptera can be highly vulnerable because of their need to migrate to the surface of the water to obtain atmospheric oxygen (Cooper 1984a, 1988; Hemphill and Cooper 1984; Morgan and Ringler 1994; Closs 1996). Some of these species possess chemical defences against predation that render them distasteful to fish and thus they can remain conspicuous without exposing themselves to excessive predation risk (Kerfoot, 1982). Small size also appears to confer some protection, as several studies have found the effects of fish predation to be limited to relatively large and conspicuous prey taxa (Cooper 1984a, 1988; Hemphill and Cooper 1984; Morgan and Ringler 1994; Closs 1996). Vulnerable prey taxa have also been shown to alter their habitat utilisation patterns to reduce or avoid predation risk (Cooper 1984a, 1984b, 1988; Closs 1996). This type of behavioural change by prey taxa can cause stress to individuals and significantly reduce their fitness by reducing feeding rate, growth rate, size at maturity and fecundity, thus altering the characteristics of future populations and assemblages (Bailey 1986; Kohler and McPeck 1989; Jeffries 1990; Peckarsky *et al.* 1993; Huryn, 1998; Peckarsky and McIntosh 1998).

Invertebrate predators can become considerably more effective in the absence of fish. They generally do not detect their prey visually, but rather utilise mechanoreception or

chemoreception and many prey species rely upon escape responses to reduce their risk of being eaten (Pekarsky and Penton, 1993; Lancaster, 1990), although the use of interstitial refugia and protective cases are also prevalent strategies. Predation by invertebrates can compensate for the absence of fish and lead to conclusions that fish do not influence the assemblage structure of their prey (Soluk and Collins, 1998).

In streams where drift rates are high, immigrants can replace prey items consumed by fish and predation effects are unlikely to be identified (Culp, 1986; Reice and Edwards, 1986; Cooper *et al.*, 1990; Reice, 1991b; Dahl and Greenberg, 1998).

Predator-prey interactions are likely to be weaker in streams with high substrate heterogeneity than in those with uniform substrates. Complex habitats provide more “niche space”, allowing the coexistence of predators and prey (Power, 1992; Dahl and Greenberg, 1998). Furthermore, complex substrates provide prey with predation refugia, which in turn reduce the predation efficiency of fish (Allan, 1982; Crowder and Cooper, 1984; Flecker and Allan, 1984; Cook and Streams, 1984; Power, 1992). The influence of predation is also thought to intensify in “benign” environments in comparison to harsh, variable or unpredictable environments (Bergon *et al.*, 1990). In streams this equates to a greater likelihood of strong predator effects in pools than riffles, and during “benign” low-flow periods when physical disturbance is minimal than during high-flow “harsh” periods (Peckarsky, 1983; Power *et al.*, 1988; Resh *et al.*, 1988; Statzner *et al.*, 1988; Power, 1990). The likelihood of strong predation effects can be further increased in ephemeral systems as pools are isolated and contract in size, forcing predators and prey into closer proximity (Dudgeon, 1992; Closs, 1996). Furthermore, in isolated pools, there is no opportunity for prey immigration by drift to compensate for the effects of fish predation (Closs, 1996).

In some cases the lack of a detected effect of fish predation may be due to low power of experimental designs to detect such effects (*see* Allan, 1982).

5.1.2 Potential role of fish predation in the study streams

The study pools can be considered to have a high potential for the development of strong predation effects for several reasons. The predominant fish species in the

streams occurs in pools and is known to be primarily a benthic feeder, so terrestrial inputs are not likely to form a large component of their diet. During baseflow conditions pools represent a “benign” environment where biotic interactions may be expected to be strong (Peckarsky, 1983). Low flows conditions result in relatively isolated pools most of the time in these streams and disturbances are short-lived and episodic (*see* Chapter 2). Under such conditions, the study streams experience very low drift rates (Kerby *et al.*, 1995) so consumed prey would not readily be replenished from within the stream. Furthermore, pools are small, forcing predators and prey into closer proximity. The high substrate complexity of the pools may however mitigate predation effects by providing abundant refugia for prey.

Four species of fish have been recorded from pools in the two tributaries of Stony Creek: the long finned eel *Anguilla reinhardtii*; freshwater catfish *Tandanus tandanus*; Australian smelt *Retropinna semoni* and purple spotted gudgeon *Mogurnda adspersa*. Of these *M. adspersa* was the only species to occur commonly and in high abundances in small pools, at the higher altitudes of the study streams. *A. reinhardtii* was the only species recorded upstream of bigger waterfalls, but was uncommon and only observed in very large pools. *T. tandanus* rarely occurred in the study streams and again was only observed in large pools. *R. semoni* occurred and bred in some of the study pools but in very low abundances. Furthermore, it is a surface/plankton feeding species in the study streams (*unpublished data*) and thus unlikely to play a significant role in structuring the benthos dominated pool assemblages (*see* Chapter 3).

5.1.3 Aims

The broad objective of this chapter is to determine whether or not the presence of *M. adspersa* influences the structure of faunal assemblages in small pools in rainforest streams. A three-stage approach was adopted to achieve this.

a) Correlative relationships between M. adspersa and pool faunal assemblages

Existing quantitative data from Chapter 3 were investigated for correlative evidence of the influence of *M. adspersa* on the faunal assemblage structure of pools and the abundances of individual taxa. Analyses addressed two questions:

- Is there evidence that the structure of pool assemblages is related to the presence/absence or density of *M. adspersa* in pools?
- Is there evidence that the abundances of individual taxa are related to the presence/absence or density of *M. adspersa* in pools?

b) Diet of M. adspersa

The diet of *M. adspersa* in these pools was described by means of analysis of dietary items in the stomach contents. The degree to which diet varied between individual fish and whether this variation was determined by characteristics of the fish themselves (size and gender) or their environment (size and depth of pools and density of fish) was also determined. The latter may lead to marked spatial and temporal variation in the effects of predation due to individual feeding preferences (Amundsen *et al.*, 1995; Warburton *et al.*, 1998).

The habitat within pools where individual fish fed was determined from the habitat preferences of prey taxa in their stomach contents. Variation between individuals and factors accounting for this were explored.

The following specific questions were addressed:

- What is the average diet of *M. adspersa* in these pools and how much variation is there in the diets of individual fish?
- Is the diet of individual fish influenced by their own characteristics (size or sex) and/or attributes of the pool from which they were collected (area, depth or density of *M. adspersa*)?
- Did individual fish feed in different pool habitats and was this influenced by attributes of the fish?

c) Pool-scale manipulation of M. adspersa density

The density of *M. adspersa* was manipulated on a whole-pool scale under controlled experimental conditions to directly determine their role in structuring faunal assemblages in this system and the abundances of key prey taxa. Analyses were also

conducted to identify relationships between natural abundances of *M. adspersa* and the size of pools.

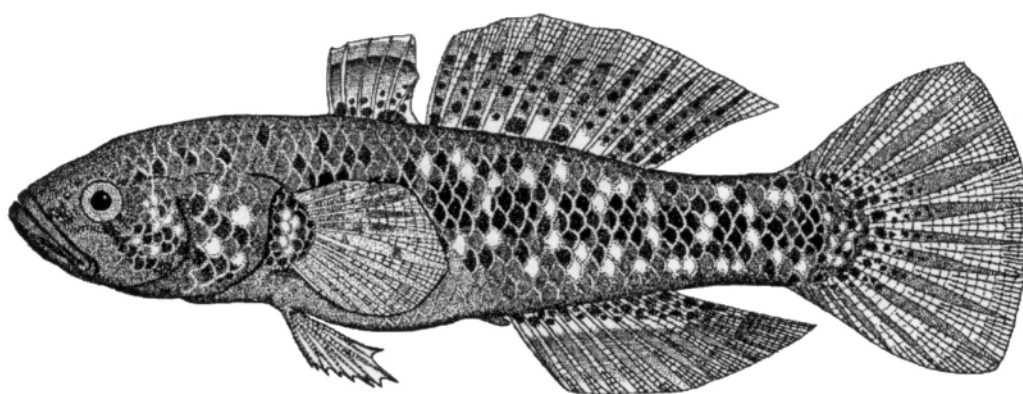
5.2 Methods

5.2.1 *Mogurnda adspersa*

Mogurnda adspersa (Figure 5.1) is a member of the family Elotrididae (gudgeons), which are common inhabitants of streams in tropical and temperate latitudes (Allen, 1989). It occurs in the Murray-Darling Basin and in streams east of the Great Dividing Range from northern New South Wales to far north Queensland where it usually inhabits still or slow flowing waters. It grows to a maximum total length of approximately 140 mm but commonly reaches only 70 mm. Fish reach maturity at approximately 50 mm total length and breeding occurs in summer at temperatures over 19 °C. Females may produce several broods in a season. Eggs are laid in a cluster which adheres to solid objects such as rocks and are guarded by males until they hatch. Larvae are planktivorous while larger fish are carnivorous with a varied diet ranging from aquatic insects and crustacea to fish (Allen, 1989; Merrick and Schmida, 1984; Hoese *et al.*, 1980; Arthington, 1992; Hurtle and Pearson, 1990; Pusey *et al.*, 1995).

Figure 5.1. Adult *Mogurnda adspersa*. The maximum total length of this species is approximately 140 mm (Merrick and Schmida, 1984).

Unpublished drawing by Brad Pusey, used with artist's permission.



5.2.2 Correlative Evidence of the Influence of *M. adspersa* Density on Pool Fauna

Data collected as the baseline component of the experiment conducted to investigate the influence of *Paratya australiensis* on pool ecosystems (see Chapter 5) provided quantitative estimates of the natural abundances of *M. adspersa* and of the fauna of various pool habitats. These were explored to identify relationships between the abundance of *M. adspersa*, the structure of pool habitat assemblages and the abundances of specific taxa.

a) Collection Method

Sampling methods are described in detail in Chapters 3 and 5. Samples of the fauna from gravel, cobble and general pool habitats (*i.e.* sweep samples) and from the drift emigrating from pools were collected from 16 pools. Gravel patches were sampled using a modified Hess sampler, cobbles were lifted into a net and fauna gleaned from their surfaces and general pool fauna was sampled by sweep sampling for 30 seconds. Fauna from these samples were identified and enumerated. The pools were sampled for *M. adspersa* shortly afterwards using multiple passes with an electroshocker and dip nets. The wetted area of each pool was estimated as the product of mean pool length and mean pool width, each calculated from three to six measurements made using a tape measure. The maximum depth of each pool was recorded. The abundance of *M. adspersa* in the pools was expressed as the density of fish per square metre.

b) Univariate Analyses

The total number of taxa, total number of individuals and Shannon-Wiener Diversity Index was calculated for each pool from invertebrate samples from each habitat. Analyses were conducted to test for differences in these variables between pools with *M. adspersa* present, and pools with *M. adspersa* absent. T-tests were used when variances were homogeneous, and Mann-Whitney U tests when they were not (Zar, 1984).

c) Multivariate Analysis

Faunal abundance data were $\log(x+1)$ transformed following the removal of rare taxa (see Chapter 3) and Bray-Curtis differences calculated between all pools for each of the sampling methods. A second set of Bray-Curtis differences was calculated for each sampling method after transforming the faunal abundance data into relative abundance, again following the removal of rare taxa. Each of the six difference matrices (two data treatments by three sampling methods) were ordinated in three dimensions, rotated to display most variation in the plane of two axes, and plotted in those two dimensions as bubble plots indicating the position of pools in ordination space and the density of *M. adspersa* in the pools. Correlation vectors (PCC) were calculated between the ordinations and the density of *M. adspersa* in pools at the time of sampling. The significance of these correlations was tested using Monte-Carlo simulations with 100 random starts. Further detail of these techniques is provided in Chapter 3.

The pools were divided into three categories based on the density of *M. adspersa* they contained. These were no *M. adspersa*, low-density *M. adspersa* ($< 0.1 \text{ fish m}^{-2}$) and moderate-density *M. adspersa* ($> 0.1 \text{ fish m}^{-2}$). One-way ANOSIMs were used to test for differences in the assemblage structure of pools in these categories using each of the six Bray-Curtis difference matrices. Where significant differences were found, SIMPER was used to identify taxa contributing most to the differences.

d) Analysis of Relationships

Scatter plots were drawn between the density of *M. adspersa* in pools and the abundances of individual taxa collected in each of the habitats. Taxa were considered to be potentially influenced by *M. adspersa* density when:

a tight curve could be fitted to the relationship,

when only low abundances occurred in pools with high densities while high and/or low abundances occurred at pools with low densities

when only low abundances occurred in pools with low densities while high and/or low abundances occurred at pools with high densities.

5.2.3 The Diet of *M. adspersa*

Data on the diet of *M. adspersa* were obtained from 15 randomly chosen pools in Unnamed Tributary. These were pools that were not used for other components of the study. Pools were electroshocked in September 1997 and a random selection of the *M. adspersa* caught from each pool was anaesthetised using MS222 (tricaine methane sulphonate) at a concentration of approximately 100 mg L⁻¹ (Prince-Iles, 1999), and preserved in 10% buffered formaldehyde. Six fish at most were taken from any single pool. The wetted area of each pool was estimated as the product of mean pool length and mean pool width, each calculated from three to six measurements made using a tape measure. The maximum depth of each pool was recorded.

The standard length (SL) and maximum gape width (MGW) of each fish was measured to the nearest millimetre and their stomach removed. The sex of the fish was determined by examining their gonads. The fullness of the stomachs was estimated as a percentage and they were dissected open in a Petrie dish of water. The contents of the stomachs were identified under a dissecting microscope to the lowest convenient taxonomic level. Gut contents were recorded as the number of items of each prey category within the stomach of each fish.

a) Average Gut Contents

The contributions of each prey item to the overall diet of *M. adspersa* were expressed as: (a) the mean percentage contribution (calculated as the proportion of the combined gut contents of all fish), (b) the percentage of fish with the item present in their guts and (c) the mean number of each item in guts per fish.

b) Factors Influencing Gut Contents of Individual Fish

Analyses were performed to describe differences between the gut contents of individual fish and to identify environmental factors influencing these differences.

Relationships between the gut contents of individual fish were investigated using multivariate techniques. Full details of these methods are provided in Chapter 3. Abundances of prey items were $\log(x+1)$ transformed and Bray-Curtis differences calculated between all fish. These were ordinated in three dimensions, rotated to display most variation in the plane of two axes and plotted in those two dimensions. Correlation vectors were calculated between the ordination and the $\log(x+1)$ abundances of the prey items as well as the stomach fullness, SL and MGW of the fish, the area, maximum depth, abundance of *M. adspersa* and density of *M. adspersa* in pools when they were collected. The significance of these correlations was tested using Monte-Carlo simulations with 100 random starts.

The distribution of SL amongst the fish was investigated by plotting a frequency histogram. If distinct size classes were present, ANOSIM was used to test for differences in gut contents between the classes. ANOSIM was also used to test for differences in gut contents between sexes of *M. adspersa* and the pool from which the fish were collected. Where significant differences were found between any of these categories, SIMPER was used to identify prey items contributing most to the differences.

Differences in test variables describing aspects of the stomach contents of the fish (stomach fullness, the number of prey items per gut, the number of prey taxa per gut and the Shannon-Wiener diversity of prey items per gut) were investigated between categories of imposed factors (size class, sex). One way ANOVAs and t-tests were used where appropriate to test the null hypotheses that there were no differences in the test variables between categories of the imposed factors. Pearson's correlation coefficients were calculated between the same test variables and selected environmental characteristics of the pools from which the *M. adspersa* were caught (pool area, pool maximum depth, number of *M. adspersa* in the pool and density of *M. adspersa* in the pool).

c) Pool habitats in which M. adspersa fed

Investigations were made to determine the pool habitat(s) in which *M. adspersa* fed. The taxa of prey items were classified according to the habitat in which they occur based on Chapter 3 results. The habitat categories used were epibenthic, epilithic, nektonic, leaf litter, pneustonic and uncertain. The diet of each fish was then expressed as the abundance of items in each of the habitat categories. These were log (x+1) transformed and Bray-Curtis differences calculated between all fish. Data were ordinated in three dimensions, rotated to display most variation in the plane of two axes and plotted in those two dimensions. Correlation vectors (PCC in PATN) were calculated between the ordination and the log (x+1) abundances of the prey items in the categories. The significance of these correlations were tested using Monte-Carlo simulations with 100 random starts.

ANOSIM (PRIMER) was used to test for differences in the habitat composition of gut contents between any distinct groups of size class, sex or pool which were identified from the earlier analyses. Where significant differences were found between any of these categories, SIMPER was again used to identify habitat categories contributing most to differences where they were significant.

5.2.4 The Effects of M. adspersa on Pool Fauna: Manipulative Experiment

An experiment was conducted to test the hypothesis that altering the density of *M. adspersa* in pools would result in changes in the structure of pool faunal assemblages.

a) Experimental Design

The experiment was performed using a randomised block multivariate BACIP design (*sensu* Faith *et al.*, 1995). Twenty pools in Logger Branch were grouped into five spatial blocks with each block consisting of four pools. Thus the four pools furthest downstream formed block one, the next four pools moving upstream block two and so on. Within blocks, pools were randomly assigned to one of four experimental treatments. These were experimental control, procedural control, *M. adspersa* addition and *M. adspersa* removal. Faunal samples were collected from gravel, cobble and sweep samples types (*see* Chapter 3) before and after manipulation of *M. adspersa*

densities in pools and assessment made of the multivariate differences between the assemblage composition of these samples. Timing of manipulations and samples is summarised in Table 5.1.

Table 5.1. The time of key events in the manipulative experiment.

Date (1997)	Experiment Day	Activity
3-4 July	-13 and -12	Pre-manipulation pool fauna samples collected
8 July	-8	Nets erected
14-15 July	-2 and -1	Pools electroshocked and fish removed
16 July	0	Fish stocked at manipulated densities
1 August	16	Pools electroshocked and fish counted
18-19 August	33 and 34	Post-manipulation pool fauna samples collected
20-21 August	35 and 36	Pools electroshocked and fish counted

b) Manipulation of M. adspersa Density in Pools: Methodology

Nets were erected at the upstream and downstream ends of all pools except experimental controls on 8 July 1997 (experiment day –8). The purpose of the nets was to prevent *M. adspersa* from moving between pools. Preliminary trials for this experiment indicated that, without the constraint of nets, *M. adspersa* moved readily between pools even when there was very little connecting flow. The nets used were constructed from 8mm (stretched mesh size) nylon “polynet” of the type commonly used to package fruit and vegetables. Two lengths of this material were sewn together to produce a net with a drop of 1m. The tops of these nets were attached to lengths of rope tightly strung across the stream approximately 0.3m above the surface of the water. The bottoms of the nets were sealed against the stream bed by layers of cobbles, gravel and sand. Once erected, the nets were checked for holes and cleared of debris every two to three days.

The wetted area of each pool was estimated as the product of mean pool length and mean pool width, each calculated from three to six measurements made using a tape measure. The maximum depth of each pool was recorded.

All pools, except experimental control pools, were electroshocked using a Smith Root Type VII backpack electrofisher, with the aim of removing all *M. adspersa* present. The electrofisher was set on 300 V with a medium pulse width. Pools were sampled,

beginning at the downstream end and working progressively upstream, with a slow sweeping action of the anode of the electrofisher held above the stream bed, until their entire area had been covered. Efforts were taken not to upset fine sediments in the pools by working from the edges as much as possible. *M. adspersa* were stunned by this process and removed from the pools using either a net attached to the anode of the electroshocker, or a small hand held net operated by a second person. They were placed into buckets partially filled with clean stream water where they soon regained consciousness. All fish caught were categorised as either “large” or “small” with a cut-off of 60 mm SL. This size corresponded to fish with a mouth gape of greater than 8 mm, at which size they would be unable to swim through the mesh of the nets erected to isolate pools. The time taken to complete a thorough pass of each pool (measured in electroshocker units) and the number of fish removed in the two size categories were recorded. Electroshocking was repeated, following a 30 minute break to permit fine sediment to settle, until a pass was completed in which no *M. adspersa* were stunned. Pusey *et al.* (1998) demonstrated that multiple-pass electroshocking is a suitable method for determining population sizes of fish in small to medium sized streams in south-east Queensland. This process was completed for blocks one and two on 14 July 1997 (experiment day -2) and for the remaining three blocks on the following day.

Pools designated for the removal treatment were not restocked. Procedural control pools were restocked with the same number of large and small *M. adspersa* that were removed and addition pools were stocked at a density of 1.5 *M. adspersa* m⁻² using only large category fish. This stocking density was the highest recorded within the system during preliminary surveys. Stocking was completed on 16 July 1997 (experiment day 0) using fish removed from the pools plus additional large size category fish collected from nearby Stony Creek (*see* Chapter 2). Between collection and stocking, fish were stored in aerated, insulated and covered containers (60 L eskies) with frequent water changes. Ten fish were returned to the laboratory and kept in an aquarium until the completion of the experiment in order to monitor mortality.

On 1 August 1997 (experiment day 16), all pools, except experimental controls, were electroshocked with two passes using the same procedure described above. Any *M. adspersa* caught were sorted into large and small size categories and counted. The

objective of this was to ensure that fish had not moved between pools since the initial manipulation. Any fish found in removal pools were kept out. The fish caught in other pool types were returned. Additional large *M. adspersa* were stocked into any addition pools in which the numbers appeared depleted. These extra fish were caught from Stony Creek.

The experiment was terminated after 35 days on 20 August 1997 for blocks one and two and the next day for the remaining blocks. The final densities of *M. adspersa* in all pools were assessed in the same way as they were before the manipulation and the nets were removed.

c) Relationships between the abundance of M. adspersa and pool attributes

Relationships between the number of *M. adspersa* occurring naturally in pools, sampling effort and pool size and depth were investigated. Pearson product-moment correlation coefficients were calculated between the wetted area and maximum depth of pools and the abundances of large and small *M. adspersa* collected within the pools. The two tailed significance of these correlation coefficients was assessed (Zar, 1984).

Relationships were also investigated between the number of *M. adspersa* caught at the end of the experiment, the number naturally present before the experiment and the number stocked, and pool size and depth. Pearson product-moment correlation coefficients were again calculated between the wetted area and maximum depth of pools, the abundances of large and small *M. adspersa* collected within the pools before and after the experiment and the number of small and large fish stocked. The two tailed significance of these correlation coefficients was assessed (Zar, 1984).

d) Sampling of Pool Fauna

Before the manipulation of *M. adspersa* density, fauna was sampled from all pools. The habitats sampled were:

gravel fauna by means of a single modified Hess sample,
cobble fauna by means of three cobble samples, and
sweep sample fauna by means of a standard sweep sample.

Details of the methods used to collect and process these samples are presented in Chapter 3. These samples were collected from blocks one and two on 3 July 1997 and from the remaining blocks on 4 July 1997 (experiment days –13 and –12).

Final samples of all the types collected before the manipulation, were retaken from all pools on 18 August for blocks one and two and the following day for the remaining blocks (experiment days 33 and 34). Manipulations of *M. adspersa* densities were therefore in place for 33 days for blocks one and two and 34 days for the remaining blocks.

e) Analysis of Pool Fauna

Samples were processed and fauna identified and enumerated as described in Chapter 3. Abundances of all taxa present in each sample were recorded. Thus for every pool there were data from before and after the *M. adspersa* manipulation for gravel, cobble and sweep samples. A data matrix was created for each of the three habitat types which included all taxa recorded and their abundances in each pool both before and after the manipulation. Rare taxa were removed and taxon abundances were transformed to generate log abundance and log relative abundance data matrices (*see* Chapter 3 for details). A Bray-Curtis dissimilarity matrix was calculated from each data matrix. These were ordinated in three dimensions, rotated to maximise the variation displayed along the axes and plotted in the pair of axes explaining most of the variation. Full details of these procedures are presented in Chapter 3.

The difference score between the pre- and post-manipulation samples at each pool was extracted from the Bray-Curtis dissimilarity matrices. These values indicated the multivariate change in the fauna in each pool between samples collected before and after the manipulation. They were used to test the null hypothesis that Bray-Curtis differences between samples collected before and after the *M. adspersa* manipulation were equal for all experimental treatments.

Differences were tested using a mixed model (model III) two-way ANOVA without replication (Zar, 1984). Experimental treatment was the fixed factor and block was the random factor in the ANOVA model. Analyses were performed using the General

Factorial Analysis of Variance procedure in SPSS (SPSS Inc., 1997a; 1997b). The residual was set as the error term. Estimates of effect size were calculated as the proportion of total variability explained by a factor. Approximate power for 0.05 significance level was estimated (SPSS Inc., 1997a; 1997b). When the null hypothesis was rejected, simple contrasts were made with the experimental control treatment set as the reference category. Following the recommendations of Zar (1984), the null hypothesis of equal Bray-Curtis differences between blocks was not tested.

Separate analyses were performed for the difference scores derived from log abundance and log relative abundance data matrices for each of the three habitat types.

Differences in the abundances of key prey taxa were calculated between before and after the manipulation in each pool. Taxa that were common before the manipulation were considered. For each taxon the null hypothesis was tested that differences in abundance between before and after the manipulation were equal for all experimental treatments. The same two-way ANOVA model described for assessing multivariate differences between treatments was used for these analyses.

5.3 Results

5.3.1 Correlative Evidence of the Influence of *M. adspersa* Density on Pool Fauna

The abundance of fish in pools sampled for this component of the study ranged from 0 to 12 individuals, which corresponded to a range of density of 0 to 0.47 fish m⁻² (see Appendix IV). This was lower than the maximum density recorded during preliminary investigations for the manipulative experiment (1.5 fish m⁻²) and possibly reflects a change in the overall abundance of fish in the study streams between the two surveys.

a) Univariate analyses

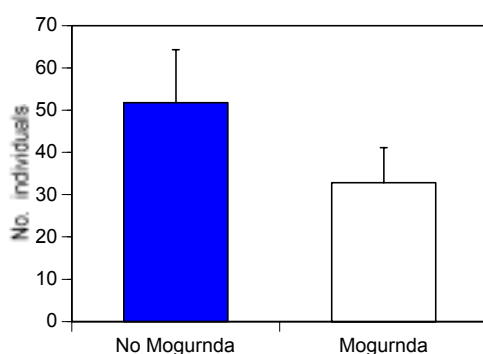
All analyses were conducted using Mann-Whitney U tests as variances were heterogeneous. There were no significant differences between the number of taxa or Shannon-Wiener Diversity of pools with and without *M. adspersa* in any of the habitats. The total number of individuals present in sweep samples from pools in which *M. adspersa* was present was significantly smaller than in pools without *M. adspersa* ($U =$

12.0, $p = 0.05$) (Figure 5.2). There were no significant differences in the total number of individuals in the other habitats.

b) Multivariate analyses

There is evidence that the structure of pool faunal assemblages was related to the density of *M. adspersa* in pools.

Figure 5.2. The mean number of individuals in sweep samples from pools with and without *M. adspersa*. Bars indicate the standard errors of the means.



Ordination of abundance and relative abundance data gave similar results for all habitats and only those generated from abundance data are presented. Correlation vectors between the ordination and the density of *M. adspersa* in pools were significant in the case of gravel and sweep sample fauna but not significant for cobble or drift fauna (Figure 5.3). For sweep sample fauna this correlation is evident as a gradation in *M. adspersa* density in pools in the direction of the vector arrow, from the left to the right in ordination space. However there is no such gradation evident in the ordination of gravel fauna. Despite the significant correlation vector, the linear relationship between *M. adspersa* density and the position of pools in ordination space appears weak. Instead, pools with *M. adspersa* present are located toward the outside of the plot and pools without *M. adspersa* on the inside. These results indicate that the presence of *M. adspersa* had a predictable effect on sweep sample fauna, which increased in magnitude with increasing density of fish, but had an unpredictable effect on gravel fauna. There is no evidence from the ordinations that the fauna of cobble or drift samples was influenced by the presence or density of *M. adspersa* in pools.

The *M. adspersa* density categories into which pools were divided are indicated in Table 5.2. Sweep samples were the only sample type in which significant differences were found between density categories (Table 5.2). Pairwise comparisons indicated that the fauna of both medium and low density pools was different from the fauna of pools with no *M. adspersa* (ANOSIM, medium vs absent $R = 0.380$, $p = 0.05$; low vs absent $R = 0.457$, $p = 0.04$) but there was no difference between medium and low density pools (ANOSIM, $R = -0.074$, $p = 0.70$). SIMPER identified that most of this difference was due to pools with *M. adspersa* having lower average abundances of Notonectidae sp.B and *Paratya australiensis*, than pools without *M. adspersa*. Once again results from the analysis of abundance and relative abundance data were very similar and only those pertaining to abundance are presented.

Figure 5.3. Bubble plots indicating the relationships between faunal assemblage structure in different pool habitats and the density of *M. adspersa* in the pools from which the faunal samples were collected. The centre of the bubbles represents of the position of samples in ordination space and the area of the bubbles represents the density of *M. adspersa* in the pools. Arrows indicate the direction of significant correlation vectors between the ordinations and *M. adspersa* density ($p > 0.05$). (Stresses: Gravel Fauna = 0.16, Sweep sample Fauna = 0.05, Cobble Fauna = 0.14 and Drift Fauna = 0.13.).

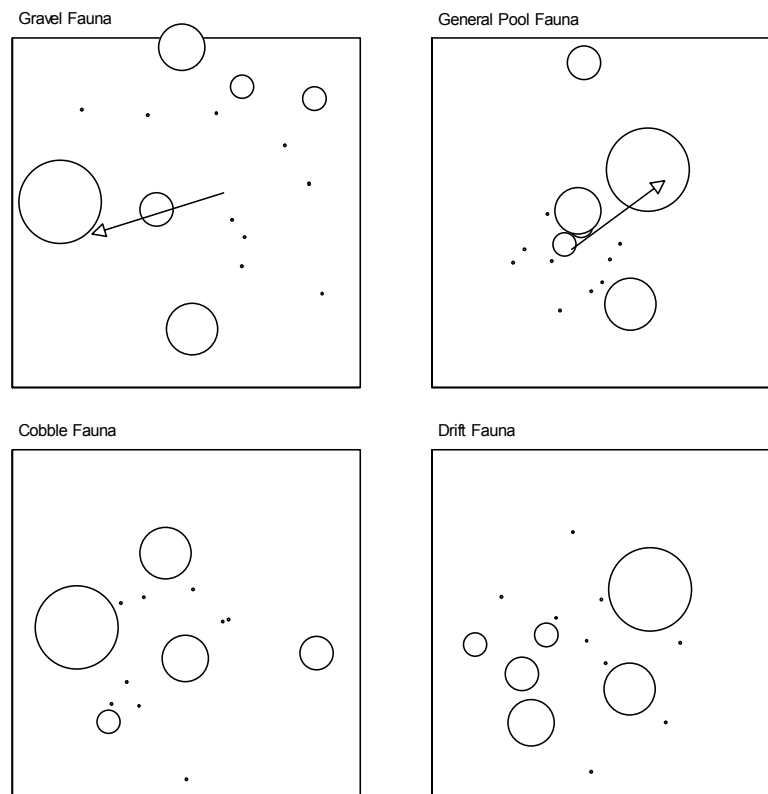


Table 5.2. Results of one-way ANOSIMs testing for differences between the fauna of pools with medium *M. adspersa* densities, low *M. adspersa* densities and no *M. adspersa* for each of the pool habitats sampled. Shaded rows indicate significant differences.

Habitat	R	p
Gravel	0.01	0.45
General Pool	0.41	0.02
Cobble	-0.056	0.63
Drift	-0.058	0.64

c) Analysis of relationships

There is evidence that the abundances of some taxa were related to the density of *M. adspersa* in pools.

Of the many taxa investigated there were only 10 that showed signs that there may be a relationship (Figure 5.4). Those collected from the gravel, sweep sample and cobble habitats show a relationship in which abundances are low or zero in pools with medium *M. adspersa* densities and range from high to low in pools with low densities or no *M. adspersa*. In the case of *P. australiensis* in the sweep samples, this relationship is not strong but it was included because of its relevance to other aspects of this study (see Chapter 5). The taxa included from the drift samples show a different relationship. They had low or zero abundances when *M. adspersa* densities were low and only had high densities (from single samples only) when *M. adspersa* densities were higher. It is possible that the presence of *M. adspersa* at medium densities may induce these taxa to drift, but additional data are required to confirm this.

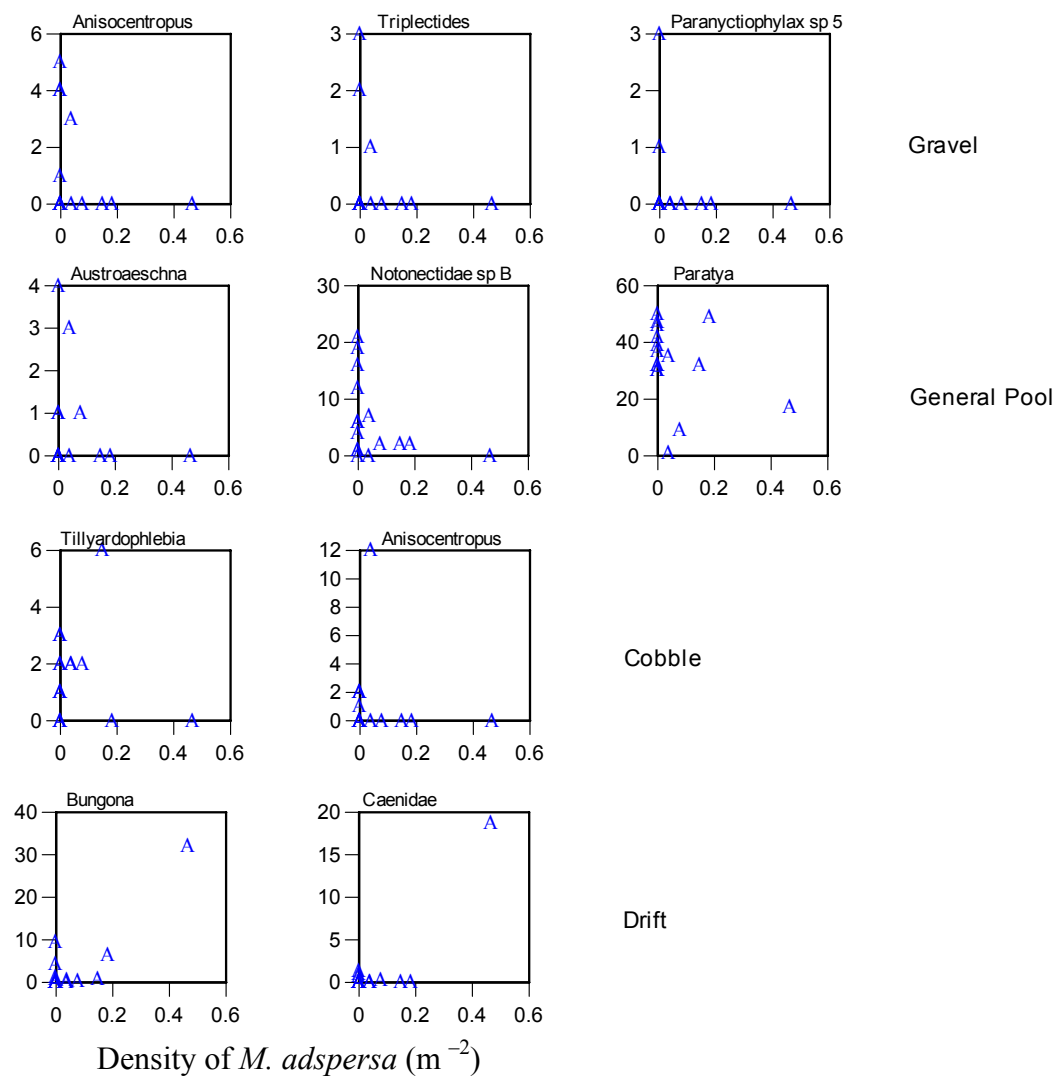
5.3.2 The Diet of *M. adspersa*

a) Average Gut Contents

Of the 36 fish collected, 3 had empty guts and were excluded from further analysis. Forty taxa of aquatic invertebrates were identified from the remaining 33 *M. adspersa* gut contents. Terrestrial arthropods did not form a major dietary component and they were combined into a single prey category for analysis. Fish had a mean of 10.4 (SE =

0.5) prey items in their guts comprising a mean of 4.4 (SE = 0.3) taxa. The average gut contents of the fish were dominated by Ostracoda, leptophlebiid mayfly nymphs and culicid larvae (Table 5.3).

Figure 5.4. Scatter plots of the density of *M. adspersa* (x axes, fish m⁻²) versus the abundance of specific taxa (y axes, abundance in a sample) in samples from different habitats. Plots are presented only for taxa where there is evidence of a relationship between the two variables.



b) Factors Influencing Gut Contents of Individual Fish

There was considerable variation among the gut contents of individual fish. The mean Bray-Curtis dissimilarity index between fish was 0.83 (SE = 0.02) with a range of 0.33 to 1.0. Expressing this in another way, fish had, on average, only 17.4% (SE = 1.8%) of their gut contents in common with other fish and some fish had none of their gut contents in common.

The diet of individual fish was influenced by the size of the fish but not by the sex of the fish, the pool from which it was collected or the density of fish in the pool from which it was collected (Figure 5.5). Bigger fish tended to have more *Paratya* and large (*Triplectides*, and *Atalophlebia*) or active insects (*Bungona*) than smaller fish, while smaller fish tended to have more Culicidae and Ostracoda.

The position of individual fish in ordination space, calculated from the composition of their gut contents, was significantly correlated ($p < 0.05$) with SL, MGW and with the abundances of a number of prey taxa in their guts (Figure 5.5). MGW and SL were highly correlated with each other (Pearson's correlation, $r = 0.97$) and therefore represent the size of the fish equally well. MGW is more likely to influence the gut contents of fish as it determines the maximum ingestible prey size. The composition of fishes' gut contents was not significantly correlated with the fullness of their stomachs, the area or maximum depth of the pool from which they were collected, the number of fish present in the pool, or the density of fish present in the pool.

A discontinuity in the size of fish examined occurred between 50 mm and 60 mm SL or between 7 mm and 8 mm MGW (Figure 5.6). This divided the fish into two groups of approximately the same number (large and small fish), which may represent age classes.

Small fish had gut contents significantly different from large fish (ANOSIM $R = 0.146$, $p = 0.002$) (Figure 5.7, Tables 5.3a and 5.3b). SIMPER analysis indicated that differences between the two groups were due to small fish having smaller average abundances of ephemeropterans (notably *Atalophlebia* and *Tillyardophlebia*) and *Sclerocyphon minimus*, and larger average abundances of Ostracoda, chironomid larvae

and Veliidae, in their gut contents than large fish. A single large fish (which appears in the upper left area of the plot in Figure 5.7) had gut contents typical of small fish (Ostracoda, Veliidae and Culicidae).

Figure 5.5. Ordination plot representing the differences between individual fish based on their gut contents and indicating significant correlations with (a) attributes of the fish and (b) the log (x+1) abundances of prey taxa in the fish gut contents. Stress = 0.12.

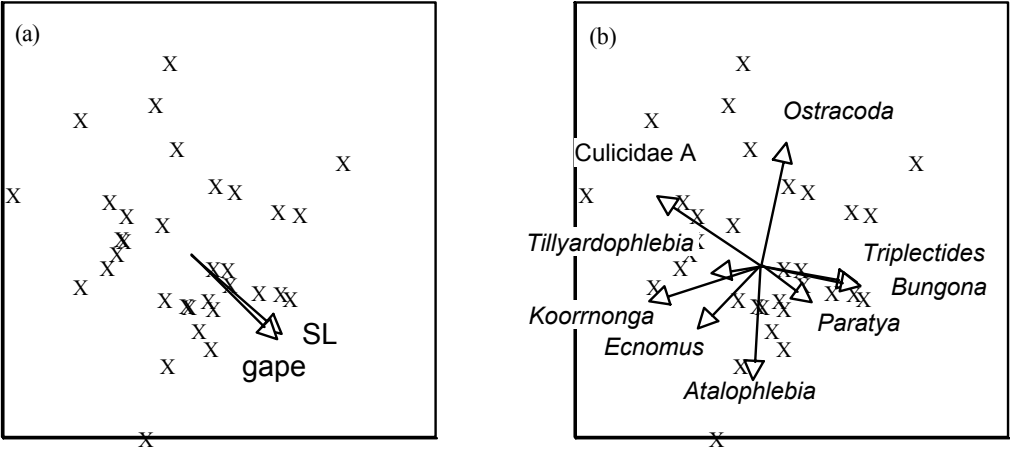


Figure 5.6. Histogram demonstrating the discontinuity in the size of *M. adspersa* examined which occurred between 50mm and 60mm SL. The x axis indicates 5mm size classes of fish SL and the y axis number of fish in each size class.

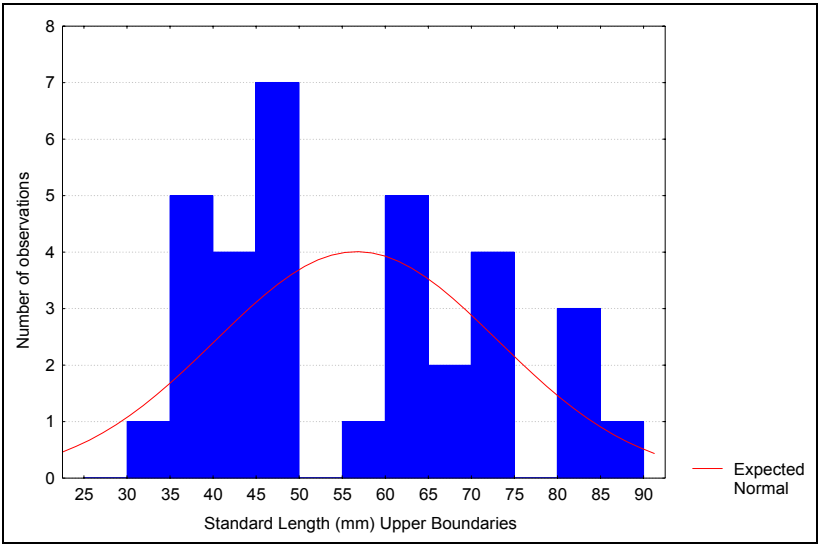


Figure 5.7. Ordination plot of individual fish based on the composition of their gut contents. Fish are coded to indicate small (SL<50mm) and large (SL>60mm) size classes. Stress = 0.12.

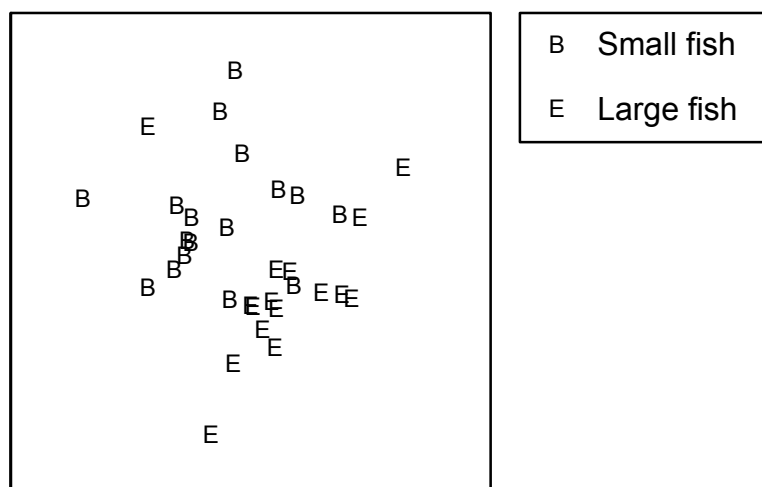


Table 5.3a. Prey items recorded in the gut contents of small *M. adspersa* (< 50 mm SL).

Prey Item	Mean % contribution to gut contents	% fish with item in gut	Mean no. in gut per fish (SE)	Micro-habitat of prey item ¹
Ostracoda	34.16	41.18	4.06 (0.66)	N/B
Culicid A	21.29	52.94	2.53 (0.45)	N
<i>Tillyardophlebia</i>	8.91	58.82	1.06 (0.27)	EL
<i>Atalophlebia</i>	5.45	35.29	0.65 (0.25)	EB
<i>Koorrnonga</i>	4.46	23.53	0.53 (0.25)	L
Veliidae	3.96	17.65	0.47 (0.26)	P
Tanypodinae larvae	3.47	17.65	0.41 (0.24)	?
<i>Ferissia</i>	1.98	11.76	0.24 (0.21)	EL
<i>Bungona</i>	1.49	17.65	0.18 (0.15)	N/B
<i>Tasmanocoenis</i>	1.49	11.76	0.18 (0.18)	EB
Chironominae larvae	0.99	11.76	0.12 (0.14)	?
Dytiscidae adults	0.99	11.76	0.12 (0.14)	N
Notonectid juv	0.99	5.88	0.12 (0.17)	N
Orthocladinae larvae	0.99	5.88	0.12 (0.17)	?
<i>Paratya</i> larvae	0.99	11.76	0.12 (0.14)	N/B
Scirtidae	0.99	11.76	0.12 (0.14)	EB
Terrestrial arthropods ²	0.99	11.76	0.12 (0.14)	P
Aeshnidae	0.50	5.88	0.06 (0.12)	EB
<i>Archichaulioides</i>	0.50	5.88	0.06 (0.12)	EL
Diphlebia	0.50	5.88	0.06 (0.12)	EL
<i>Ecnomus</i> sp.AV20	0.50	5.88	0.06 (0.12)	EB
Hydrobiidae	0.50	5.88	0.06 (0.12)	EL
Orthocladinae pupae	0.50	5.88	0.06 (0.12)	?
<i>Paratya</i> adults	0.50	5.88	0.06 (0.12)	N/B
<i>Plectrocnemia</i>	0.50	5.88	0.06 (0.12)	EL
<i>Sclerocyphon minimus</i>	0.50	5.88	0.06 (0.12)	EL
Stratyomyidae larvae	0.50	5.88	0.06 (0.12)	N
Tanypodinae pupae	0.50	5.88	0.06 (0.12)	?
<i>Triplectides</i>	0.50	5.88	0.06 (0.12)	L
<i>Ulmerophlebia</i>	0.50	5.88	0.06 (0.12)	EB

¹ EB - epibenthic, EL - epilithic, L - leaf litter, N - nektonic, P - pneustonic, N/B - nektonic at some times, benthic at others, ? - uncertain

² Terrestrial Arthropods consisted of ants, adult Diptera and a coccoid bug.

Table 5.3b. Prey items recorded in the gut contents of large *M. adspersa* (> 60 mm SL).

Prey Item	Mean % contribution to gut contents	% fish with item in gut	Mean no. in gut per fish (SE)	Micro-habitat of prey item ¹
<i>Atalophlebia</i>	31.43	68.75	2.75 (0.47)	EB
<i>Tillyardophlebia</i>	18.57	56.25	1.63 (0.38)	EL
<i>Koorrnonga</i>	7.86	43.75	0.69 (0.26)	L
<i>Sclerocyphon minimus</i>	7.14	43.75	0.63 (0.25)	EL
Notonectid juv	3.57	18.75	0.31 (0.21)	N
Terrestrial arthropods ²	3.57	12.5	0.31 (0.23)	P
<i>Bungona</i>	2.86	25	0.25 (0.17)	N/B
<i>Ecnomus</i> sp.AV20	2.86	12.5	0.25 (0.22)	EB
Veliidae	2.86	12.5	0.25 (0.22)	P
<i>Triplectides</i>	2.14	18.75	0.19 (0.16)	L
<i>Ulmerophlebia</i>	2.14	12.5	0.19 (0.18)	EB
<i>Atalomicria</i>	1.43	12.5	0.13 (0.15)	EB
<i>Cherax depressus</i>	1.43	12.5	0.13 (0.15)	EB
Dytiscidae adults	1.43	6.25	0.13 (0.18)	N
Ostracoda	1.43	12.5	0.13 (0.15)	N/B
<i>Anisocentropus</i>	0.71	6.25	0.06 (0.13)	L
Corixidae	0.71	6.25	0.06 (0.13)	N
Culicid A	0.71	6.25	0.06 (0.13)	N
<i>Diphlebia</i>	0.71	6.25	0.06 (0.13)	EL
<i>Episynlestes</i>	0.71	6.25	0.06 (0.13)	EB
Leptophlebiidae juv	0.71	6.25	0.06 (0.13)	?
<i>Paratya</i> adults	0.71	6.25	0.06 (0.13)	N/B
<i>Plectrocnemia</i>	0.71	6.25	0.06 (0.13)	EL
Ptylodactylidae larvae	0.71	6.25	0.06 (0.13)	EB
<i>Sclerocyphon striatus</i>	0.71	6.25	0.06 (0.13)	EL
Anuran Tadpole	0.71	6.25	0.06 (0.13)	N
<i>Tasiagma</i>	0.71	6.25	0.06 (0.13)	EL
Trichoptera	0.71	6.25	0.06 (0.13)	?
indeterminate				

¹ EB - epibenthic, EL - epilithic, L - leaf litter, N - nektonic, P - pneustonic, N/B - nektonic at some times, benthic at others, ? - uncertain

² Terrestrial Arthropods consisted of ants, adult Diptera and a coccoid bug.

There was no significant difference in gut contents between fish sexes allowing for differences between size classes (two way crossed ANOSIM, $R = 0.16$, $p = 0.08$).

There was no significant difference in stomach fullness, the number of prey taxa per gut, number of prey items per gut or the Shannon-Wiener diversity of prey items per gut between large and small fish, or fish sexes (Table 5.4).

There were small but significant, or near significant correlations between the number of prey items per gut and the density of *M. adspersa* in pools when they were collected (positive relationship) and between the number of prey taxa per gut and the area of the pools (negative relationship). No additional significant correlations were found between stomach fullness, the number of prey taxa per gut, number of prey items per gut or Shannon-Wiener diversity of prey items per gut, and pool area and maximum depth, the number of fish in pools, or the density of fish in pools (Table 5.5).

There was no significant difference between the gut contents of fish from different pools (ANOSIM, $R = 0.035$, $p = 0.334$).

Table 5.4. Results of t-tests for differences between gut fullness of *M. adspersa*, the number of prey taxa per gut, the number of prey items per gut and the Shannon-Wiener diversity of prey per gut for (a) size classes, (*large and small*) and (b) sex of fish, (*male and female*).

a) Size Class

	df	t	p
Gut Fullness	31	0.12	0.91
No. Prey Taxa per Gut	31	-0.18	0.86
No. Prey Items per Gut	31	1.15	0.26
Shannon-Wiener Diversity of Prey per Gut	31	-1.37	0.18

b) Sex

	df	t	p
Gut Fullness	31	-0.12	0.91
No. Prey Taxa per Gut	31	-0.08	0.94
No. Prey Items per Gut	31	1.01	0.32
Shannon-Wiener Diversity of Prey per Gut	31	-1.14	0.26

Table 5.5. Pearson's correlation coefficients between aspects of the gut contents of *M. adspersa* and selected environmental parameters. Figures in brackets are the significance levels of the correlations. Shaded cells highlight correlations that were significant or near significant ($p < 0.05$).

Factors	Number of Fish in Pool	Density of Fish in Pool	Pool Area	Pool Maximum Depth
Gut Fullness	-0.01 (0.98)	-0.08 (0.67)	0.06 (0.75)	0.23 (0.20)
No. Prey Taxa per Gut	-0.11 (0.53)	0.28 (0.12)	-0.34 (0.06)	0.01 (0.93)
No. Prey Items per Gut	0.12 (0.51)	0.41 (0.02)	-0.25 (0.15)	-0.07 (0.70)
Shannon-Wiener Diversity of Prey per Gut	-0.16 (0.37)	0.17 (0.34)	-0.29 (0.10)	0.05 (0.79)

c) Pool habitats in which M. adspersa fed

Contributions to the overall gut contents of *M. adspersa* by prey items derived from different habitats varied between individual fish. Some of this variation was related to the size of the fish.

The habitat into which each prey item was classified is included in Table 5.3. Taxa classified into the “uncertain” category were chironomid larvae and early instar trichopterans and Leptophlebiidae. These taxa are certainly benthic but it was unclear as to which of the benthic categories they belonged. The category containing taxa which are both benthic and nektonic at different times includes some taxa, such as Ostracoda and *Paratya* larvae, which move into the water column on a diel basis (see Hancock, 1995) and others, such as adult *Paratya* and *Bungona* nymphs, which swim into the water column as an escape mechanism when disturbed. There was no way to determine whether individuals in this category were displaying benthic or nektonic behaviour when they were consumed by the *M. adspersa*.

The composition of prey items from different habitats varied between individual fish. The mean Bray-Curtis dissimilarity index between fish was 0.63 (SE = 0.01) with a range of 0.14 to 1.0. There were significant differences between large and small *M. adspersa* (ANOSIM, $R = 0.16$, $p = 0.002$). This was due to small fish having fewer items from epibenthic, epilithic and leaf litter habitats and more items from

nektonic/benthic and nektonic habitats than large fish (SIMPER) (Figure 5.8 and Table 5.6). It appears that large fish were predominantly benthic feeders while small fish fed more in the water column and from the surface of the water.

Figure 5.8. Ordination of individual fish based on the log (x + 1) abundance of prey items from different habitats in their stomach contents (a) coded to show size categories of the fish and (b) showing significant correlation vectors of the log (x + 1) abundance of prey items from different habitats with the ordination. Stress = 0.16. (EB - epibenthic, EL - epilithic, N - nektonic, L - leaf litter, P - pneustonic, ? - uncertain)

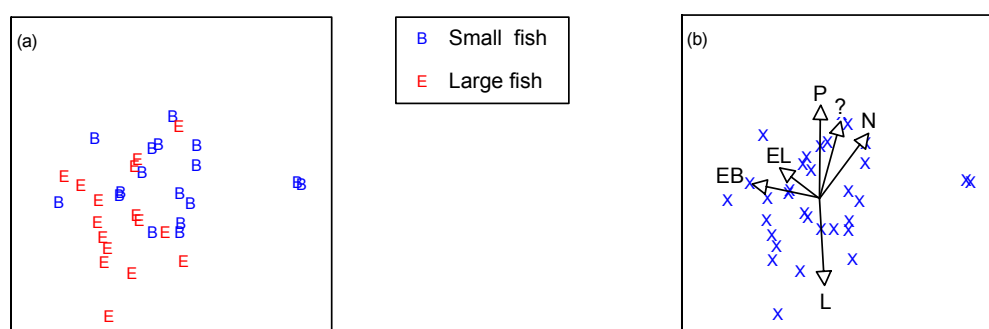


Table 5.6. Contribution of prey items from different micro-habitats to the mean gut contents of *M. adspersa*.

micro-habitat	Mean % contribution		
	All Fish	Small fish	Large fish
N/B	23.98	37.13	5.00
EB	22.22	9.41	40.71
EL	19.59	13.37	28.57
N	16.96	23.76	7.14
L	7.31	4.95	10.71
P	5.56	4.95	6.43
?	4.39	6.44	1.43

N/B - nektonic at some times, benthic at others, EB - epibenthic, EL - epilithic, N - nektonic, L - leaf litter, P - pneustonic, ? - uncertain

5.3.3 The Effects of *M. adspersa* on Pool Fauna: Manipulative Experiment

a) Manipulation of *M. adspersa* density in pools

The wetted area of pools used for the experiment ranged from 16.0 to 67.2 m² (mean = 33.9 m², standard error = 4.7 m²). Maximum depth ranged from 0.27 m to 0.86 m (mean = 0.47 m, standard error = 0.05 m) (see Appendix IV).

Before the manipulation, no *M. adspersa* were caught in any of the pools in block five (Table 5.7). These pools were upstream of a cascade which rose 2 m over a distance of 10 m and which appears to have formed a natural barrier to the upstream dispersal of *M. adspersa*. Pools from the remaining blocks contained between 0 and 18 large *M. adspersa* (mean = 5, standard error = 2) and between 0 and 59 small *M. adspersa* (mean = 15, standard error = 5). The sampling of block five pools was stopped after two passes of the electroshocker because no fish were caught. Pools in the other blocks required between three and seven passes before no *M. adspersa* were caught. This used between 666 and 3978 electroshocker units (mean = 1465 units, standard error = 254 units).

Relationships existed between properties of the pools and the number of *M. adspersa* present before the manipulation (Table 5.8). Block five pools were excluded from these analyses for the reasons outlined above. There were significant correlations between the wetted area of pools and the number of small *M. adspersa* collected in them and between the numbers of large and small fish collected in pools. There was no significant relationship between the area of pools and the number of large *M. adspersa* collected in them. There were significant correlations between the maximum depth of pools and the numbers of both large and small fish collected in pools.

Table 5.7. Number and density of *M. adspersa* of large (L) and small (S) size categories recorded from pools before the manipulation, 16 days after manipulation and at the end of the experiment. The number of electroshocker units used to sample the pools before the manipulation and after the experiment are also presented. The figures in brackets are the number of sampling passes used. Actions taken (additions (+) and removals (-) of large and small *M. adspersa*) following the 16 day sample are summarised. Shaded rows highlight pools where the density of *M. adspersa* at the end of the experiment deviated markedly from the stocking density.

Pool	Block	Treatment	Before Treatment		Density Stocked (fish m ⁻²)	After 16 days		At Termination	
			Density (fish m ⁻²)	Units (Passes)		Density (fish m ⁻²)	Action (fish)	Density (fish m ⁻²)	Units (Passes)
1	1	PC	0L, 0.36S	1812 (7)	0L, 0.36S	0.01L, 0.12S		0.10L, 0.16S	941 (3)
2	1	A	0L, 0.12S	1084 (3)	1.5L	0.21L, 0.07S	+ 36L	0.40L, 0.14S	1435 (4)
3	1	EC							679 (3)
4	1	R	0.54L, 0.39S	1125 (5)	0	0.12S	- 4S	0L, 0.39S	866 (3)
5	2	EC							656 (4)
6	2	A	0L, 0.17S	1314 (4)	1.5L	0.47L, 0.04S	+ 4L	0.47L, 0.04S	1016 (5)
7	2	PC	0L, 0.25S	1764 (5)	0L, 0.25S	0.05S		0L, 0.13S	500 (3)
8	2	R	0.13L, 0.35S	1059 (5)	0	0.13S	- 4S	0	495 (3)
9	3	PC	0.28L, 0.96S	3978 (7)	0.28L, 0.96S	0.15L, 0.2S		0.24L, 0.16S	1305 (3)
10	3	EC							1344 (3)
11	3	A	0.25L, 0.69S	666 (5)	1.5L	0.44L	+ 4L	0.31L, 0.06S	511 (3)
12	3	R	0.43L, 1.11S	1643 (5)	0	0.09S	- 2S	0.04L, 0.09S	516 (3)
13	4	A	0.11L, 0S	939 (3)	1.5L	0.54L	- 1L ¹ , + 2L	0.11L, 0.11S	718 (3)
14	4	EC							420 (3)
15	4	R	0.05L, 0.78S	1481 (5)	0	0.05L	- 1L	0L, 0.27S	374 (3)
16	4	PC	0.05L, 0.10S	712 (3)	0.05L, 0.10S	0.05L, 0.1S		0.05L, 0.10S	361 (3)
17	5	EC							520 (3)
18	5	A	0	540 (2)	1.5L	0.51L	+ 1L	1.23L, 0S	1154 (3)
19	5	R	0	782 (2)	0	0		0	543 (2)
20	5	PC	0	715 (2)	0	0		0	396 (2)

¹ Large *M. adspersa* removed because it had obvious tufts of fungus growing on its head.

Table 5.8. Pearson product-moment correlation coefficients (r) and their two-tailed significance levels (p) between the wetted area and maximum depth of pools, and the abundances of large and small *M. adspersa* caught in the pools. Shaded cells indicate $p \leq 0.05$.

Max. Depth	r = 0.1530 p = 0.635		
No. Large <i>M. adspersa</i>	r = 0.1915 p = 0.551	r = 0.6357 p = 0.026	
No. Small <i>M. adspersa</i>	r = 0.6087 p = 0.036	r = 0.7579 p = 0.004	r = 0.6257 p = 0.030
	Wetted Area	Max. Depth	No. Large <i>M. adspersa</i>

Pools were stocked with *M. adspersa* as indicated in Table 5.7. Sixteen days later all pools (excluding experimental controls) were sampled for *M. adspersa* with two electroshocking passes. This was insufficient sampling to accurately determine the numbers of *M. adspersa* present, but gave an estimation of the success or otherwise of stocking. Fewer large category *M. adspersa* than expected were caught in addition pools and one large fish was caught in a removal pool (pool 15). Small category fish were caught in many pools in which they were not stocked. All fish caught in removal pools were kept out and additional large *M. adspersa* were stocked in addition pools as indicated in the table. A single large fish was removed from pool 13 because it had a large fungal infection on its head, which was considered likely to be terminal. *M. adspersa* are particularly susceptible to infection by the fungus *Saprolegnia* (Merrick and Schmida 1984). No other *M. adspersa* showed signs of illness and all appeared to be in good condition.

The ten large fish removed at random from those used for the experimental stocking and returned to the laboratory survived in an aquarium until the end of the experiment. Furthermore, they displayed neither outward signs of disease nor atypical behaviour.

The numbers of large and small category *M. adspersa* recorded at the end of the experiment, following thorough sampling, did not accurately reflect the numbers stocked a little over a month earlier and further adjusted on day 16 (Table 5.7 and Figure 5.9). After completion of the experimental manipulations, a total of 225 large and 85 small fish were stocked into procedural control and addition pools. At the end of

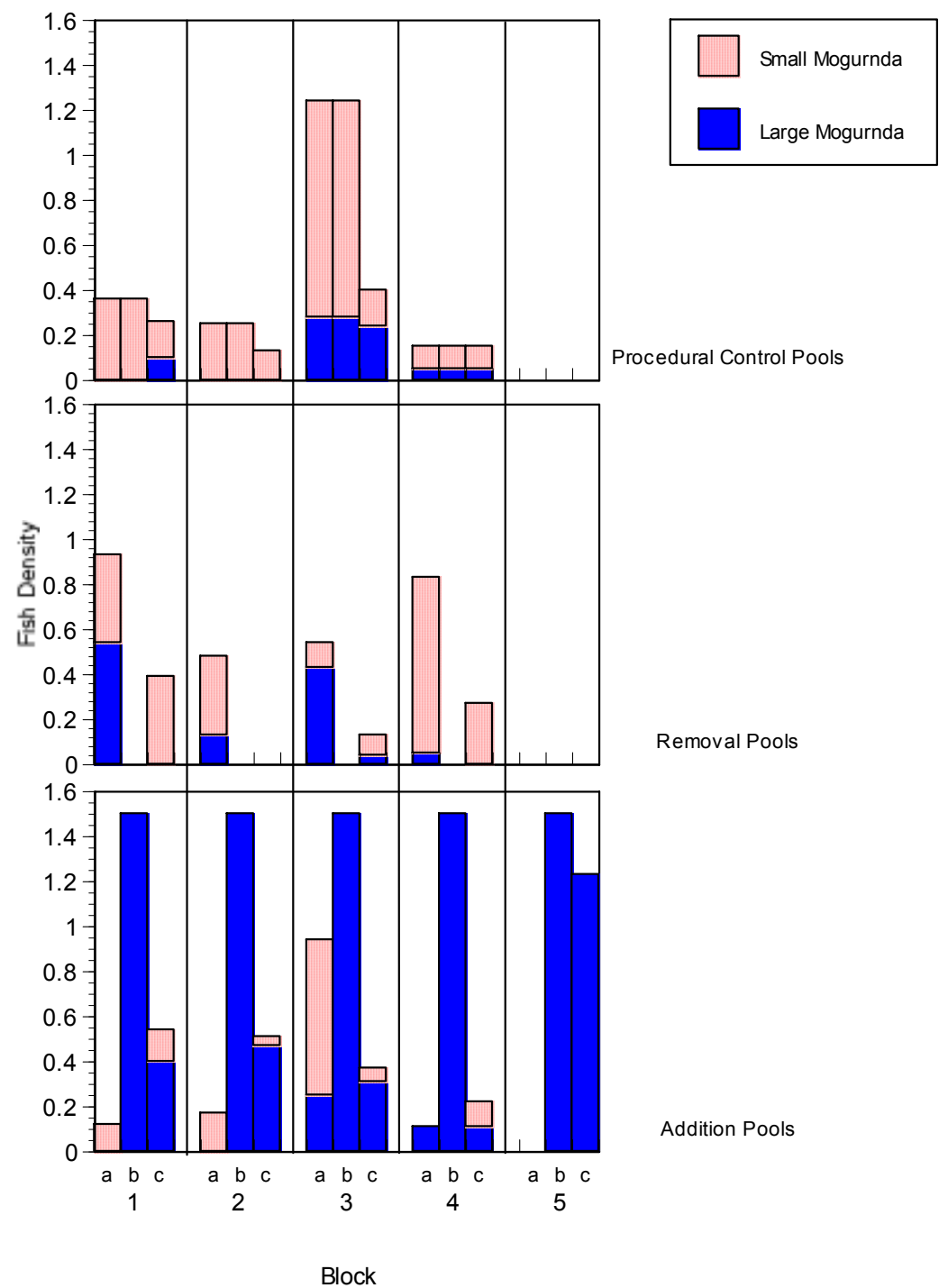
the experiment, 94 large and 55 small *M. adspersa* were collected from these and the removal pools. This equates to persistence rates of 35% and 65% of the fish stocked for the two size classes. Besides the single large fish with a severe fungal infection mentioned above, no sick or dead fish were observed throughout the experiment. It is possible that predators, such as birds, may have eaten some fish.

Small category fish were collected where they were not stocked in many addition and removal pools and occurred at lower densities than they were stocked in some procedural control pools. The densities of large category fish in procedural control pools were similar to those stocked in most cases. The exception to this was in block one where no large category *M. adspersa* were stocked yet seven were collected at the end of the experiment.

In all cases there were fewer large fish collected in addition pools than were stocked. The addition treatments in blocks one, two and five were successful, in the sense that the densities of large *M. adspersa* in these pools at the end of the experiment were considerably higher than their natural densities before the experiment. The addition treatment in block five was particularly successful in that a high proportion (81%) of the large fish stocked were recaptured at the end of the experiment. The addition treatments in blocks three and four were unsuccessful as the densities of large *M. adspersa* in these pools at the end of the experiment were equal to, or only slightly higher than, their natural densities before the experiment.

The removal treatment was successful in all blocks as large category fish were absent or at very low densities at the end of the experiment. However, in block five the removal treatment cannot be considered a true removal as there were no fish present before the experiment.

Figure 5.9. Stacked columns showing the densities (fish m⁻²) of large and small size category *M. adspersa* before manipulation (a), at stocking (b) and at the end of the experiment (c) in procedural control, removal and addition pools for the five experimental blocks.



For both size classes of fish, there were significant correlations between the number of *M. adspersa* present in procedural control, addition and removal pools at the end of the experiment and the number of fish stocked into the pools (Table 5.9). The final abundances of large *M. adspersa* were also significantly correlated with the maximum depth of pools and the final abundances of small *M. adspersa* with their wetted area. This may be partially explained by stocking, as there was a significant correlation between the number of small *M. adspersa* stocked and the wetted area of pools ($r = 0.78$, $p = 0.003$). However, there was no significant association between the number of large *M. adspersa* stocked and the maximum depth of pools ($r = -0.0431$, $p = 0.879$). The relationship between the abundances of small fish in pools at the end of the experiment and the area of the pools can thus be explained by the stocking history of the pools. However, the relationship between the final abundances of large *M. adspersa* and the maximum depth of the pools cannot be explained in this way. This suggests that a greater proportion of the large fish stocked persisted in deeper pools than in shallower pools

Table 5.9. Pearson product-moment correlation coefficients (r) and their two-tailed significance levels (p) between the wetted area and maximum depth of pools, the abundances of large and small *M. adspersa* caught in the pools before the manipulation, the number of large and small *M. adspersa* stocked into the pools and the abundances of large and small *M. adspersa* caught in the pools at the end of the experiment. Shaded cells indicate $p \leq 0.05$. Data from experimental control pools were not used in this analysis.

	Wetted Area	Max. Depth	No. Large <i>M. adspersa</i> Before	No. Small <i>M. adspersa</i> Before	No. Large <i>M. adspersa</i> Stocked	No. Small <i>M. adspersa</i> Stocked	No. Large <i>M. adspersa</i> After
No. Large <i>M. adspersa</i> at End	$r = 0.4940$ $p = 0.103$	$r = 0.5415$ $p = 0.037$	$r = 0.0112$ $p = 0.972$	$r = 0.3263$ $p = 0.301$	$r = 0.6313$ $p = 0.012$	$r = 0.2118$ $p = 0.442$	-
No. Small <i>M. adspersa</i> at End	$r = 0.6967$ $p = 0.012$	$r = -0.0518$ $p = 0.854$	$r = 0.4952$ $p = 0.102$	$r = 0.4804$ $p = 0.114$	$r = -0.0666$ $p = 0.814$	$r = 0.5426$ $p = 0.037$	$r = -0.0308$ $p = 0.913$

b) *Analysis of Pool Fauna*

Altering the density of *M. adspersa* in pools did not result in changes to the structure of pool faunal assemblages.

Seventy-eight taxa were recorded from gravel samples, 34 from cobble samples and 19 from sweep samples.

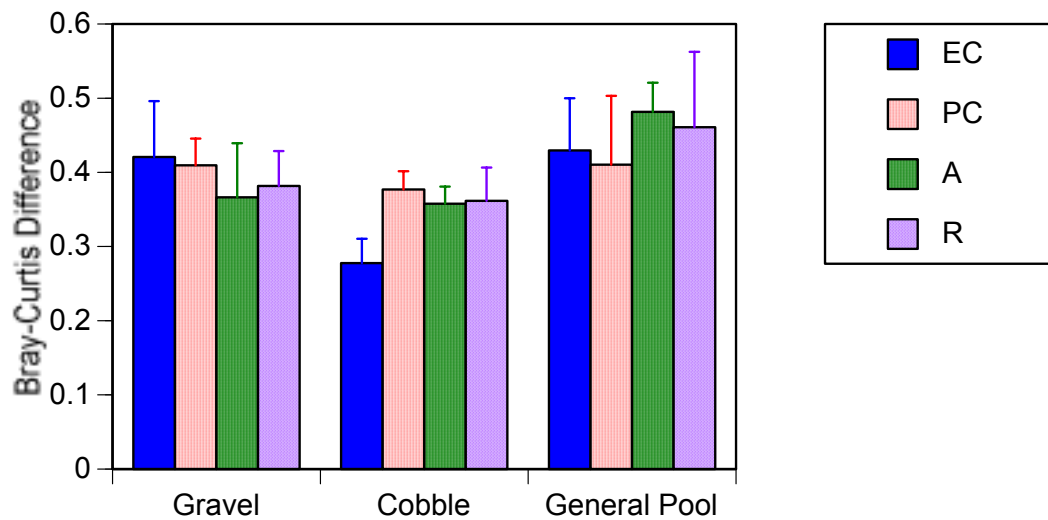
Analysis of faunal abundance and relative abundance data gave very similar results. Only those pertaining to the abundance data are presented. Bray-Curtis differences between the abundances of fauna from samples collected before and after the *M. adspersa* manipulation ranged from small (0.14) to very large (0.92) (Table 5.10, Figure 5.10).

Table 5.10. Bray-Curtis differences between the log (x+1) abundances of fauna following the removal of rare taxa, from samples collected before and after the experiment. Results are presented for gravel, cobble and sweep samples.

EC – experimental control, PC – procedural control, A – addition, R – removal.

		Habitat		
Pool		Gravel	Cobble	General Pool
Block 1	EC	0.2686	0.2084	0.4706
Block 1	PC	0.4187	0.3699	0.1429
Block 1	A	0.3738	0.3864	0.4545
Block 1	R	0.2834	0.3992	0.6078
Block 2	EC	0.4942	0.296	0.3750
Block 2	PC	0.5319	0.2876	0.6190
Block 2	A	0.1817	0.4239	0.5652
Block 2	R	0.4605	0.3653	0.6970
Block 3	EC	0.2839	0.3347	0.5385
Block 3	PC	0.3116	0.4395	0.9190
Block 3	A	0.3777	0.3375	0.3455
Block 3	R	0.2914	0.1885	0.5625
Block 4	EC	0.3823	0.191	0.1833
Block 4	PC	0.4168	0.3897	0.3220
Block 4	A	0.2788	0.2891	0.5306
Block 4	R	0.5239	0.4024	0.2195
Block 5	EC	0.6738	0.3565	0.5800
Block 5	PC	0.3676	0.397	0.3509
Block 5	A	0.6191	0.3521	0.5140
Block 5	R	0.3484	0.4512	0.2182

Figure 5.10. Mean Bray-Curtis difference between the log (x+1) abundance of taxa in faunal samples from three habitats collected before and after the experiment for pools in the for experimental treatments. Bars indicate the standard errors of the means. EC - experimental control, PC - procedural control, A - addition, R - removal.



The null hypotheses were accepted that there was no significant difference in the magnitude of Bray-Curtis dissimilarity between experimental treatments allowing for differences between blocks for all three habitats. Results for the three habitat types were similar and only those for gravel samples are presented (Table 5.11, *see* Appendix IV for other habitats). The effect size of experimental treatment was very small for gravel and sweep samples and larger, although still small, for cobble habitat. The proportions of total variability between samples, taken before and after the experiment, explained by experimental treatment were therefore small. The power to detect differences between treatments was also low in all three ANOVAs, again with cobble habitat higher than the other two.

Faunal differences in pools between before and after the experiment for treatments within blocks are further explored in Figure 5.11, for gravel fauna. Results for the other two habitats were similar and are presented in Appendix IV. These ordination plots graphically illustrate the findings of the ANOVAs that there were no differences in the magnitude of the change in fauna in pools between before and after the experiment. They also show that the multivariate direction of changes, as represented by movement through ordination space over time, varied between treatments within blocks and also between the same treatment in different blocks. In summary, the experimental

manipulation of *M. adspersa* density in pools did not detectably influence change in the structure of pool fauna over time, in terms of magnitude or direction, in any of the habitats sampled.

Table 5.11. Results of mixed model two-way ANOVA without replication testing for differences in the magnitude of Bray-Curtis dissimilarity between the log (x+1) abundance of gravel faunal samples collected before and after the experiment in experimental treatments. Experimental treatment was the fixed factor and experimental block the random factor in the model. The residual was used as the error term. Estimates of effect size and power are also presented.

Source of Variation	SS	DF	MS	F	Significance of F	Effect Size	Power
Experimental Treatment	0.01	3	0.00	0.18	0.906	0.044	0.076
Residual (error)	0.20	12	0.02				

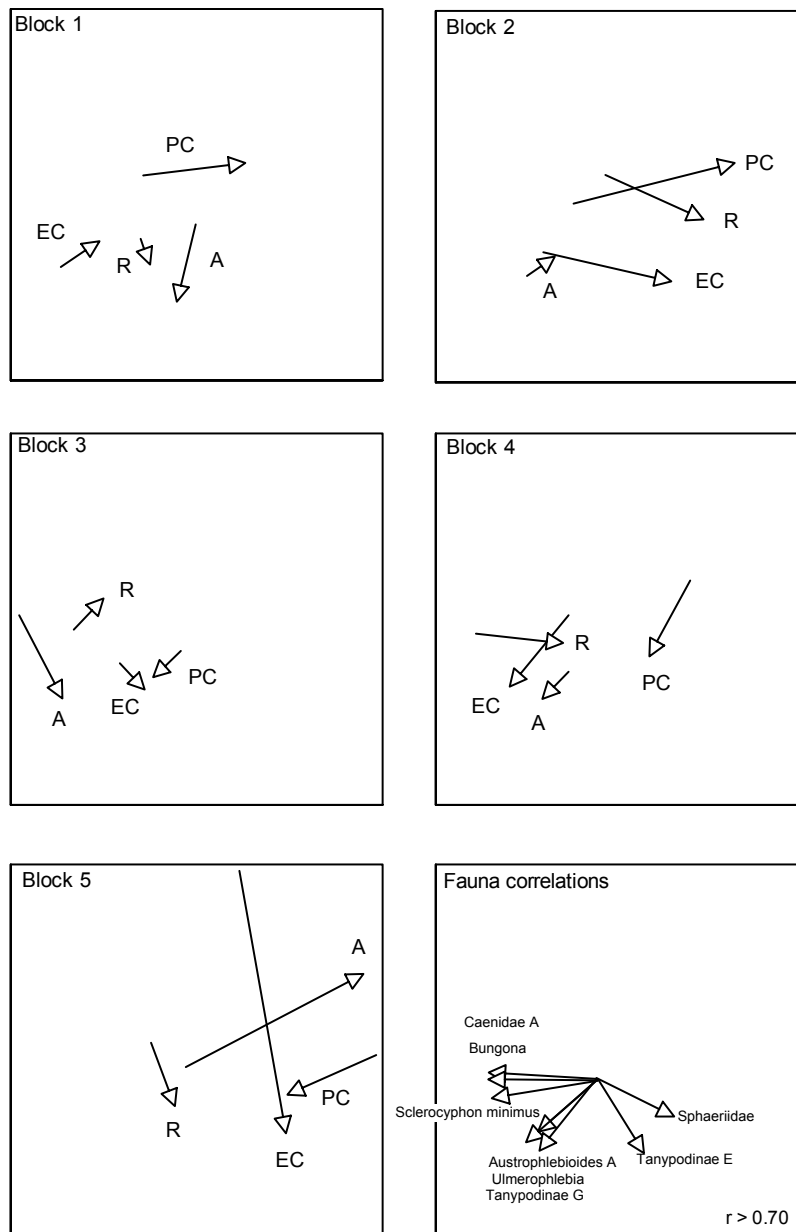
There was no evidence that manipulation of the density of *M. adspersa* affected the abundances of any individual taxa, as there were no significant differences in abundance between before and after the manipulation for all taxa tested ($p > 0.05$) (see Appendix IV).

c) Additional Correlation Analyses

The movement of fish between pools discussed above may have contributed to the failure of the pre-determined analytical methods to detect any effects resulting from experimental manipulation. This movement resulted in the experimental treatments being less defined than desired. To investigate the effects of the manipulation of pool fish density that was actually achieved (as opposed to planned as was used in preceding ANOVA analyses), additional Pearson's correlation analyses were conducted. These investigated correlations between the Bray Curtis difference between before and after the experiment in each pool (log abundance and log relative abundance for each sampling method) and: (a) the change in density of *M. adspersa* in pools, (b) the percent change in density, (c) the change in abundance and (d) the percent change in abundance. Differences in fish populations were calculated both between before manipulation and after 16 days, and before manipulation and the end of the experiment.

None of these correlations were significant or even near significant ($p > 0.05$) indicating that the magnitude of change in pool fauna sampled before and after fish manipulation was not influenced by changes in fish populations in pools.

Figure 5.11. Ordination of the log (x+1) abundance of gravel fauna showing the magnitude and direction of changes between samples taken before and after the experiment for each pool. Plots are divided into blocks and pools within blocks are labeled by experimental treatment. The tail of each arrow indicates the location of the pool in ordination space before the experiment and the head the location after the experiment. All plots are to the same scale and from the same ordination. Correlation vectors of taxa with strong and significant correlations with the ordination ($r > 0.7$, $p < 0.05$) are presented in the final plot. Stress = 0.11.



5.4 Discussion

Analysis of the diets of *M. adspersa* in tributaries of Stony Creek confirmed that they consume a wide diversity of macroinvertebrate taxa. The correlations identified suggest that there is a relationship between the natural density of the fish in pools, the structure of pool faunal assemblages and the abundance of some prey species. Despite this, experimental manipulation of the density of *M. adspersa* in pools did not result in detectable changes in pool fauna.

The diets of *M. adspersa* were dominated by conspicuous and abundant epibenthic and some nektonic invertebrate prey taxa. Previous studies have identified species such as these as being highly vulnerable to predation by fish (e.g. Cooper, 1984a; 1988; Hemphill and Cooper, 1984; Culp, 1986; Holomuzki and Short, 1988; Closs, 1996). One possible explanation for the large variation in the diet of individual fish is simply that *M. adspersa* may feed opportunistically. Further evidence for dietary plasticity is provided by the observed variations between the mean diet of *M. adspersa* in this system and other streams and rivers (see Appendix V). If the observed differences between fish were a result of random opportunistic encounters with prey, fish collected from the same pool may be expected to show some similarity in diet because their probability of encountering a prey species would be similar. Conversely, fish from different pools would have quite different probabilities of encountering a prey species, and may be expected to have less dietary similarity than fish from the same pool. This was not the case, as the pool from which fish were collected did not explain any of the variance in their diets. It is also possible however, that individual fish have differing preferences for particular prey species and concentrate their feeding effort on these species. Such behaviour can result in fish with quite specific individual prey preferences being mistaken for generalist feeders (see Amundsen *et al.*, 1995; Warburton *et al.*, 1998). A consequence of this would be a different influence of predation on prey assemblages in each pool depending upon the feeding preferences of individual fish present.

There was an ontogenetic change in the diets of *M. adspersa* that occurred at approximately the size at which they attain sexual maturity (Merrick and Schmida, 1984). Not surprisingly, small fish fed on smaller prey items and large fish on larger

items. However, the change also involved a shift in the habitat in which feeding occurred. Large fish favoured benthic prey while small fish had a significantly higher nektonic and pneustic component to their diets. Large fish therefore fed mostly at the bottom of the water column while small fish fed more in the water column and from the surface of the water. This cannot be explained by availability of potential prey, as there is an abundance of benthic fauna in pools small enough to be eaten by small size fish (see Chapter 3). Fish feeding near the surface of the water and the edges of pools are more vulnerable to predation than fish feeding deeper (Gelwick *et al.*, 1997). For example, birds such as the azure kingfisher (*Alcedo azurea*), which forage for fish along these streams, capture prey from the surface layer of pools including their edges (*personal observation*). This suggests that based on their feeding habits, small fish may have been exposed to greater predation risk than large fish.

Relationships between the multivariate composition of pool faunal assemblages and the natural density of *M. adspersa* in pools suggested that pool fauna (as collected by sweep samples) changed progressively as the density of *M. adspersa* increased. Furthermore, greater total numbers of individuals (summed across all taxa) and higher abundances of two conspicuous taxa occurred in pools without than those with *M. adspersa*. The faunal composition of gravel habitats in pools with *M. adspersa* present in high densities was also different from the composition in pools without fish. However, these pools were also very different from each other. This suggests that high densities of *M. adspersa* unpredictably influence the fauna of gravel habitats. The possibility discussed above of differing prey preferences between individual fish, provides a mechanism for this relationship. Random combinations in pools of high densities of fish with various individual prey preferences could produce the observed relationships.

A limited number of taxa displayed a strong negative relationship with the presence of *M. adspersa*, suggesting that their abundances were possibly mediated by fish predation. Most of these taxa were not major components of the diets of the fish examined. However, analysis of the gut contents of predators does not necessarily identify prey taxa most susceptible to predation. These taxa can be severely depleted, or even eliminated, by antecedent predation and may therefore be rare or altogether absent from the gut contents of established predators (Paine, 1988; 1992; Closs, 1996).

Despite these correlative relationships, the manipulative experiment found no effects of *M. adspersa* density on pool fauna in any of the habitats examined. Several intrinsic characteristics of the experiment may have contributed to its failure to detect a predation effect. The fish were much more mobile than expected. The assumption that pools under base flow conditions represented isolated populations of *M. adspersa* proved wrong. It appears on the contrary that this is a highly mobile species of fish capable of travelling between pools through riffles containing very little water. Furthermore they have strong preferences for larger, deeper pools and migrate to these from smaller shallower pools. Even the erection of nets at the top and bottom of each pool failed to totally curtail this behaviour. This may represent an adaptive response to life in these streams, which during severe drought dry up except for a few large, deep pools (see Chapter 2). Chances of persistence in the system would be increased by this behaviour. This rendered manipulation of their density in pools problematical and resulted in two of the five fish addition treatments having much lower densities than expected at the end of the experiment. Although there were low densities of fish in these treatments at the end of the experiment, they were included in analyses because they were exposed to increased predation by *M. adspersa* for at least some of its duration. The change in fauna in the three pools where the addition was successful was no greater than in these two pools and correlations between the change in fish populations and the change in faunal composition were small and not significant.

It is possible that the experiment was not run long enough for predation effects to become evident. However other experiments have identified strong interactions between fish predators and their prey in streams over comparable periods (e.g. Gilliam *et al.*, 1989; Peckarsky and McIntosh, 1998). Furthermore, the experiment concluded shortly before the start of the wet season (see Chapter 2) and prolongation would quite probably have resulted in catastrophic termination by a spate without collection of final samples.

The statistical power of the analyses performed was fairly low. It is therefore possible that an effect was present, but was not detected. This is a common problem with such experiments (Allan, 1983). It must be noted however, that not only were changes to

assemblage structure as a result of *M. adspersa* manipulation not significant, but there were no trends in the multivariate direction or magnitude of the changes. This implies that there was no effect present. The only way power could have been increased in this case is by the inclusion of more replicates within each treatment. This would have necessitated the inclusion of additional spatial blocks of pools, which would have been logistically difficult to accomplish.

Other studies have concluded that fish predation had no effect on the assemblage structure of their invertebrate prey (e.g. Allan, 1982; Reice, 1991; Bechara et. al., 1993). A number of the explanations proposed for this lack of effect can be discounted here.

Fish that feed primarily on drift or from the surface of the water are less likely to affect benthic invertebrates (Morgan and Ringler, 1994 Waters, 1993; Dahl and Greenberg, 1998). Dietary analysis has shown that *M. adspersa* were not feeding primarily on drift or from the surface of the water. *M. adspersa* in these pools clearly feed primarily on the benthos, although smaller individuals do take a higher proportion of their prey from the water column and surface. Terrestrial arthropods, which form an important component of the diet of many drift feeding fish (Pusey and Kennard, 1995), were an insignificant component of the diet of *M. adspersa*. Several of the taxa displaying the highest drift rates in these streams (e.g. Simuliidae and Hydropsychidae larvae) (Kerby et al. 1995), were absent from the diet of *M. adspersa*. Furthermore, these streams are known to exhibit low drift rates particularly during periods of low flow (Kerby et al. 1995). As flows were very low during the experiment, to the extent that pools were almost isolated, it is likely that drift was also very low.

The effects of predation can be masked if prey items consumed by fish are replaced by immigrants from upstream (Culp, 1986; Cooper et al., 1990; Sih and Wooster, 1994). Lack of significant drift in these streams (Kerby et al. 1995) and the relative isolation of the pools also negate this explanation.

Soluk and Collins (1988) demonstrated that in the absence of fish, invertebrate predators can become more effective. They suggested that predation by invertebrates may compensate for the presence of fish in manipulative studies removing fish

predation in streams. This phenomenon may have contributed to the failure of *M. adspersa* addition and removal to induce an effect. For this to occur there would have to be invertebrate predators present which responded in this way to fish and which were capable of exerting the same predation pressure as the fish. Many of the invertebrate predators in these pools occur sporadically and in low densities, and are not likely to exert strong predation pressure with or without fish. The only abundant invertebrate predators during the experiment were nymphs of the zygopteran *Episynlestes albicauda* (up to 5 m⁻²), Notonectidae sp.B (up to 10 m⁻²) and to a lesser extent nymphs of the mayfly *Mirawarra* (difficult to estimate, but perhaps up to 1 m⁻²). Nothing is known concerning the potential predation pressure exerted by two of these taxa, but an individual Notonectidae sp.B can consume 10 nymphs of the baetid *Bungona narilla* in 24 hours under laboratory conditions (J. Marshall, *unpublished data*). While it is possible that these taxa change their behaviour, and thus the predation pressure they place on their prey, in response to the presence of fish (*see* Cooper, 1984b; 1988; Closs, 1996), it seems unlikely that changes would in fact mask the effects of the fish. For this to occur the predation pressure and target prey taxa of the invertebrate predators alone would need to approximate that for the invertebrate predators plus the fish. Differing attributes of the predator taxa, such as size, density, prey preferences, feeding behaviour and mechanisms, as well as prey taxon specific vulnerability to predation, make the proposed scenario unlikely. Further experimentation would be necessary to clarify whether or not a balanced relationship exists between predation by *M. adspersa* and these invertebrates.

It has been suggested that the effects of fish predation on prey assemblages are likely to be weak in streams with high substrate heterogeneity. Such substrates are thought to provide a multitude of refugia for prey to avoid predation (*e.g.* Flecker and Allan, 1984; Gilliam *et al.*, 1989; Power, 1992; Closs, 1996). The pools used in this study had highly heterogeneous substrates (*see* Chapters 2 and 3), yet many taxa were vulnerable to predation by *M. adspersa*. The large number of taxa recorded in the diets of the fish bears testimony to this. An alternative explanation for the lack of detectable predator effects in the experiment is that the prey consumed by the fish represented a very small component of total available prey in each pool. Assuming that the gut contents of the fish examined represented all prey consumed in half a day, each fish consumed an

average of 10 prey items per half day or 20 items per day. Over the 36 days of the experiment each fish would have consumed an average of 720 prey items. The average size of pools used in the experiment was 35 m² and fish were stocked into addition treatment pools at 1.5 fish m⁻². Assuming all stocked fish remained in the pools and fed at this rate, 37 800 prey items were consumed in this average pool during the experiment. How does this compare with the number of prey items available in the average pool? Using fauna of the gravel habitat as an example, a sample covers an area of 0.01 m² (see Chapter 3) and this habitat forms 5% of the substrate of the average pool (see Chapter 3). An average gravel sample contained 200 animals which corresponds to 20 000 m⁻² or 35 000 animals living in gravel habitat in the average pool. If it is assumed fish apportion their feeding effort equally between all benthic habitats, they would spend 5% of their time feeding over gravel. Of the total of 37 800 prey items consumed, 1890 would be taken from gravel habitat. This represents only 5.4% of the total gravel fauna in the pool. Such a small change to the fauna would not be detected and may be replaced by natural recruitment (see Reice, 1991b). In practice only conspicuous and vulnerable taxa such as *Paratya*, *Episynlestes* and Notonectidae were likely to be affected by *M. adspersa* predation during the experiment. The fact that they were not may be because they were able to reduce the effectiveness of predation by altering their behaviour and/or seeking refuge in the heterogeneous pool substrates (Cooper, 1984b; 1988; Power *et al.*, 1985; Sih and Wooster, 1994; Wooster, 1994; Closs, 1996; Pierce and Hinrichs, 1997; Peckarsky and McIntosh, 1998).

Conflicting results from the manipulative experiment and correlation analyses can be accounted for by considering the properties of the two approaches. Results of the experimental manipulation are considered to be inconclusive for two reasons. Firstly, success of the manipulation of fish density was variable, as despite efforts to contain the fish they apparently moved between pools. Secondly, because the composition of pool fauna was highly variable in space and time (see Chapter 3), the power of the experiment to detect a predation effect was low. Because of this, the failure of the experiment to demonstrate an effect of *M. adspersa* predation on pool fauna cannot be considered as indicative that such an effect did not exist.

Correlation analyses between non-manipulated populations of *M. adspersa* and the abundances of their prey identified patterns, but such “natural” experiments, by their nature, cannot attribute causation to these patterns (*see* Cooper and Dudley, 1988). One of the reasons for this view is that in natural experiments, variation in extrinsic environmental factors is uncontrolled and one or more such factors may be responsible for observed patterns. However, the results of Chapter 3 indicate that, in this case, pool scale environmental variation explains almost none of the faunal variation in pools. Given this, predation effects are perhaps the most plausible agents for the relationships identified by correlation.

It thus appears that predation can have an effect on the structure of pool assemblages, but that the nature of this effect can be unpredictable. The variable nature of the effect is supported by high variability in the diets and apparent feeding preferences of individual fish.

CHAPTER 6: GENERAL DISCUSSION

6.1 Understanding the drivers of spatial and temporal variation in communities

Identification of the factors that give rise to observed patterns of species distribution and abundance is a key goal in ecology. The importance of abiotic and biotic factors in determining the organisms present at a location has long been recognised and separating their relative influence has been a core theme in ecological research. Abiotic attributes of habitat influence assemblages via the tolerances and preferences of species (Hutchinson, 1957), but biotic processes such as competition and predation can alter patterns predicted from abiotic relationships alone, and thus can also play a significant role.

Classical community theory suggests there should be deterministic convergence in the structure of communities in environmentally similar patches governed by resource limitation and competition for those resources (Cody and Mooney, 1978). In this vein there is evidence that in streams species richness can be strongly deterministic at the local habitat scale (e.g. Lake *et al.*, 1985; Giller *et al.*, 1991; Death and Winterbourn, 1994; Downes *et al.*, 1998a). This theory would further predict that physically similar habitats within a region should support similar communities. In this sense a “community” can be considered a repeatable interacting set of species. An equilibrium view of community composition is however not supported by evidence from streams (e.g. Lake *et al.*, 1985; Minshall *et al.*, 1985; Downes *et al.*, 2000). An opposing non-equilibrium view is that other forces such as parasites and pathogens, predation, seasonality, disturbance and environmental stochasticity hold population densities at levels such that resources do not become limiting (Connell, 1975; Birch, 1979; Strong, 1984), so that species occupy a location largely independently of one another (Lawton, 1984) and can thus be thought of as “multi-species assemblages” rather than communities.

The primary aim of this thesis was to determine the factors that give rise to patterns of spatial and temporal variation observed in the structure and composition of the fauna of rainforest stream pools, based on (a) observation, (b) exploration of causality through correlation with environmental (and biotic) parameters that are often thought to be drivers, and (c) manipulative experiments.

6.2 Habitat/abiotic drivers of faunal patterns

There is a substantial body of evidence indicating that the abiotic attributes of habitat strongly influence the distribution and abundance of species in streams, and thus the composition of stream faunal assemblages (Hynes, 1970; Vannote *et al.*, 1980; Statzner and Borchardt, 1994; Poff, 1997). If habitat were an important driver in these streams, then spatial and temporal patterns in fauna would be explained by environmental variation. This was not so, and at best habitat was a weak predictor.

6.2.1 Spatial patterns

There were few obvious pool-level environmental filters influencing faunal assemblages (*sensu* Poff, 1997). Within habitat types, spatial patterns observed in the fauna were unrelated to environmental variation. Expectations that the fauna living on cobbles would be influenced by the size of the stones, or the quantity of epilithon on their surfaces, were not realised. In a similar manner, fauna living in gravel accumulations varied independently of the mass of the gravel in the sample, the particle size composition of the gravel, or the quantity and quality of organic matter in the gravel, and general pool fauna was not governed by the size of the pool, its substrate composition, or the availability of primary food resources.

The lack of relationship between pool size and faunal composition is contrary to expectations. These pools can be considered “*islands*” as they meet the definition of Simberloff (1974) of an island being “*any patch of habitat isolated from similar patches by different and relatively inhospitable terrain traversable only with difficulty by the organisms dwelling in the habitat patch.*” Island biogeography theory (McArthur and Wilson, 1967) would therefore predict a correlation between pool size and species richness, and such relationships have been found in ephemeral freshwater pools (*e.g.* Ebert and Balko, 1987; March and Bass, 1995) and on individual cobbles within streams (Hart and Horwitz, 1991; Douglas and Lake, 1994; Downes *et al.*, 1998a). This is only one of many possible predictions concerning the influence of habitat on biota that were not met in these streams.

At the stream level there were consistent faunal differences, but it is unclear what factor or factors were responsible. Stream CPOM load is implicated, as there were consistent differences between the streams in the mass of CPOM in pools, but the mechanism for this influence is not clear. The observation that differences in CPOM mass between pools in the same stream or within individual pools over time did not explain faunal variation further confuses this issue. This simply implies that whatever influences faunal differences between the streams also influences CPOM.

6.2.2 Temporal patterns

If temporal variation in habitat attributes were important drivers of faunal patterns, then trajectories of temporal changes in pool fauna would be expected to follow temporal change in environmental properties. In fact, there was no clear sequence of change that related to temporal change in environmental parameters and individual pools often followed quite different temporal trajectories. Contrary to expectations, the fauna of these stream pools showed no seasonality despite marked seasonal environmental patterns. Likewise, the life histories of grazing caddisflies in these streams show no clear response to a marked seasonal temperature cycle (Bunn, *unpublished data*).

6.3 Biotic drivers

Could the observed lack of influence of abiotic factors upon pool fauna be the result of strong biotic processes in the mostly “benign” pool environment (*sensu* Peckarsky *et al.*, 1990)?

6.3.1 *Mogurnda adspersa* – predator with a patchy distribution

If predation were a key driver of faunal patterns, then a strong effect would be predicted from the predominant benthivorous fish predator, *Mogurnda adspersa*. There was some evidence of an effect, but this was not strong enough to explain the magnitude of observed spatial and temporal faunal variation.

There was some evidence, in the form of natural correlations, that predation by *Mogurnda*, influences the composition of pool fauna and the abundances of some prey species in pools. In one habitat, the faunal compositions of pools with naturally high

fish densities were as different from each other as they were from those pools with naturally low fish densities. This is the type of pattern that would be predicted as a consequence of the highly variable prey preferences of individual fish identified from dietary analyses. Large and conspicuous taxa were predicted to be the most vulnerable to predation, and there was a direct relationship between their composition and abundance in sweep samples, and the natural density of *Mogurnda* in pools.

Despite these natural correlations, manipulation of the density of *M. adspersa* in pools resulted in no significant changes in pool faunal assemblages. Although there were problems encountered with fish density manipulation, the refugium hypothesis; whereby heterogeneity of substrate provides numerous places where prey species can avoid predation (*e.g.* Flecker and Allan, 1984) offers a plausible explanation of the results. Another possible explanation is that predation rates were low with respect to the overall availability of prey (*i.e.* lots of prey and few fish), so that predation had little influence on prey assemblage structure (*see* Reice, 1991b).

Predation by fish thus had some influence on the composition and abundance of fauna in pools but the consequences were unpredictable, due in particular to the effects of variation in the diet preferences of individual fish. The effects of predation were weak and once again, were overwhelmed by some other stochastic process.

6.3.2 Bioturbation – the role of Paratya australiensis

There was an expectation that the atyid shrimp *Paratya australiensis* would play an important role in influencing the fauna of the study pools, given its large biomass in pools and the known effects of atyids from other studies (*e.g.* Pringle *et al.*, 1993). Furthermore, it is one of the few species that showed a weak association between abundance and pool attributes, so shrimp effects on other biota may have been mediated by environmental factors such as pool size and depth. If bioturbation from *Paratya* had a strong influence on pool biota, then manipulation of their density would result in faunal responses. Again however, there was no marked effect from manipulation and no major correlative evidence of positive or negative associations with other biota. Bio-removal of fine sediment deposited upon the bed of streams has been demonstrated to be an important process in some systems and was expected to be equally important in

the study streams. However, the rate at which fine sediment settled from suspension and was deposited in the study pools was low. Removal of shrimp from pools thus had no effect on the build-up of deposited fine sediments. There was consequently no cascading effect on the biomass of epilithic algae, or on the composition of pool fauna. This is in stark contrast to predictions based on the results of atyid shrimp removal in systems where the rate at which fine sediment is deposited is high (Pringle *et al.*, 1993) and indicates that under base-flow conditions, sediment deposition is not a dominant process in the study streams.

6.4 What underpins the unpredictable patterns?

To summarise the results of this study, spatial and temporal variation was observed in the structure and composition of the fauna of rainforest stream pools. Pools within and between streams were different from each other, despite similarities in physical features or close proximity. Pool fauna also displayed unpredictable temporal variability, which did not follow a defined seasonal signal, nor could it be related to obvious temporal change in flow or other factors. Predation had a small effect but was not responsible for the overall patterns. Both abiotic and biotic processes that are commonly considered to be the most important drivers of faunal patterns in streams were thus found to exert very little influence on stream pool fauna at the scales studied.

A possible and plausible explanation of these results is offered by considering the effects of stochastic processes associated with the supply of recruits to pools. Under this explanation, the fauna present in a pool at any time is determined by low-level random recruitment events from a regional pool of potential recruits. As a consequence, biotic and abiotic influences are overwhelmed, and the composition of fauna in pools varies at random in both space and time. This explanation is supported by population genetics studies of several taxa in the study area (Schmidt *et al.*, 1995; Bunn and Hughes, 1997; Hughes *et al.*, 1998). Such control of species assemblages by recruitment is not a novel concept and has been well documented in marine and terrestrial environments, where they have been referred to as "*supply-side*" ecology (see Underwood and Fairweather, 1989).

6.4.1 *Stochastic effects of recruitment in other ecosystems*

Many species including marine plants and invertebrates, many insects, many fish, parasites and some terrestrial plants have life history stages that undergo obligate, broad-scale dispersal. As a consequence of this life history strategy, areas subject to local extensions of a species can be readily recolonised from other population sources (*e.g.* Arnolds *et al.*, 1998). Furthermore, widespread dispersal means that different life history stages do not compete with each other for resources (*e.g.* Uriz *et al.*, 1998).

Variability in the success of dispersal in species with obligate dispersal stages can result in recruitment variability at a location (*e.g.* Campus and Lagos, 1996; Harris *et al.*, 1998; Satumanatpan *et al.*, 1999; Connell and Green, 2000). If the dispersal stages of the species do not arrive at a habitat with sufficient regularity and quantity to saturate available resources, local population sizes will be governed by recruitment success (*e.g.* Doherty and Fowler, 1994; Schmitt and Holbrook, 2000). When many species are involved there is a high chance that some species may fail to recruit to a habitat patch and it is unlikely that all areas of the same habitat type will contain the same assemblage of species (*e.g.* Ault and Johnson, 1998). Under these circumstances the structure of assemblages become both spatially and temporally variable and unpredictable (Underwood and Fairweather, 1989).

6.4.2 *Support for this in streams*

Bunn and Hughes (1997) proposed the hypothesis that much of the spatial and temporal variation in aquatic populations within the study streams is controlled by stochastic low-level recruitment. Evidence to support this was provided by population genetics studies of several aquatic insect species with winged adult phases capable of wide spread dispersal (Schmidt *et al.*, 1995; Bunn and Hughes, 1997; Hughes *et al.*, 1998; see Section 3.4.5). Allowing for reasonable levels of egg and larval mortality, Bunn and Hughes (1997) estimated that the total population of a species of caddisfly in a stream reach could be the offspring of between only 3 and 12 females. The results of this body of work presents strong evidence that recruitment rates for some species are very low and patchy in Conondale Range streams.

For recruitment to govern spatial and temporal patterns in the faunal composition of stream pools, the pools must also experience low levels of connectivity. If this were not the case, movement of individuals between pools would override any effects of patchy recruitment and homogenise fauna occupying similar habitat patches throughout the stream. Results of the above-mentioned population genetics studies provide strong evidence that larval movement is negligible in Conondale Range streams, as genetic differences at the scale of individual pools were greater than those between streams and subcatchments. Low pool connectivity in these streams is a consequence of very low stable flow levels for much of the time, local topography with bedrock controls forming barriers between pools and very low levels of drift (Kerby, 1991; Kerby *et al.*, 1995). During periods of elevated discharge further genetic evidence suggests connectivity and in-stream movement of fauna may increase (Hughes *et al.*, 2000).

The results of this study support those of Downes *et al.* (2000) that faunal composition can display large differences between sites relative to those between whole rivers and furthermore, stochastic low-level supply of recruits, as discussed above, provides a plausible mechanism for such localised fluctuations. However, further research into recruitment processes in these streams is required to support this proposed model.

6.5 Conclusions: Implications for the ecology and management of streams

The unpredictable patterns of spatial and temporal variation in stream pool fauna described by this study have consequences for both our understanding of stream ecology and the means by which streams are managed.

Under this mechanism, taxa can have individual habitat preferences, and strong evidence for this was provided by this study. For example, *Koornonga* sp.AV1 occurs only in leaf litter habitat and net spinning caddisfly larvae such as *Plectrocnemia* sp.AV1 are likely to require a specific range of flow velocity. However, the presence or absence and abundance of species are unpredictable. For this reason, the presence of habitat alone cannot be used to predict resulting assemblage composition. This has important implications for the management of streams.

Biomonitoring to establish the ecological health of aquatic systems is becoming increasingly important worldwide and in Australia where this study was conducted. This process depends on an understanding of the biophysical processes influencing the structure and function of communities (Norris and Norris, 1995). There is an implicit assumption that empirical and predictable relationships exist between habitat condition and the composition of the fauna living in the habitat. This study has demonstrated that such relationships do not necessarily exist in all streams at the spatial scales commonly applied to Australian biomonitoring studies (*i.e.* the stream pool as an example of a habitat unit). This does not imply that the results of previous studies that have demonstrated strong correlations between biotic patterns and environmental conditions are invalid, but does show that such strong relationships are not universal. Accurate prediction of the composition of fauna in one of the study pools at a particular time is not possible because of the stochastic nature of spatial and temporal faunal variation. Furthermore, it is unreasonable to assume that a site is representative of larger spatial units such as stream reaches, or that a single sample from a site is representative of a longer time interval (*see also* Downes *et al.*, 2000). It would however, be possible to accurately predict the composition of the composite fauna of all of the pools within a particular stream reach or of one particular pool over a period of time. The accuracy of any such prediction would increase with the size of the reach or the length of the period of time, as the larger the spatial or temporal scale over which prediction is made, the greater the proportion of stochastic variation that is explained. In effect, such predictions would be of the pool of species available for colonisation to each habitat type.

The extent to which streams in southeast Queensland and elsewhere follow the patterns identified in this study is not known. Genetic evidence suggests that variation in faunal assemblages in other streams in the Conondale Range at least, is similarly unpredictable (Schmidt *et al.*, 1995; Bunn and Hughes, 1997; Hughes *et al.* 1998). If this phenomenon is more widespread it has significant implications for the design and interpretation of biomonitoring programmes. Further research may be warranted to identify the spatial extent of streams that follow these patterns.

The findings of this study also have implications for our understanding of the role of biotic processes such as competition and predation in streams. Under benign environmental conditions, such as those experienced in the study pools during base flow, competition has the potential to become important amongst similar species such as the guild of grazers on hard substrates (Negus, 1995). It is unlikely that this would ever lead to competitive exclusion, as a local extinction in one pool would not occur in another because of the chance absence or low abundance of the competitively superior species. Similarly, predation effects may never be consistent. A fish arriving in a particular pool may encounter certain abundant taxa and form a search image and thus feeding preference for those taxa. Predation upon these taxa would shift the resulting assemblage structure in a particular direction. Different pools would shift in different directions as a result of chance variations in which species constitute abundant taxa and subsequently fish feeding preferences.

In these stream pools, where much of the observed spatial and temporal faunal variation is unpredictable, the notion of “*community*” as a repeatable, interacting set of species is not appropriate. Rather, the fauna present within a habitat patch at any time appears to represent a random selection of potentially available species, and as such the notion of “*multi-species assemblage*” appears more apt.

CHAPTER 7: REFERENCES

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APPENDIX I: EXAMPLES OF PHOTOGRAPHIC SAMPLES

Figure A. Two examples of the photographs that were used to confirm identifications of pool fauna. Intervals on the scale bar represent 1 mm. Note that reproduction of these images has reduced their resolution from that of the originals.

a) Sweep sample



b) Cobble sample



APPENDIX II: TAXONOMIC LISTING OF FAUNA

Table A. Classification of all taxa collected throughout the study, with authorities for species and abbreviated short names and codes used in some tables and figures throughout the text. All insect taxa are larvae unless indicated: (a) adults, (l) larvae.

Classification	Taxon	Short Name	Code
<u>Cnidaria</u>			
Hydrozoa	Hydra	Hydra	HYDRA
<u>Platyhelminthes</u>			
Turbellaria			
Dugesiidae	<i>Dugesia</i> sp.	Turbellaria	TURB
<u>Nematoda</u>	Nematoda	Nematoda	NEMATOD
<u>Nematomorpha</u>			
Gordioidea			
Gordiidae	Gordiidae	Gordiidae	GORD
<u>Annelida</u>			
Oligochaeta	Oligochaeta	Oligochaeta	OLIGO
<u>Mollusca</u>			
Bivalvia			
Sphaeriidae	<i>Pisidium (Pisidium)</i> sp.A	Sphaeriidae	SPHAE
Gastropoda			
Ancylidae	<i>Ferissia</i> sp.A	<i>Ferissia</i>	FERISS
Gastropoda <i>continued</i>			
Hydrobiidae	Hydrobiidae sp.A.	Hydrobiidae	HYDROBII

Classification	Taxon	Short Name	Code
<u>Arthropoda</u>			
Crustacea			
Copepoda	Copepoda	Copepoda	COPE
Ostracoda	Ostracoda sp.A	Ostracoda A	OSTRACOA
	Ostracoda sp.B	Ostracoda B	OSTRACOB
Cladocera	Cladocera	Cladocera	CLAD
Decapoda			
Atyidae	<i>Paratya australiensis</i> (a) Kemp 1917	<i>Paratya</i>	PARAA
	<i>Paratya australiensis</i> (l) Kemp 1917	<i>Paratya</i> (l)	PARAL
	<i>Australatya striolata</i> (Mculloch and McNeil 1923)	-----	-----
Palaemonidae	<i>Macrobrachium australiense</i> Holthuis 1950	<i>Macrobrachium</i>	MACRO
Parastacidae	<i>Euastacus hystriacus</i> Riek 1951	<i>Euastacus</i>	EUAST
	<i>Cherax depressus</i> Riek 1951	<i>Cherax</i>	CHERAX
Arachnida			
Acari	Mite J	Mite J	MITEJ
	Mite L	Mite L	MITEL
Aturidae	<i>Albia lundbladi</i> Cook 1986	Mite K	MITEK
Hygrobatidae	<i>Australiobates violaceus</i> Lundblad 1941	Mite B	MITEB
Limnesiidae	<i>Limnesia brinvosa</i> Cook 1986	Mite H	MITEH
Momoniidae	<i>Momoniella parva?</i> Cook 1986	Mite F	MITEF
Unionicolidae	<i>Koenikea</i> sp.	Mite C	MITEC
	<i>Recifella</i> sp.	Mite D	MITED
Malaconothridae	<i>Trimalaconothrus</i> sp.	Mite I	MITEI

Classification	Taxon	Short Name	Code
Hexapoda			
Ephemeroptera			
Caenidae	<i>Tasmanocoenis queenslandica</i> (Soldan 1978)	<i>Tasmanocoenis</i>	CAENA
Baetidae	<i>Bungona narilla</i> Harker 1957	<i>Bungona</i>	BUNGONA
Amelotopsidae	<i>Mirawara</i> sp.	<i>Mirawara</i>	MIRA
Leptophlebiidae	<i>Atalomicria</i> sp.AV1	<i>Atalomicria</i>	ATALOMIC
	<i>Atalophlebia</i> sp.AV13	<i>Atalophlebia</i>	ATALOPH
	<i>Austrophlebioides</i> sp.AV6	<i>Austrophlebioides</i> C	AUSTROC
	<i>Koorrnonga</i> sp.AV1	<i>Koorrnonga</i>	KOORR
	<i>Tillyardophlebia</i> sp.AV6	<i>Tillyardophlebia</i>	TILLYARD
	<i>Ulmerophlebia</i> sp.AV3	<i>Ulmerophlebia</i>	ULMERO
Megaloptera			
Corydalidae	<i>Archichaulioides</i> sp.A	<i>Archichaulioides</i>	ARCHI
Odonata			
(Zygoptera)	Zygoptera juveniles	Zygoptera juv	ZYGO
Isostictidae	<i>Labidosticta vallis</i> (Fraser 1955)	<i>Labidosticta</i>	LABIDO
Megapodagrionidae	<i>Austroargiolestes</i> sp.	<i>Austroargiolestes</i>	AUSTARG
Synlestidae	<i>Episynlestes albicauda</i> (Tillyard 1913)	<i>Episynlestes</i>	EPI
	<i>Synlestes tillyardi</i> Fraser 1948	<i>Synlestes</i>	SYNLEST
Diphlebiidae	<i>Diphlebia coerulescens</i> Tillyard 1913	<i>Diphlebia</i>	DIPHL
(Anisoptera)	Anisoptera juveniles	Anisoptera juv.	ANIS
Telephlebiidae	<i>Austroaeschna sigma</i> Theischinger 1982	<i>Austroaeschna</i>	AUSTROAE
Gomphidae	<i>Austrogomphus amphi-clitus</i> (Selys 1873)	<i>Austrogomphus</i>	AUSTGOM
	<i>Hemigomphus gouldii</i> (Selys 1854)	<i>Hemigomphus</i>	HEMGOM
Austrocorduliidae	<i>Austrocordulia refracta</i> Tillyard 1905	<i>Austrocordulia</i>	AUSTCORD
Cordulephyidae	<i>Cordulephya pygmaea</i> Selys 1870	<i>Cordulephya</i>	CORDU
Synthemistidae	<i>Eusynthemis nigra</i> (Tillyard 1906)	<i>Eusynthemis</i>	EUSYN

Classification	Taxon	Short Name	Code
Plecoptera			
Eustheniidae	<i>Stenoperla australis</i> Tillyard 1921	<i>Stenoperla</i>	STENO
Gripopterygidae	Gripopterygidae juveniles	Gripopterygidae	GRIP
Trichoptera			
Hydroptylidae	<i>Hellyethyra simplex</i> (Mosely 1934)	<i>Hellyethyra</i> A	HELLYA
	<i>Hellyethyra</i> sp.B	<i>Hellyethyra</i> B	HELLYB
	<i>Orthotrichia</i> sp.	<i>Orthotrichia</i>	ORTHOTR
Philopotamidae	<i>Chimarra australica</i> (Ulmer 1916)	<i>Chimarra</i>	CHIM
Hydropsychidae	<i>Cheumatopsyche</i> sp.	<i>Cheumatopsyche</i>	CHEUM
Polycentropodidae	<i>Parayctiophylax</i> juveniles	<i>Parayctiophylax</i> juv	NYCTJUV
	<i>Parayctiophylax</i> sp.AV3	<i>Parayctiophylax</i> sp.3	NYCTIO3
	<i>Parayctiophylax</i> sp.AV5	<i>Parayctiophylax</i> sp.5	NYCTIO5
	<i>Plectrocnemia</i> sp.AV1	<i>Plectrocnemia</i>	PLECTRO
Ecnomidae	Ecnomidae juveniles	Ecnomidae juv	ECNOMJUV
	<i>Ecnomina</i> F sp.AV5	<i>Ecnomina</i>	ECNOMAF5
	<i>Ecnomus continentalis</i> Ulmer 1916	<i>Ecnomus continentalis</i>	ECNOMSC
	<i>Ecnomus</i> sp.AV20	<i>Ecnomus</i> sp.AV20	ECNOMS20
Tasimiidae	<i>Tasiagma ciliata</i> Neboiss 1977	<i>Tasiagma</i>	TASIAGMA
	<i>Tasimia palpata</i> ? Mosely 1936	<i>Tasimia</i>	TASIMIA
Antipodoecidae	<i>Antipodoecida</i> sp.AV2	<i>Antipodoecida</i>	ANTIPOD
Helicopsychoidea	<i>Helicopsyche Ptychopteryx</i> (Brauer 1865)	<i>Helicopsyche</i>	HELICOPS
Calocidae	<i>Pliocaloca</i> sp.AV1	<i>Pliocaloca</i>	PLIOCALO
Calamoceratidae	<i>Anisocentropus</i> sp.	<i>Anisocentropus</i>	ANISO

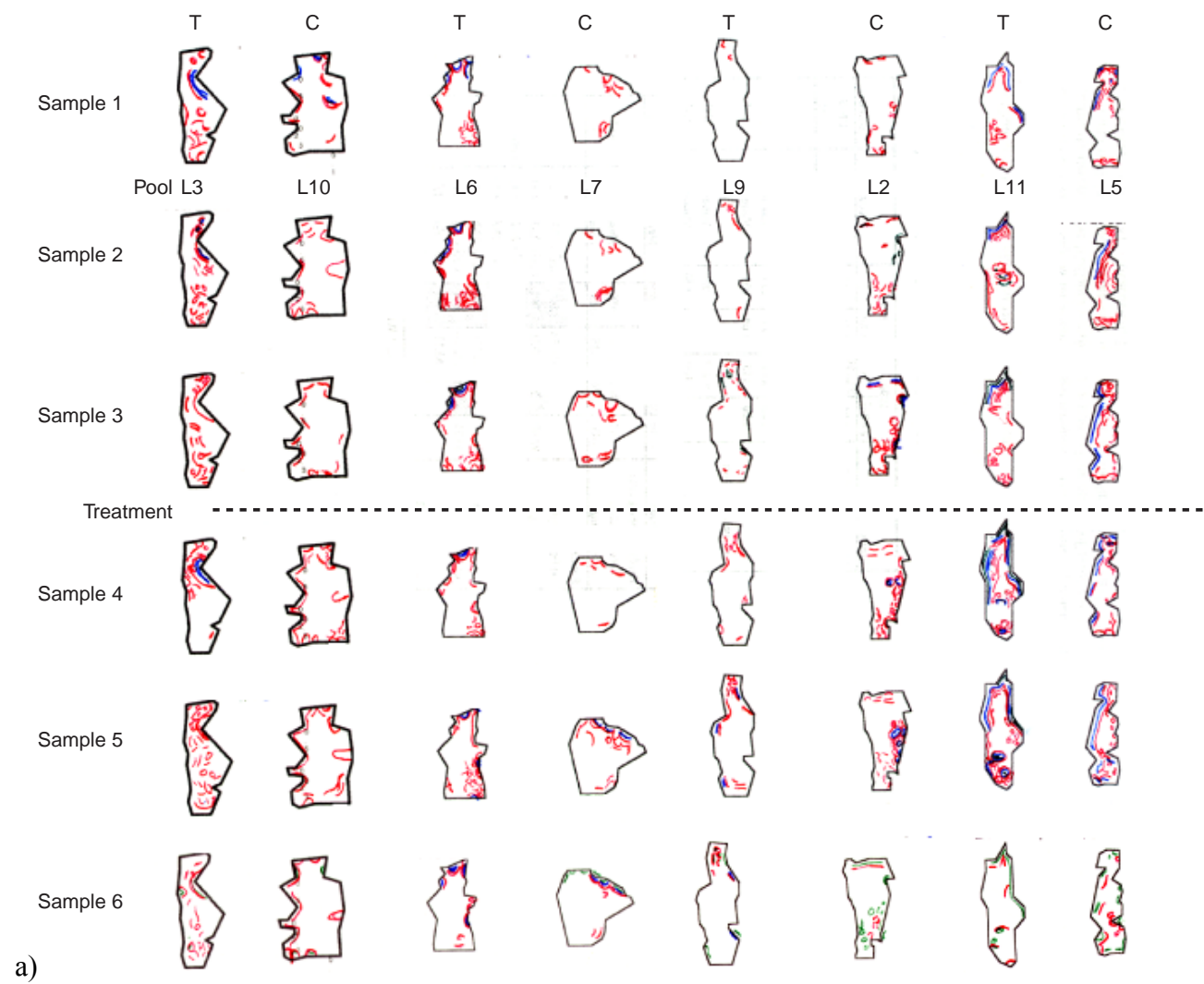
Classification	Taxon	Short Name	Code
Trichoptera <i>continued</i>			
Leptoceridae	Leptoceridae juveniles	Leptoceridae juv	LEPCER
	<i>Oecetis</i> sp.	<i>Oecetis</i>	OECETIS
	<i>Triplectides altenogus</i> Morse and Neboiss 1982	<i>Triplectides altenogus</i>	TRIALT
	<i>Triplectides ciuskus</i> Moseley 1953	<i>Triplectides ciusleus</i>	TRICIU
	<i>Triplectides elongatus</i> Banks 1939	<i>Triplectides elongatus</i>	TRIELO
	<i>Triplectides</i> juveniles	<i>Triplectides</i> juv	TRIJUV
	<i>Triplectides</i> sp.AV10	<i>Triplectides</i> sp.AV10	TRIAV10
Lepidoptera			
Pyralidae	Pyralidae sp.A	Pyralidae	PYRAL
Hemiptera			
Gelastocoridae	Gelastocoridae	Gelastocoridae	GELASTO
Corixidae	Corixidae	Corixidae	CORIX
Notonectidae	Notonectid juveniles	Notonectid juv	NOTOJUV
	Notonectid sp.A	Notonectid A	NOTOA
	Notonectid sp.B	Notonectid B	NOTOB
	Notonectid sp.C	Notonectid C	NOTOC
	Notonectid sp.D	Notonectid D	NOTOD
Coleoptera			
Hydrophilidae	Hydrophilidae sp.C (a)	Hydrophilidae C (a)	HYDPHAC
	Hydrophilidae sp.F(a)	Hydrophilidae F (a)	HYDPHAF
	Hydrophilidae sp.A (l)	Hydrophilidae A (l)	HYDPHLA
Hydraenidae	Hydraenid sp.A (a)	Hydraenid A	HYDRAEA
Scirtidae	Scirtidae sp.A (l)	Scirtidae A (l)	SCIRT

Classification	Taxon	Short Name	Code
<i>Diptera continued</i>			
	Unknown Dipteran G	Unknown Dipteran G	DIPG
	Unknown Dipteran H	Unknown Dipteran H	DIPH
	Unknown Dipteran I	Unknown Dipteran I	DIPI
Tipulidae	Tipulid pupa	Tipulid pupa	TIPPUP
	Tipulid sp.A	Tipulid A	TIPA
	Tipulid sp.B	Tipulid B	TIPB
	Tipulid sp.C	Tipulid C	TIPC
	Tipulid sp.D	Tipulid D	TIPD
Ceratopogonidae	Ceratopogonid sp.A	Ceratopogonid A	CERATO A
	Ceratopogonid sp.B	Ceratopogonid B	CERATO B
	Ceratopogonid sp.C	Ceratopogonid C	CERATO C
	Ceratopogonid sp.D	Ceratopogonid D	CERATO D
	Ceratopogonid sp.E	Ceratopogonid E	CERATO E
Simuliidae	Simuliid sp.A	-----	-----
Chironomidae			
Aphrotaeniinae	Aphrotaeniinae sp.A	Aphrotaeniinae	APHRO
Chironominae	Chironominae sp.AB	ChironominaeAB	CHIRONAB
	Chironominae sp.B	ChironominaeB	CHIRONB
	Chironominae sp.C	ChironominaeC	CHIRONC
	Chironominae sp.D	ChironominaeD	CHIROND
	Chironominae sp.Y	ChironominaeY	CHIRONY
Orthocladinae	Orthocladinae sp.I	Orthocladinae I	ORTHOCLI
	Orthocladinae sp.X	Orthocladinae X	ORTHOCLX

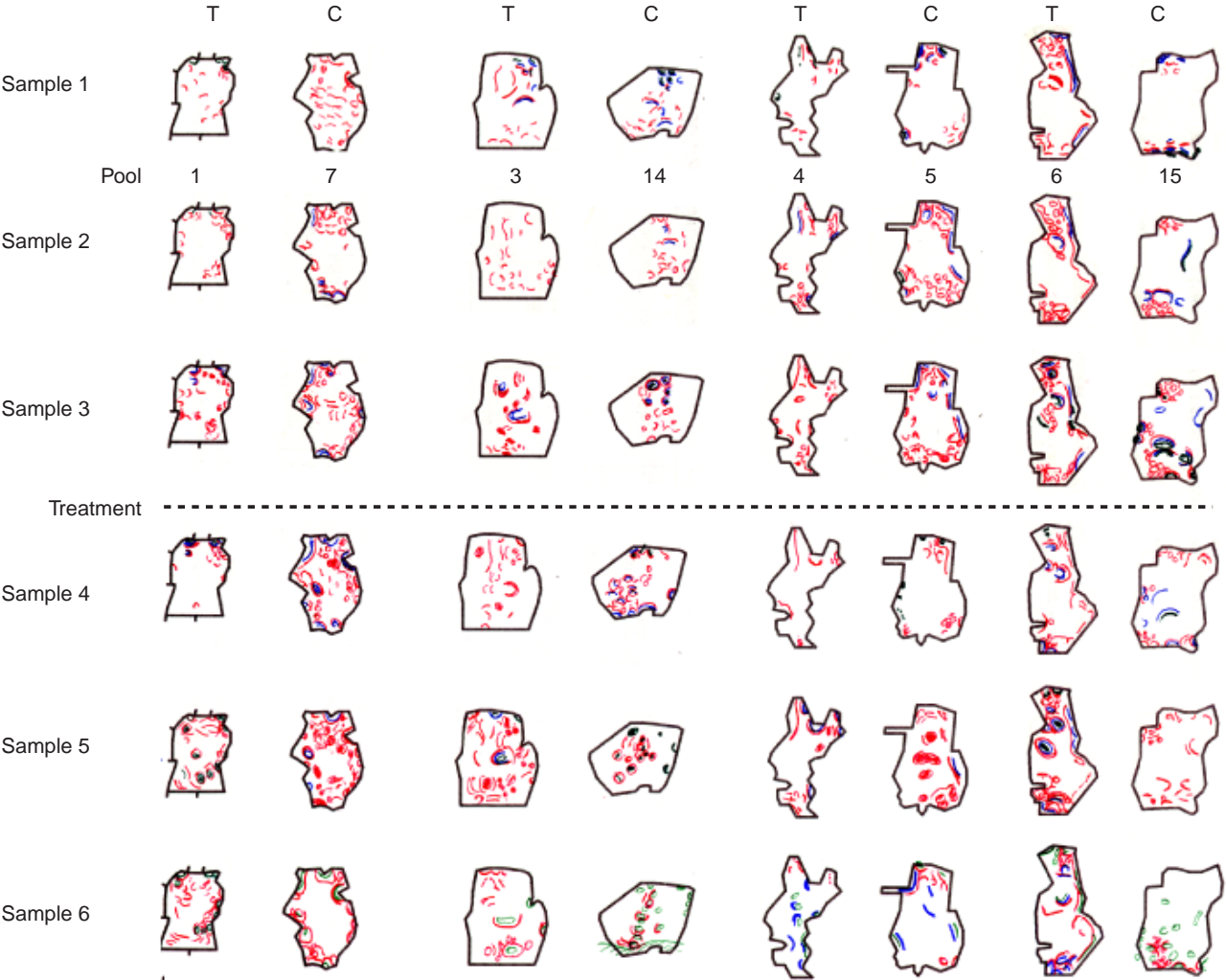
Classification	Taxon	Short Name	Code	
Diptera <i>continued</i>				
Tanypodinae	Tanypodinae sp.A	Tanypodinae A	TANYA	
	Tanypodinae sp.AA	Tanypodinae AA	TANYAA	
	Tanypodinae sp.E	Tanypodinae E	TANYE	
	Tanypodinae sp.G	Tanypodinae G	TANYG	
	Tanypodinae sp.J	Tanypodinae J	TANYJ	
	Tanypodinae sp.K	Tanypodinae K	TANYK	
	Dixidae	Dixidae	DIX	
	Culicidae	Culicidae sp.A	Culicidae A	CULIA
		Culicidae sp.B	Culicidae B	CULIB
	Psychodidae	Psychodidae sp.A	Psychodidae A	PSYCHOA
	Stratyomyidae	Stratyomyidae sp.A	Stratyomyidae	STRATYO
	Athericidae	Athericidae B	Athericidae B	ATHERB
	Tabanidae	Tabanidae	Tabanidae	TABAN
	Dolichopodidae	Dolichopodid sp.A	Dolichopodid A	DOLIA
		Dolichopodid sp.B	Dolichopodid B	DOLIB
	Empididae	Empididae sp.A	Empididae A	EMPIDA
		Empididae sp.B	Empididae B	EMPIDB
<u>Chordata</u>				
Teleostomi				
Amphibia	Anguillidae	<i>Anguilla reinhardtii</i> Steindachner 1867	-----	
	Retropinnidae	<i>Retropinna semoni</i> Steindachner 1866	<i>Retropinna</i> SMELT	
	Plotosidae	<i>Tandanus tandanus</i> Mitchell 1838	-----	
	Eleotridae	<i>Mogurnda adspersa</i> Castelnau 1878	<i>Mogurnda</i> MOGURNDA	
		Tadpole juveniles	Tadpole juveniles TADPJUV	
	Myobatrachidae	<i>Adelotus brevis</i> tadpoles (Gunther 1863)	<i>Adelotus</i> ADEL	
		<i>Mixophyes</i> spp. tadpoles	<i>Mixophyes</i> MIXO	
Hylidae	<i>Litoria</i> spp. tadpoles	<i>Litoria</i> LITORIA		

APPENDIX III: GRAZER DISTRIBUTION MAPS

Figure B (over page). Schematic maps of the distribution of grazing Tasimiidae (*Tasiagma ciliata* and *Tasimia palpata*?) in each experimental pool on each sampling occasion in a) Logger Branch and b) Unnamed Tributary from the *Paratya* manipulation experiment (Chapter 5). Red indicates the presence of grazers within the pools (*i.e.* under water), blue indicates grazers on rocks at the air water interface, and green indicates grazers on rocks out of the water.



b)



**APPENDIX IV: ADDITIONAL DATA
ON THE EFFECTS OF PREDATION BY
THE FISH *MOGURNDA ADSPERSA* ON
POOL FAUNAL ASSEMBLAGES**

Table E. The abundance, density and density category of *M. adspersa* and the area of each pool. Pools prefixed with “L” are in Logger Branch, and the remainder in Unnamed Tributary.

Pool	Abundance	Density (fish m ⁻²)	Category	Area (m ²)
1	0	0.00	1	24.3
3	3	0.08	2	38.1
4	0	0.00	1	26.6
5	0	0.00	1	28.4
6	2	0.04	2	50.4
7	0	0.00	1	33.8
14	1	0.04	2	25.5
15	7	0.15	3	46.9
L2	9	0.18	3	48.9
L3	0	0.00	1	24.2
L5	0	0.00	1	29.5
L6	0	0.00	1	24.7
L7	0	0.00	1	21.5
L9	0	0.00	1	52.2
L10	0	0.00	1	15.8
L11	12	0.47	3	25.7

Table F. Allocation of pools to experimental blocks and treatments and the area and maximum depth of pools (EC - experimental control, PC - procedural control, A - addition, R- removal).

Pool	Block	Treatment	Area (m ²)	Depth (m)
1	1	PC	66.9	0.33
2	1	A	42.6	0.32
3	1	EC	-	-
4	1	R	33.1	0.41
5	2	EC	-	-
6	2	A	23.5	0.27
7	2	PC	39.3	0.39
8	2	R	31.7	0.30
9	3	PC	61.5	0.81
10	3	EC	-	-
11	3	A	16.0	0.50
12	3	R	23.5	0.59
13	4	A	27.8	0.36
14	4	EC	-	-
15	4	R	21.9	0.40
16	4	PC	19.1	0.54
17	5	EC	-	-
18	5	A	27.7	0.86
19	5	R	67.2	0.36
20	5	PC	64.0	0.56

Table G. Results of mixed model two-way ANOVA without replication testing for differences in the magnitude of Bray-Curtis dissimilarity between the log (x+1) abundance of cobble faunal samples collected before and after the experiment in experimental treatments. Experimental treatment was the fixed factor and experimental block the random factor in the model. The residual was used as the error term. Estimates of effect size and power are also presented.

Source of Variation	SS	DF	MS	F	Significance of F	Effect Size	Power
Experimental Treatment	0.03	3	0.01	1.63	0.235	0.289	0.322
Residual (error)	0.07	12	0.01				

Table H. Results of mixed model two-way ANOVA without replication testing for differences in the magnitude of Bray-Curtis dissimilarity between the log (x+1) abundance of sweep sample faunal samples collected before and after the experiment in experimental treatments. Experimental treatment was the fixed factor and experimental block the random factor in the model. The residual was used as the error term. Estimates of effect size and power are also presented.

Source of Variation	SS	DF	MS	F	Significance of F	Effect Size	Power
Experimental Treatment	0.02	3	0.01	0.17	0.913	0.41	0.074
Residual (error)	0.35	12	0.03				

Figure C. Ordination of the log (x+1) abundance of cobble fauna showing the magnitude and direction of changes between samples taken before and after the experiment for each pool. Plots are divided into blocks and pools within blocks are labelled by experimental treatment. The tail of each arrow indicates the location of the pool in ordination space before the experiment and the head the location after the experiment. All plots are to the same scale and from the same ordination. Correlation vectors of taxa with strong and significant correlations with the ordination ($r > 0.65$, $p < 0.05$) are presented in the final plot. Stress = 0.18.

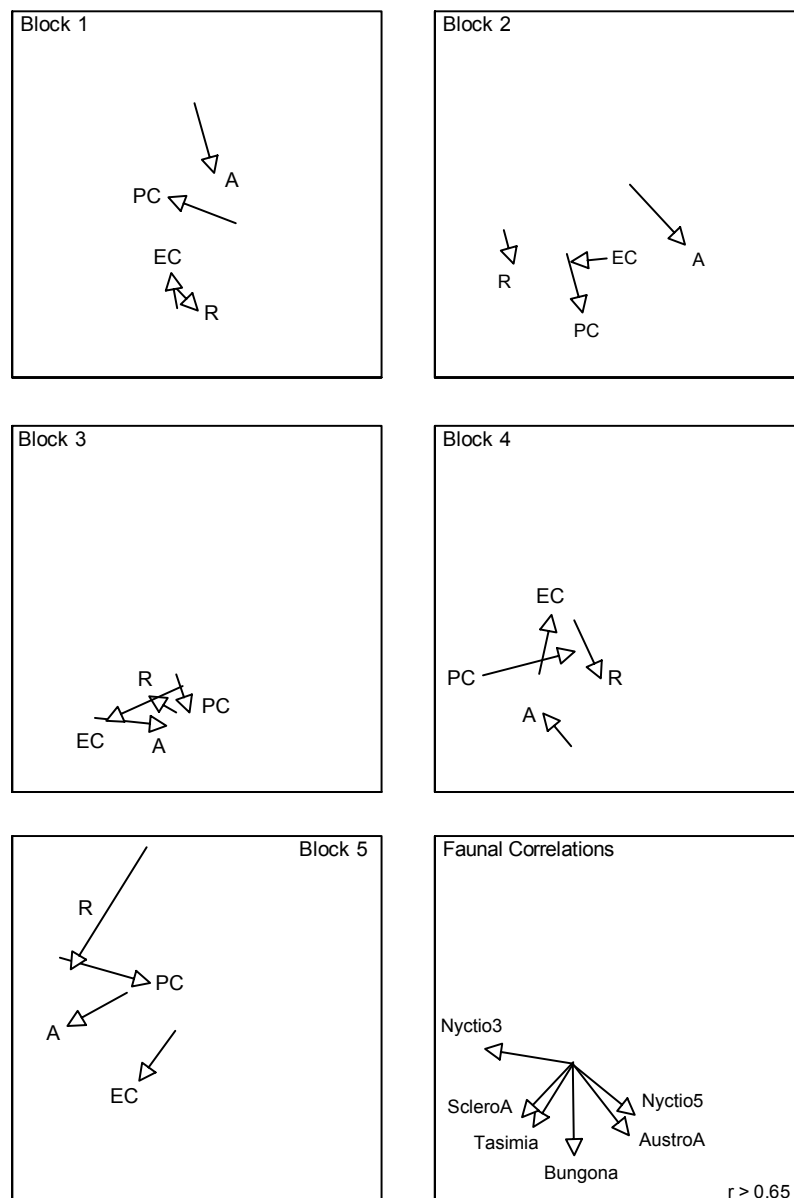


Figure D. Ordination of the log (x+1) abundance of sweep sample fauna showing the magnitude and direction of changes between samples taken before and after the experiment for each pool. Plots are divided into blocks and pools within blocks are labelled by experimental treatment. The tail of each arrow indicates the location of the pool in ordination space before the experiment and the head the location after the experiment. All plots are to the same scale and from the same ordination. Correlation vectors of taxa with strong and significant correlations with the ordination ($r > 0.7$, $p < 0.05$) are presented in the final plot. Stress = 0.08.

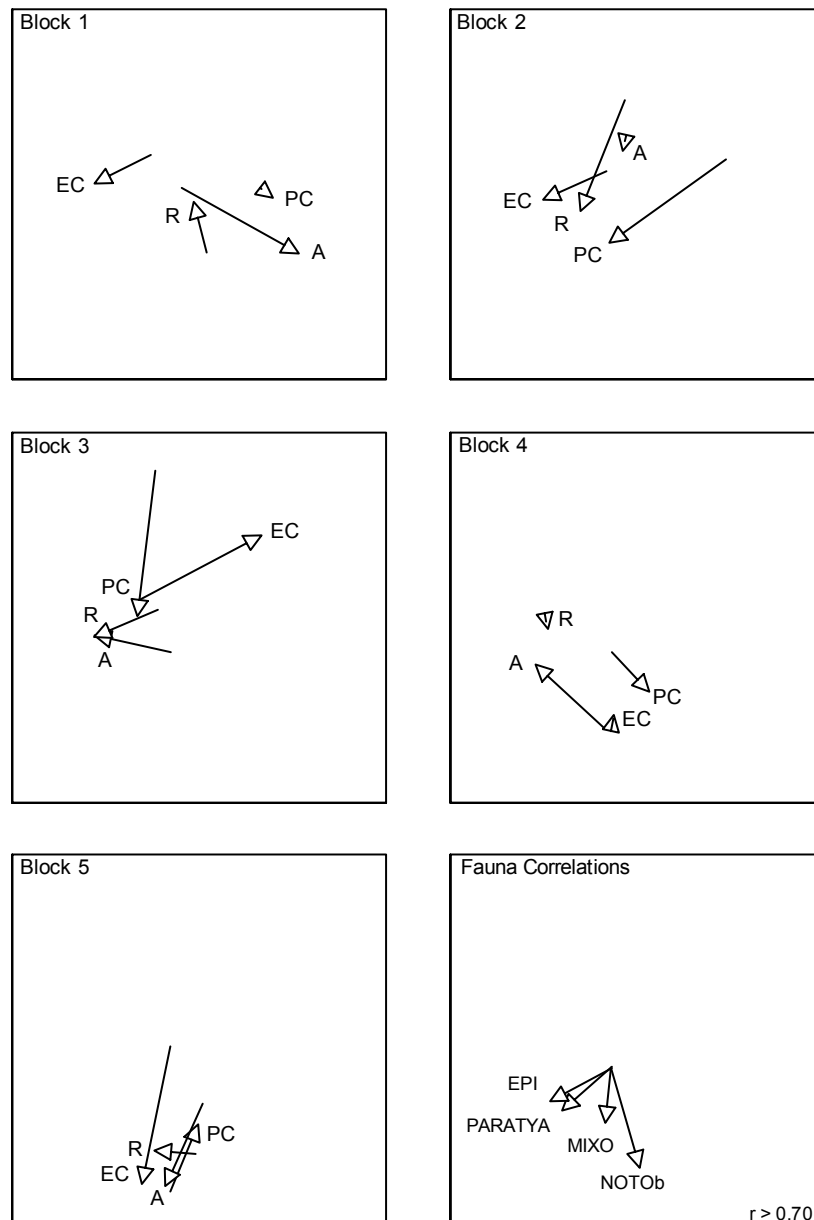


Table I. Results of mixed model two-way ANOVA without replication testing for differences in the abundance of common taxa collected in gravel habitat before and after the experiment in experimental treatments. Experimental treatment was the fixed factor and experimental block the random factor in the model. The residual was used as the error term.

Atalophlebia sp. AV13

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	362	3	120	1.39	0.2
Residual (error)	1043	12	86		

Koorrnonga sp. AV1

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	3541	3	1180	1.5	0.2
Residual (error)	8889	12	740		

Bungona narilla

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	513	3	171	0.91	0.5
Residual (error)	2259	12	188		

Tasmanocoenis queenslandica

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	576	3	192	1.8	0.2
Residual (error)	1251	12	104		

Chironominae sp.D

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	3019	3	1006	0.4	0.7
Residual (error)	26658	12	2221		

Oligochaeta

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	515	3	171	0.5	0.7
Residual (error)	3898	12	325		

Ulmerophlebia sp. AV3

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	10386	3	3434	1.3	0.3
Residual (error)	31733	12	2644		

Table J. Results of mixed model two-way ANOVA without replication testing for differences in the abundance of common taxa collected in cobble habitat before and after the experiment in experimental treatments. Experimental treatment was the fixed factor and experimental block the random factor in the model. The residual was used as the error term.

Atalophlebia sp. AV13

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	99	3	32	2.4	0.1
Residual (error)	168	12	14		

Tillyardophlebia sp. AV6

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	450	3	150	2.5	0.1
Residual (error)	719	12	60		

Bungona narilla

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	2080	3	683	1.3	0.3
Residual (error)	6358	12	530		

Paranyctiophylax sp. AV5

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	5	3	2	0.2	0.9
Residual (error)	84	12	7		

Sclerocyphon minimus

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	291	3	97	0.5	0.7
Residual (error)	2414	12	201		

Ulmerophlebia sp. AV3

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	1.8	3	0.6	0.4	0.7
Residual (error)	16	12	1		

Table K. Results of mixed model two-way ANOVA without replication testing for differences in the abundance of common taxa collected in sweep samples before and after the experiment in experimental treatments. Experimental treatment was the fixed

factor and experimental block the random factor in the model. The residual was used as the error term.

Episynlestes albicauda

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	181	3	60	1.2	0.3
Residual (error)	580	12	48		

Mixophyes spp. tadpoles

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	32	3	10	0.5	0.7
Residual (error)	243	12	20		

Notonectidae sp.B

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	197	3	66	0.3	0.8
Residual (error)	2875	12	240		

Paratya australiensis

Source of Variation	SS	DF	MS	F	Significance of F
Experimental Treatment	61	3	20	0.5	0.7
Residual (error)	523	12	43		

**APPENDIX V: COMPARISON OF THE
DIET OF *M. ADSPERSA* IN THIS STUDY
WITH OTHER PUBLISHED STUDIES**

Methods

Analyses were performed to compare the diets of *M. adspersa* recorded in this study with the published diets of *M. adspersa* in other regions. Pusey *et al.* (1995) reported mean gut contents as a proportion by volume of each prey class for fish collected from the South Johnstone and Mulgrave Rivers in north Queensland. Hortle and Pearson (1990) and Arthington (1992) reported mean gut contents as the proportion by number of each prey class for fish collected from the Annan River in north Queensland and Brisbane creeks in south east Queensland respectively. As the units of these studies were different, direct comparison was not possible. The only legitimate basis for comparison was on the basis of presence/absence of prey categories. Furthermore, it was also necessary to combine taxa into the lowest common taxonomic unit. For example *Paratya* larvae and adults, *Cherax* juveniles, and Ostracoda from this study were combined to match the “crustacea” category used by Arthington (1992).

A meta-analysis was performed by creating a combined data matrix containing the mean gut contents of *M. adspersa* from this and other studies, calculating Bray-Curtis differences between studies and ordinating the resulting matrix (*see* Chapter 3 for details). Correlation vectors were calculated between the ordination and the individual prey items. The significance of these was tested using Monte-Carlo simulations with 100 random starts.

Results

The diet of *M. adspersa* was found to be variable between different stream systems. This suggests they adapt their diet to local conditions.

The diet of *M. adspersa* described in this study was more similar to the diet in Brisbane Creeks than in any of the rivers in north Queensland (Figure E and Table L). Gastropods and tadpoles, which were recorded in the diets of fish in this study, were absent from the published diets. The diets of *M. adspersa* from the Annan River were quite different from those from other sites due to the presence of fish as a prey item and the absence of many other prey categories. It must be noted however that these results were based on the gut contents of only four individuals and that the aquatic fauna of the sampling site may have been impacted as a result of heavy metal pollution (Hortle and Pearson, 1990). Fish were also recorded in the diets of *M. adspersa* from the South Johnstone River.

Figure E. Ordination comparing the mean gut contents of *M. adspersa* from this study (labelled Stony Creek) with published gut contents on the basis of presence/absence of prey categories and showing prey items significantly correlated with the ordination. Stress = 0.10.

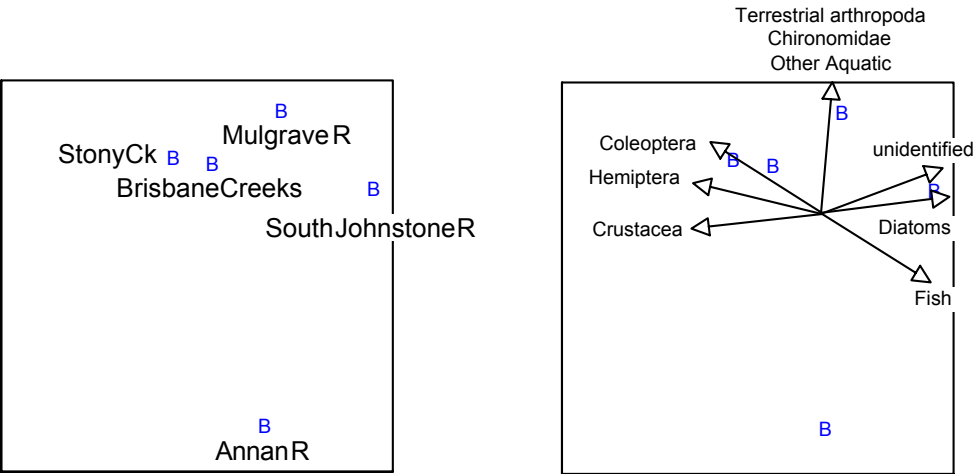


Table L. Comparison of the presence/absence of prey items in the gut contents of *M. adspersa* in this study with other published studies. The symbol * indicates the presence of a prey item.

Prey Item	Stony Ck ¹	Brisbane Creeks ²	South Johnstone R ³	Mulgrave R ³	Annan R ⁴
unidentified			*	*	
detritus				*	
diatoms			*		
terrestrial	*	*	*	*	
arthropods					
Gastropoda	*				
Crustacea	*	*		*	*
Ephemeroptera	*	*	*	*	*
Odonata	*	*	*		
Hemiptera	*	*			
Trichoptera	*	*	*	*	*
Chironomidae	*	*	*	*	
Coleoptera	*	*		*	
other aquatic	*	*	*	*	
insects					
fish			*		*
tadpoles	*				
Fish examined	33	137	60	23	4

¹ This study, ² Arthington (1992), ³ Pusey *et al.* (1995), ⁴ Hurtle and Pearson (1990)