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Spatial Autocorrelation of Benthic Invertebrate Assemblages in Two Victorian Upland Streams

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Abstract

Spatial patterns have important implications for the design of studies in freshwater environments. For sites to be considered independent replicates, they should not be autocorrelated. Autocorrelated data can decrease the accuracy of inferential statistical tests. The benthic macroinvertebrate faunas of the Wellington and Wonnangatta Rivers in Victoria's Alpine National Park were sampled at 16 riffle sites over scales of 50m to 40 km to investigate spatial autocorrelation patterns. Both rivers were sampled in 1996, but in 1997 only the Wellington River was sampled. The spatial patterns of the faunal assemblages were analysed using the multivariate Mantel test, a matrix comparison test, which was used to relate the ecological distance (Bray-Curtis dissimilarity) to the geographical distance between each site-pair within each river. Despite similarities in the fauna, catchment characteristics, and instream habitat, these adjacent rivers showed marked differences in faunal spatial patterns. A strongly autocorrelated spatial pattern was found in the Wellington River data, however the fauna of the Wonnangatta River showed no relationship with geographic distance. The patterns of autocorrelation found in the Wellington River were similar for the two years, despite differences in the fauna sampled. Significant autocorrelation was found at the small scales in the Wellington River, but there was no support for large scale longitudinal patterns in the Wellington River fauna. The fauna of the Wonnangatta River was not autocorrelated at any scale studied. These findings imply that autocorrelation can be, but is not always, an important factor determining the patterns of distribution and abundance of macroinvertebrates. The spatial patterns of environmental variables comprising some abiotic components of the habitat for benthic macroinvertebrates were also investigated. Environmental data was autocorrelated in both the Wellington River and the Wonnangatta River. Environmental dissimilarity was correlated with invertebrate dissimilarity in Wellington River samples, but not in Wonnangatta River samples. Therefore the lack of spatial autocorrelation in the Wonnangatta River invertebrate fauna did not appear to be related to the spatial pattern of the environmental variables. Ecological and statistical implications of autocorrelation in benthic invertebrate assemblages are discussed and recomendations for analysing autocorrelated data and planning study design to incorporate autocorrelation are included.

Statement of Responsibility

The material presented in this thesis has not been submitted for the award of any degree of 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 when due reference is made in the text of the thesis.

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Natalie J. Lloyd.

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Chapter 1

Introduction

The spatial distributions of organisms have long interested ecologists. Ecologists have sought to identify the adaptive significance of distributions such as aggregations, even spacing and gradients. There are many factors influencing these spatial patterns including social behaviours, responses to prey (or predator) species and responses to underlying spatial patterns of environmental variables.

Spatial patterns such as gradients or patches are frequently the result of contagious processes- processes that occur in one location and affect nearby locations (Legendre & Fortin, 1989). This is known as spatial autocorrelation. Autocorrelation of a variable occurs "when it is possible to predict the values of this variable at some points of space (or time), from the known values at other sampling points, whose spatial (or temporal) positions are also known" (Legendre & Fortin, 1989, p. 109). Autocorrelation of organisms implies that the system in which they inhabit is 'open'. That is, movement occurs between populations or patches (Begon *et al.*, 1990) and therefore changes in population size may reflect regional circumstances rather than purely local conditions (Wiens, 1989).

Sites that are spatially autocorrelated are not independent from one another because changes at one site may affect another site by contagious processes. If the spatial pattern is a gradient, these processes attenuate with distance, so that closely situated sites experience very similar events, whereas more distantly separated sites experience more different events or conditions. The degree to which a second site is affected will depend on the distance between the two and the relationship of the contagious process(es) with distance.

Patches and other spatial patterns may be caused by underlying contagious processes with thresholds. In this situation, autocorrelation may be strong over a particular range of distances, but at some boundary, become random. For example, vegetation patterns based

on soil type may exhibit this type of autocorrelation. Territorial behaviour can cause negative spatial autocorrelation at the scale of the territory size because the presence of one individual is related to the absence of conspecifics.

Spatial autocorrelation in two and three dimensions has been documented in terrestrial and marine ecosystems, from chemical variables such as acid rainfall patterns in the USA (Cressie, 1991) to species distributions such as mountain hares in Finland (Ranta *et al.*, 1997b). Autocorrelation analysis that separated two spatial dimensions revealed that the north-south range of autocorrelation in sugar-maples (*Acer saccharum*) is much larger than the east-west range (Legendre, 1993).

Rivers are ecologically unusual due to the unidirectional flow of water. Consequently, many chemical and physical properties of the environment experienced by aquatic organisms, including energy flow and metabolic processes, follow longitudinal gradients from the source to the mouth of the river. Examples of such variables include water temperature, river width, shading from riparian vegetation, and size of organic particles. Metabolic processes such as nutrient spiralling, primary production and the form of organic matter also follow longitudinal patterns (Statzner & Borchardt, 1994; Webster & Meyer, 1997). The spiralling length of a nutrient can be considered as the distance required for one atom to pass from a dissolved state through the food web and to return to a dissolved state (Newbold *et al.*, 1982). Similarly, invertebrates often show longitudinal patterns and are considered to move primarily downstream by drifting. Due to the migration of individuals between patches, rivers are considered to be open systems at all but "the largest scales" (Cooper *et al.*, 1998, p. 30). Many stream ecologists have sought to explain the spatial distribution of stream fauna in the light of longitudinal patterns of environmental variables. Hynes (1970) compiled the evidence of zonation patterns of macroinvertebrates, fish, algae and macrophytes known in 1970. The River Continuum Concept (RCC) (Vannote *et al.*, 1980) sought to explain the longitudinal patterns of macroinvertebrate functional groups in terms of organic matter, nutrients and energy flow. Upstream reaches could be characterized by larger particles of organic matter such as large woody debris and entire leaves. This resource may be used by shredders and wood eaters. The prevalence of these functional groups was hypothesized to decrease downstream as organic matter particles became smaller on average, due to a decreasing input of organic debris from the riparian zone. Abundances of scrapers should be maximal in the middle of the continuum, as algae is most available there. Downstream reaches may be dominated by filter feeders and detritivores, which ingest small organic particles. The invertebrate communities are therefore dependant upon the form of available energy in the river (Vannote *et al.*, 1980). Whilst the RCC has not proven to be widely applicable (Winterbourn *et al.*, 1981; Lake, 1986; Statzner & Resh, 1993), longitudinal patterns of

invertebrate communities are generally accepted (Lake & Barmuta, 1986).

Many researchers have documented that events occurring upstream have influenced downstream locations due to these strong upstream-downstream linkages. For example, upstream disturbances such as fire, deforestation, and point-source pollution lead to changes in water and habitat quality downstream via the water-borne movement of solutes, organic and inorganic particles, temperature and organisms. Therefore, one might expect that downstream sites will not be independent from upstream sites and that this spatial autocorrelation may be one-dimensional. One of the implications of this spatial autocorrelation is that sites on the same stream within the area of influence of the contagious processes will not be legitimate replicates (Hurlbert, 1984; Cooper & Barmuta, 1993).

Spatial autocorrelation is important to freshwater ecology for two reasons. First, spatial autocorrelation may be a useful tool in attempting to understand the distribution of invertebrates in streams. Autocorrelation analysis can be used to relate the spatial distributions of environmental variables and biotic interactions, and the scaling of these patterns, to the spatial distribution of invertebrates. Second, the issue of independent replicates (i.e. sites) and valid design has important ramifications for the field of freshwater ecology in general, and the detection of human impacts in freshwater systems in particular. This latter implication of spatial autocorrelation is the emphasis of this work.

1.1 Biological causes of spatial autocorrelation

Spatial autocorrelation is most likely to result from contagious processes (Legendre & Fortin, 1989). Contagious processes that may affect the composition of benthic invertebrate assemblages include movements by individual animals such as drift, benthic movement and aerial movement by adult insects. The patterns produced by such movements may be either eroded or reinforced by other factors. Therefore, factors that affect colonization by nymphs, egg deposition by females, or the survival of eggs and larvae may influence contagious processes in streams. Both environmental variables and biotic interactions affect egg deposition and the colonization and survival of benthic invertebrates. A spatial pattern within a steam may be a reflection of such variables, rather than being related to dispersal processes *per se*. For example, longitudinal models of invertebrate distribution, such as the River Continuum Concept (Vannote *et al.*, 1980) and those proposed by Hynes (1970), Lake (1986) and Statzner & Borchardt (1994) relate invertebrate assemblage composition to longitudinal patterns of physical and biophysical variables.

Many invertebrates move within a river by drifting (Brittain & Eikeland, 1988). The influence of this behaviour is likely to attenuate with distance. Several researchers have noted a negative exponential distribution of invertebrates caught in drift nets at different distances from a source of disturbance (McLay, 1970; Ciborowski, 1983; Larkin & McKone, 1985; Lancaster *et al.*, 1996; Allan & Feifarek, 1989). Although distances traveled are likely to be short for a single drift movement, many species have been observed to undertake multiple drifts (Giller & Campbell, 1989). Animals' entry into the drift may be deliberate, or related to increased activity such as may occur if the settlement site is suboptimal (Brittain & Eikeland, 1988). Alightment at a suitable patch reduces the chance of further drift events. Therefore, the proportion of individuals drifting decreases with increasing number of drift events. Drifting animals may also suffer predation (Dahl & Greenberg, 1996; Mathooko, 1996), so increased drifting duration (and therefore distance) reduces the chances of successful colonization. Drifting animals showed lower survivorship than benthic animals, possibly due to higher parasite loads and microbial pathogens in addition to their smaller size, in a study of drift in a second-order stream in Maryland, USA (Wilzbach & Cummins, 1989). Therefore, the number of individuals of one species moving large distances by drifting is most likely to be smaller than the number moving small or intermediate distances (Hemsworth & Brooker, 1979). Therefore, drifting behaviour within a single taxon can be seen as a contagious process that influences the composition of the invertebrate fauna. Because dispersal attenuates with distance, dispersal from one site may affect nearby locations more strongly than more distant locations, dispersal could result in a pattern of spatial autocorrelation.

At the level of assemblages, the greater the distance between sites, the lower the probability that some elements of the fauna will immigrate and colonize successfully. Drift studies frequently show that the proportions of taxa comprising the drift are different to those inhabiting the benthos (Brittain & Eikeland, 1988) and those colonizing benthic substrates (Doeg *et al.*, 1989b). Some components of benthic assemblages are rarely found in drift samples; these include cased trichopterans, beetles, oligochaetes, and water mites (Hynes, 1970). Species drift for different lengths of time due to differences in behaviour and swimming ability (Otto & Sjöström, 1986). Current speed and hydraulic transport properties of stream channels affect the distance travelled by drifting animals (Elliot, 1971; Allan & Feifarek, 1989; Lancaster *et al.*, 1996). Differences between taxa in drifting distances may cause autocorrelation of benthic fauna as closely situated sites may be more similar than more distant sites.

Animals also crawl along the substrate, both upstream and downstream (Söderström, 1987). This form of movement could also act as a contagious process. Giller & Campbell (1989) argued that crawling was as important as drifting in the colonization of artificial

substrate trays. Richards & Minshall (1988) believed that 40-50% of *Baetis* nymphs reaching a particular rock arrived there by crawling. Approximately 20% of colonists reaching test cages arrived from downstream, and 19% crawled in from the hyporheos; therefore almost 40% dispersed by crawling (Williams & Hynes, 1976). Hughes *et al.* (1995) postulated that individuals of *Paratya australiensis* (an atyid shrimp) migrate short distances in the benthos, given the species patterns of genetic differentiation. Brooks & Boulton (1991) thought that the mechanism of recolonization after small-scale disturbances in a South Australian temporary stream was primarily migration through the benthos from nearby patches. Williams & Williams (1993) demonstrated that benthic movement is quite common among invertebrates of a Welsh upland stream, and that different taxa show different patterns. Bergey & Ward (1989) suggested that upstream crawling may be sufficient to compensate for downstream drift in some taxa. However, crawling is only likely to be an important dispersal mechanism at a very small scale, such as within a single riffle or pool. For example, in a study of crawling *Dicosmoecus gilvipes*, marked individuals were relocated within a single pool on several occasions (Hart & Resh, 1980).

Aerial movements can be an important dispersal pathway in some rivers. Gray & Fisher (1981) found that aerial colonization accounted for two-thirds of recolonization following scouring spates in winter and summer in a lowland desert stream. Hughes *et al.* (1998) argued that the *Tasiagma ciliata* larvae within reaches of stream were the offspring of only a few females. Like other methods of dispersal, aerial movements by adults before oviposition are likely to attenuate with distance. Although flight by adult insects has been less well studied than drift, there is limited evidence that flight distance varies between taxa and among individuals of one taxon. Plecopterans often are poor fliers, with several species possessing rudimentary wings or none at all (Williams, 1981), whereas dipterans and odonates are usually strong fliers (Corbet, 1980; Sheldon, 1984). The latter are found on many oceanic islands whereas plecopteran, ephemeropteran and trichopteran distributions include very few islands (Sheldon, 1984). Flight distance and direction are highly dependent on wind speed and direction, which, therefore, affects different taxa and individuals differently due to differing emergence times (Brown, 1970; Hershey *et al.*, 1993; Bagge, 1995). This method of dispersal is unavailable to animals that do not undergo a terrestrial adult stage, such as most Australian elmid beetles (subfamily Elminae) (Glaister, 1999) and non-insect invertebrates. If flight is an important dispersal pathway, autocorrelation of the macroinvertebrate assemblages may result due to the different distances dispersed by different taxa and individuals.

Dispersal has been viewed in the past as a mechanism by which patches denuded by spates or droughts were recolonised, but recent work suggests that dispersal can have

strong influences on established local assemblages (Palmer *et al.*, 1996). Immigration which has a strong influence on established patches can result in regional control of assemblage structure, rather than purely local control as would occur if established assemblages prevent the colonisation of immigrants.

Successful colonization following migration via drift or benthic movement, and the survival and persistence of eggs laid by adult females after aerial dispersal may be a contagious process. The spatial patterns of invertebrate assemblages caused by dispersal may be either reinforced or altered by the colonization and persistence of invertebrates. Therefore, factors which influence recruitment can influence autocorrelation. Recruitment is related to several environmental variables. For example, some hydropsychid and simuliid females preferentially lay eggs on bare rocks (Mackay, 1992). Similarly, simuliid larvae select smooth surfaces on which to settle (Mackay, 1992). The particle size of rocky substrate has a strong influence on the density and composition of invertebrates due to the colonization substrate preferences of many different species (Mackay, 1992). Drift densities are correlated with current and water chemistry variables for several invertebrate groups (Brittain & Eikeland, 1988). These environmental variables may cause spatial autocorrelation in invertebrate assemblages by a combination of their influence on the invertebrate fauna and their intrinsic spatial patterns.

Many variables important in determining suitable habitat for invertebrates are likely to be spatially autocorrelated, as they are due to a number of physical and biological factors that are also subjected to contagious processes. For example, average substrate size decreases predictably along a longitudinal gradient (Allan, 1995). Longitudinal gradients occur in physico-chemical water variables such as temperature, current speed and hydraulic patterns, electrical conductivity, turbidity (Hynes, 1970; Petts & Foster, 1985; Statzner & Borchardt, 1994). Organic matter loading and the size of organic particles follow a longitudinal pattern, as do energy flow (Vannote *et al.*, 1980) and nutrient spiralling (Newbold *et al.*, 1982). The River Continuum Concept of Vannote *et al.* (1980) sought to explain the distribution and abundance of benthic invertebrate communities with respect to the longitudinal gradients of energy input and organic matter storage and transport. Other environmental variables may be autocorrelated at small scales rather than showing a longitudinal gradient, for example, nutrient enhancement due to point source pollution. Influences of the riparian zone, such as shading and large woody debris input, will most likely be autocorrelated. Autocorrelation in environmental variables important in the ecology of benthic invertebrates may be a cause of autocorrelation in invertebrate assemblages.

Biotic interactions also have the potential to structure spatial patterns of stream assemblages by influencing the colonization, persistence or survival of assemblage

species. Recruitment is affected by several types of biotic interactions. The presence of predaceous stoneflies deters colonization by prey species, including mayflies, stoneflies, trichopterans and dipterans (Peckarsky, 1985). Drifting in mayflies and stoneflies increases in the presence of predators (Peckarsky, 1984; Huhta *et al.*, 2000). High rates of parasitised invertebrates in drift samples suggest that parasitism may increase active entry into the drift by some invertebrates (Statzner & Bittner, 1983; Wilzbach *et al.*, 1986). Parasitism of odonates by nematodes increases the distance flown by the adult odonate, due to effects on the nervous system of the host (Corbet, 1980).

Competitive interactions for food and foraging space, in which the loser enters the drift, between several trichopteran and ephemeropteran genera and simuliids have been recorded in streams using time-lapse photography (Wiley & Kohler, 1981). Dudley *et al.* (1990) documented similar interactions between simuliids and blephacerids in California. Drift appears to be density dependent in several taxa, at least under some abiotic conditions (Brittain & Eikeland, 1988), although not all (Statzner *et al.*, 1986, 1987). The evenly spaced distributions of nets, cases or tubes of several trichopteran and dipteran species are examples of intraspecific competition determining the spatial distribution of these taxa (Wiley & Kohler, 1984; Mackay, 1992).

Food abundance can influence both colonization and persistence. The condition of epilithon either facilitated or hampered colonization by *Baetis* spp. and *Agapetus* sp. (Boulton *et al.*, 1988; Mackay, 1992). *Baetis rhodani* actively enters the drift in response to low food abundance, while *Potamophylax cingulatus* was less likely to drift from experimental channels with excess food (Brittain & Eikeland, 1988).

All of these factors have the potential to interact and determine spatial autocorrelation of stream benthic assemblages. For example, Hart (1992) documented a patchy system whereby a keystone predator, food preferences of the benthic fauna, and current speed combined to determine the patchy spatial patterns of benthic invertebrate assemblages. Where current speed was high, crayfish (*Orconectes propinquus*) could not graze and *Cladophora glomerata* (a macroalga) dominated if it colonised an empty space before sessile grazers. The presence of *C. glomerata* then influenced the composition of macroinvertebrate assemblages, with some species showing positive and others negative correlations with the density of this macroalga. In lower current areas and high current areas in which sessile grazers colonised before *C. glomerata*, the assemblage comprised a low-growing, epilithic microalgal lawn inhabited by several species of sessile grazers.

1.2 Implications of autocorrelated data from streams

Nominally independent, randomly selected replicates are the basis for almost all sampling programs and experimental designs. If random independent replicates (e.g. sites) are measured for a variable of interest, then the population value (or parameter) can be estimated from the sample statistic. If sites are not independent, then the estimation of the population value can be affected.

The error term associated with the statistic will be incorrect because the effective degrees of freedom are overestimated. If sites are independent, one degree of freedom is accrued for each additional site. However, if sites are not independent then each new site only imparts a partial degree of freedom, as the value of the variable could, in part, have been estimated by the values of the variable from other sites (Cressie, 1991). The error term and degrees of freedom influence the outcome of any inferential test.

Two contradictory assumptions exist in the steam ecology literature, particularly in those studies designed to detect anthropogenic impacts on instream fauna. The first assumption is that sites are independent regardless of the distance between them (Hurlbert, 1984). This assumption is implicit in any study using inferential statistics, including Before-After-Control-Impact designs (BACI) (Stewart-Oaten *et al.*, 1986). Inferential statistics were used in 60% of the lotic studies reviewed by Resh & McElravy (1993) on the effects of water pollution on invertebrates. The remaining studies reviewed did not contain any statistical analyses at all.

The second assumption, either stated (e.g. Quinn *et al.*, 1992) or implied (e.g. Richardson, 1985) in studies using the upstream reference or control site design, is that there are strong linkages between upstream and downstream locations and that the fauna that should occur at a site downstream of a putative impact, in the absence of any impact, can be predicted from the fauna occurring at an upstream site. This assumption is so prevalent that 63% of the lotic impact-detection studies reviewed by Voshell *et al.* (1989) and Resh & McElravy (1993) used upstream reference sites. This assumption of strong linkages between sites is equivalent to the assertion of strongly contagious processes and therefore, the reason to predict/expect that autocorrelation may be occurring in this ecosystem, and that the assumption of independence may be invalid at some scales within rivers.

The difference between these two assumptions of research is **estimation** versus **prediction**. Sampling or experimental designs incorporating the use of inferential statistics, and even some designs that do not, for example, models such as the River InVertebrate Prediction and Classification System (RIVPACS) (Wright *et al.*, 1984; Moss

et al., 1987; Wright *et al.*, 1993, 1996) and the AUStralian RIVer Assessment System (AUSRIVAS) (Coysh *et al.*, 2000), make the assumption that the sampling universe is all possible riverine sites within the scope of the study and that the reference sites sampled estimate the value of the variable of interest (e.g. taxonomic richness) for the entire population. Such **estimation** requires the use of independent replicates. Conversely, **prediction**, assumes that the variable of interest in one location is partly determined by surrounding locations. Techniques based upon prediction (e.g. kriging) require sites sampled (or times of sampling) to be autocorrelated (Legendre & Fortin, 1989). The upstream reference site design makes the assumption that value of the variable at a downstream site can be predicted from the value at the upstream site; i.e., the value of the variable should be the same in the absence of an impact. Often, studies using the upstream reference site design will perform inferential statistics upon the variable of interest, thereby confounding the two opposing assumptions and possibly producing non-sensical inferences.

The pattern of autocorrelation may be important to the assumptions of research designs. It is possible that autocorrelation could be statistically highly significant, and yet explain very little variation in the variable. The ecological significance of such a pattern of autocorrelation would be quite limited. Such a pattern would have bearing on the upstream reference site design, invalidating the assumption that downstream fauna can be predicted from upstream fauna. The implications for estimation of population values would be less important: if error terms were corrected, then inferential tests could be performed (Cressie, 1991).

1.3 Aims of this study

This study was designed to explore the nature of spatial autocorrelation in riverine benthic invertebrate assemblages. At the time of planning, no research on autocorrelation in benthic macroinvertebrates had been published, nor had there been any documentation of autocorrelation occurring in freshwater systems at all. The presence of autocorrelation in other systems suggested macroinvertebrate assemblages may well be autocorrelated, but this had not yet been ascertained. The belief that streams were open systems and the acknowledgment that this is due to the migration of individuals suggests that migration is an important contagious process in freshwater systems. The widespread assumption of strong upstream-downstream linkages and the use of the upstream reference site model imply that autocorrelation would occur in streams. Therefore the primary aim of this research was to document the patterns of spatial autocorrelation of benthic invertebrate assemblages in lotic habitats. Two rivers and two years were studied in order to gain

some idea of the generality of spatial autocorrelation patterns.

Because of the ramifications of autocorrelated data on the design of sampling protocols and experimental designs, this research was conceived as a methodological study. Consequently, I employed methods of sampling and data analysis common in recent impact-detection literature. I subsequently analysed the data in different ways to investigate the effects of common design elements. This is also why I have reviewed spatial analysis tools, so that spatial patterns can be incorporated into wider research questions.

Due to the importance of scale issues and the suggestions from recent literature that the scale of sampling may be crucial in determining the outcomes of research, I also wanted to investigate the scales at which spatial autocorrelation was apparent in the streams studied. The observation of longitudinal patterns in benthic invertebrates is widely reported, yet autocorrelation of assemblages is likely to occur at a number of spatial scales, including those much smaller than entire river lengths.

Therefore the aim of this study was to describe the pattern of autocorrelation in benthic invertebrates of two upland rivers over a variety of scales. A number of different spatial patterns could be possible and would depend on the strength of autocorrelation at different scales. For example, weak autocorrelation over a large distance could be related to longitudinal succession along a river profile. Alternatively, strong autocorrelation seen only at short geographic ranges may have a different underlying mechanism, such as the recovery of assemblage structure downstream of a point source pollution.

The final aim was to explore the relative importance of environmental factors and inferred dispersal processes in determining the spatial pattern of assemblages in upland streams. Longitudinal models and their implication that the succession of taxa downstream is related to physiographic changes in the environment have dominated thinking in community ecology in lotic habitats. Despite the acknowledgement that rivers are open systems, and the considerable research conducted on the magnitude, composition and adaptive value of invertebrate drift, there is little discussion of drift as a contagious process.

This study is the first to thoroughly investigate spatial autocorrelation patterns in riverine benthic macroinvertebrate assemblages, including long sections of river, several sites, a breakdown of different spatial scales and correlations with environmental variables. In addition to describing autocorrelation patterns, this research will place spatial autocorrelation patterns within the framework of longitudinal patterns.

Chapter 2

General Methods

2.1 General considerations

This was designed as a baseline study to investigate basic questions about the phenomenon of macroinvertebrate autocorrelation. This project was conceived as a thorough study in terms of the geographic distances covered (extent), and the number of sites studied (grain) but only a snapshot in terms of time and rivers studied. The sampling design and protocol was modeled on common practices in order to be relevant to current research. Consequently, I sampled two upland rivers, over summer, over 40 km of river length and collected multivariate data.

A multivariate approach was chosen because of the widespread and successful use of assemblage data for detecting impacts in rivers (Faith *et al.*, 1995) and stream ecology in general. Clarke & Ainsworth (1993) found assemblages to be sensitive for detecting impacts and for clearly differentiating sites within different habitats. Benthic macroinvertebrate assemblages of riffles were studied. The term 'assemblage' has been used throughout this thesis to mean organisms found together, rather than 'community', which implies a more tightly knit collection of interacting taxa (e.g. Townsend, 1989).

Because little or no previous work had been conducted on the spatial autocorrelation patterns of benthic macroinvertebrates in freshwater systems, the possible scales at which such correlation may exist were unknown. Therefore, I decided to sample large, contiguous sections of rivers.

Upland rivers were studied because there were relatively little anthropogenic environmental impacts to potentially confound the patterns of invertebrate assemblages.

Due to the large effort required to sample intensively along very long stretches of rivers, only two rivers were sampled. This would give an idea of whether spatial autocorrelation exists in these systems and gain an idea of the generality of spatial patterns in rivers, at least in these parts of Australia.

The same rationale was applied to temporal sampling. Because rivers show considerable variation in assemblages over time I did not attempt to characterise the changes in spatial autocorrelation among seasons. Two years of sampling in austral summer were planned, one river was sampled in both years, the second river was sampled only once. Sampling dates within summer were randomly allocated.

Summer sampling was chosen for three reasons. First, a considerable number of recent Australian studies were based on sampling conducted in either summer or spring. AUSRIVAS protocol (Coysh *et al.*, 2000) recommends spring and autumn sampling, but summer sampling is common (e.g. Bunn *et al.*, 1986; Barmuta, 1989; Downes *et al.*, 1993; Metzeling, 1993; Davies & Nelson, 1994). Second, Australian macroinvertebrates do not show strong seasonality due to poorly synchronised lifecycles, that is, identifiable nymphs are present throughout the year (Campbell *et al.*, 1998). Third, the patterns of invertebrate abundance and distribution should be relatively stable in summer because discharge is not generally high or variable in summer compared with spring (Hughes & James, 1989). There would be a smaller possibility of spates during the sampling season in summer. Discharge data for 1996 and 1997 confirmed that discharge was lower and less variable in summer than in spring in the Macalister and Wonnangatta Rivers, the rivers sampled (Table 2.1).

As this project was conceived as a methodological project, different analytical protocols were used to generate sub-sets of data in order to test effects on the detection of spatial autocorrelation. A variety of commonly used taxonomic-level and rare-species removal protocols were used. These issues are important to the theory and practice of impact detection and to the area of freshwater ecology in general. Despite this importance, there is little consensus in recent literature on the appropriate use of taxonomic level and rare species protocols.

2.2 Study site

This study was conducted in the Alpine National Park, in central eastern Victoria (Gippsland) (Licola 37°38′, 46°37′) (Fig. 2.1). The climate is temperate with cool winters and warm dry summers. The selected rivers, the Wellington and Wonnangatta

Rivers, are south-flowing rivers in the Victorian Alps Mountain Range. These rivers were selected because they are in adjacent catchments, which was necessary to conduct sampling quickly. The entire studied length of both rivers is accessible by walking, so randomly allocated sites could be sampled. Last, both rivers are relatively unimpacted upstream and throughout the length of the studied sections.

Upstream of the confluence of the Wellington and Carey Rivers, the Carey River was sampled because this was the larger river. Both are fourth order at this point, but the Carey River has a higher discharge (I. Campbell, unpublished data) and the Wellington River is partially regulated as it drains from Lake Tali Karng through a natural barrier caused by a rockslide 1500 years ago (Salas, 1981). The Wonnangatta River is unregulated. Both rivers are classified as spring rivers according to Haines *et al.*'s (1988) classification, and, for Australian rivers, experience relatively low hydrologic variability (Hughes & James, 1989).

Physico-chemical data were provided by Australian Water Technologies from routine monitoring programs conducted in the Macalister River at Licola (downstream of the Wellington River) (see Fig. 2.2) and the Wonnangatta River near Crooked River (see Fig. 2.3). Rainfall data for the West Gippsland region were obtained from The Meteorological Board of Victoria, (1996,1997). Discharge data from the Macalister River at Licola (downstream of the Wellington River) and Glencairn (upstream of the Wellington River) (see Fig. 2.2) and the Wonnangatta River at Crooked River (see Fig. 2.3) were provided by Theiss Environmental Services.

2.2.1 Impacts on the Wellington and Wonnangatta Rivers

2.2.1.1 Catchment condition

Despite logging activities in the past, which finished in the Wellington and Wonnangatta River catchments in 1981, both catchments are well forested with native vegetation (Council, 1982).

The forests of the Wellington and Wonnangatta catchments were surveyed to identify the major floristic components. Plants were identified using Costermans (1992).

The Wellington River catchment is covered with dry sclerophyll forest, which is dominated by red box *Eucalyptus polyanthemos*, red stringybark *E macrorhyncha* and but but *E. bridgesiana* (Table 2.2). Although invading blackberry *Rubus fructicosus* vines occur, the vegetation of the riparian zone primarily comprises native plants such as river tea tree *Leptospermum obovatum*, sedges, and long-leafed lomatia *Lomatia myricoides*

(Table 2.2).

The vegetation of the Wonnangatta catchment is similar to that of the Wellington catchment, although dominated by fewer species. The open forest of the hills comprises red box, red stringybark with an understory of shining cassinia *Cassinia longifolia* and sweet bursaria *Bursaria spinosa*. However, unlike the Wellington River, the riparian vegetation of the Wonnangatta River includes some exotic plants because, in some sections, the valley vegetation has been cleared to allow cattle grazing (Table 2.2).

Historically, cattle grazing occurred upstream of and along the studied section of the Wonnangatta River. Grazing upstream of the studied section of the Wonnangatta River ceased when the area was declared a National Park in 1981 (Johnson, 1996). Some grazing still occurs along the banks of the Wonnangatta River because 7.6 km^2 remains as freehold land. In addition to grazing, this private land has been cleared, in some cases to the river's edge.

A few roads cross both rivers, and camping occurs along 24 km of the Wellington River and 5 km of the Wonnangatta River.

2.2.1.2 Instream condition

Despite these potential impacts of camping, cattle grazing and altered riparian zones, water quality is good for both rivers, with neutral pH and low turbidity, conductivity, nitrogen and phosphorus levels (ANZECC, 1992)(Table 2.3).

2.2.2 Similarities and differences between the rivers

The Wellington and Wonnangatta Rivers are stony upland rivers. The substratum of both rivers is a tightly packed amalgam of boulders, cobbles, pebbles, and sand. Despite similarities, the rivers are considerably different in size. The Wonnangatta River is a larger river and is further from its source than the Wellington River, resulting in differences in stream order, river width, catchment area, discharge/catchment area, altitude and slope. The two rivers also occur in catchments with different geological and riparian vegetation characteristics (Table 2.4). The Wonnangatta catchment has some cleared land, cattle grazing and damaged riparian zones, unlike the Wellington catchment.

2.3 Sampling design

2.3.1 Spatial sampling protocol

A 40 km length was located in both rivers and divided into eight contiguous 5 km sections (see Figs. 2.2 and 2.3). The 40 km lengths began at the uppermost accessible part of the river. In order to prevent overlap of sampling in two adjacent sections, 500 m at both ends of each section were excluded from centre-point choice. A centre point for sampling was randomly selected for each section on each sampling occasion prior to the commencement of fieldwork. This centre point was then located in the field and 150 m lengths of river downstream and upstream of this centre location were traversed and the number of riffles counted. Two riffles were then selected randomly from those riffles.

2.3.2 Temporal sampling protocol

Sampling was conducted from January 26 to February 14 in 1996 and February 4-12 in 1997. The sampling order of sections within each river was fully randomised. However, I sampled two or three sections consecutively from each river in order to minimise travelling time between the two rivers and to keep the entire sampling period as short as possible. The sampling seasons were kept short to decrease potentially confounding factors of weather, floods and insect emergence.

2.3.3 Invertebrate sampling

Invertebrate assemblages were sampled by using a Surber sampler (Surber, 1970; Hellawell, 1978). I wanted to employ a standard procedure for sampling, but in Australia a wide variety of sampling techniques are used, including kick samples (Boulton, 1985; Chessman & Robinson, 1987; Wright *et al.*, 1995; Coysh *et al.*, 2000), artificial substrate samplers (Faith *et al.*, 1995), box samplers (Barmuta, 1989) and suction samplers (Brooks & Boulton, 1991). However, the Surber sampler is a common sampling apparatus (e.g. Bunn *et al.*, 1986; Doeg *et al.*, 1987; Metzeling, 1993; Davies & Nelson, 1994). I selected this sampling method as it is quantitative, unlike kick or sweep sampling, and is lightweight and can therefore be carried for considerable distances. It is also useful for a variety of substrates. The only potential limitation is the size of rocks around which the frame will fit. However, this was not a major problem in either the Wellington or Wonnangatta River because cobbles exceeding the capacity of the sampling frame were

uncommon. The frame was positioned randomly, although if the frame could not be pressed firmly against the substrate due to large cobbles, it was relocated. The frame was placed against the substrate with the net attached to the back. The ten largest rocks within the frame of the Surber were placed into the net for measurement and examination for attached invertebrates. The substrate was disturbed with a trowel to a depth of 8-10 cm for a period of 2 min. All material lifted by this disturbance was carried into the net by the current. Animals attached to the rocks collected during sampling were removed by hand and included in the sample, which was washed thoroughly with water to separate the organic and inorganic components. The organic component was retained and preserved in 2% formalin (1996) or 70% ethanol (1997). In some cases, there was a delay before preservation because the sampling sites, due to random site selection, were not accessible by car. This period was a maximum of 2 hours.

Five Surber samples were taken at each riffle using a 22.5 x 22.5 cm Surber sampler with 300 μm mesh. Five samples were considered sufficient to characterise the assemblage present in each riffle because cumulative richness curves for both rivers showed that taxa from five samples account for the majority of taxa found in ten samples in a pilot study (Fig. 2.4). Five samples accounted for 86%, 73% and 90% of the taxa found in 10 samples from the Wellington River 1996, 1997 and Wonnangatta River sampling programs respectively (Fig. 2.4). This is consistent with the results of Metzeling *et al.* (1984), who found that five Surber samples contained 73-85% of the species found in 10 samples in the Latrobe River, which is in the nearby western Gippsland region. Five samples were sufficient to detect significant differences in the composition of fauna at different sites by using Analysis of Similarity (ANOSIM) (Clarke, 1993) (see section 2.4.5). In all sampling seasons global one-way ANOSIM tests found differences between the fauna at different sampling sites (Table 2.5). That is, differences between sites were greater than differences within sites. Five samples were, therefore, considered sufficient to distinguish sites on the basis of their macroinvertebrate fauna.

2.3.4 Habitat description

The AUSRIVAS protocol (Coysh *et al.*, 2000) for habitat variable records was employed so as to use a standard protocol to describe habitat at the scale of the riffle. Several habitat variables were measured for each riffle sampled (Table 2.6). Measurements included: water temperature, air temperature, stream width, bank width, bank heights, water depth and corresponding current speed at 1 m, 2 m and 3 m from the water's edge. Estimates of percentage composition for periphyton, each substrate particle size, length of riffle, turbidity, land use, erosion and stability of stream bank, width and composition of riparian

zone, and shade over river were recorded.

The maximum length, height and width were measured with a ruler to the nearest cm for the 10 largest rocks collected in every Surber sample. Stone size may reflect bed roughness, which affects the turbulence of near-bed hydraulic flow (Davis & Barmuta, 1989). Stones collected from within the Surber sampler were used to calculate a relative measure of bed roughness for each sample. 'Bed roughness' was calculated by taking the mean of the height measurements of the 10 largest stones removed from each of the five Surber samples for every riffle.

2.3.4.1 Measurement of distance between riffles

The distance between the two riffles sampled in a section was paced out. The map coordinates of the riffles were ascertained by topographic features and recorded. Signal distortion by the steep valley walls precluded the use of a GPS (Global Positioning System) to calculate position. Digital image analysis of the map with coordinates marked on it was used to measure river distance between sampling (Logan, 2000).

2.3.5 Sample processing

In the laboratory, samples were washed thoroughly on a 300 μm sieve and sub-sampled. Twenty-five percent sub-samples were examined under a binocular dissector. Every invertebrate present was identified to lowest taxonomic level.

2.3.5.1 Validation of subsampling protocol

Subsampling was employed because samples contained large amounts of organic material and many invertebrates. Sufficient characterisations of samples have been obtained with 25% subsamples in previous Australian studies (Marchant *et al.*, 1989; Walsh, 1997). Ten randomly chosen samples, including samples from both rivers, comprised a pilot test for subsampling. Twenty-five per cent. subsamples were investigated, as advocated by Wrona *et al.* (1982). The sample was divided by placing the entire sample in a Folsom plankton splitter, a rotating device that splits the sample into two equal portions (McEwen *et al.*, 1954). This device has been used successfully to subsample plankton (Longhurst & Siebert, 1967) and macroinvertebrate samples (McKaige, 1986). Distributions of invertebrates within the container were randomised with an aquarium air blower (Wrona *et al.*, 1982). The Folsom splitter was used to split the sample into two 50% portions, one

of which was then randomly chosen to be split again. Both the 25% subsample and the remaining 75% of the original sample were sorted and every invertebrate was identified and counted.

The assemblage composition and presence/absence data of the 25% subsamples were compared to those of the 75% subsamples and to the entire sample (obtained by summing the abundances of each taxon found in the 25% and 75% subsamples). Data were examined at the lowest possible taxonomic level. The assemblage composition (i.e. abundance data for all taxa) was compared by using ANOSIM (Clarke, 1993) (see section 2.4.5 for explanation of this testing procedure). Taxon abundances were fourth-root transformed to reduce the influence of the abundant taxa on the analysis (Clarke, 1993). There was no difference between assemblages for all three sample portions (one-way ANOSIM, R=0.064, $P\simeq$0.95, N=10) nor in a paired comparison between the 25% subsamples and the entire samples (one-way ANOSIM, R=0.052, $P\simeq$0.80, N=10). Nor was there any difference in presence or absence of taxa between the 25% subsamples, the 75% subsamples and the entire samples (one-way ANOSIM, R=0.007, $P\simeq$0.37, N=10). Therefore, the 25% subsamples were not significantly different from whole samples in composition or presence-absence of taxa.

The 25% subsampling technique was adopted for all further samples because it appeared to adequately characterise the community composition of the entire sample.

2.3.5.2 Inclusions and Exclusions

A number of animals in the sub-samples were not included in the data-set. These included terrestrial insects such as ants, mites other than Hydracarina (Oribatida) and winged adults because these were considered to be contaminants. Data for springtails (Order Collembola) were also discarded because they are found only on the surface of the water and are not truly aquatic. In addition to non-aquatic invertebrates, aquatic pupae of trichopterans and dipterans were not identified. These animals are inactive and therefore do not comprise an interactive part of the assemblage. Due to the reorganisation of body tissues during metamorphosis they are extremely difficult to identify consistently.

A third group of animals excluded from the data-set was aquatic larvae that were judged to have been dead at the time of sampling. Insects were considered to be in this class if they were severely damaged, for example, those with only the head remaining, and the soft tissues appearing decomposed. The heads of several trichopterans and most emphemeropterans are easily detached so that isolated heads of these groups were included in the counts if they appeared to be 'fresh'. Similarly, oligochaetes

often break in the process of being separated from detritus and each other, so a single oligochaete was counted when two ends were found. However, dipteran, coleopteran, megalopteran, odonate and plecopteran heads are more firmly attached and severed heads were infrequently found for these taxa. Detached heads of these groups were not included in sample data. All insects missing one or more legs or gills were counted as these are often damaged in transit or during removal from the detritus.

One sample contained an eggsac of several hundred eggs and first instar *Orthotrichia* sp. (Order Trichoptera). These were not included in the sample total because they comprised an inactive component of the assemblage. In addition, the extreme rarity of eggsacs makes their presence a very sporadic occurrence, which could artificially increase the ecological distance between the site from which they were collected and every other site. Rare species (according to different criteria) were excluded from some analyses in order to examine effects upon autocorrelation calculations (see section 2.4).

Immature larvae were identified and included in the data-set because they comprised a substantial proportion of each sample. It is likely that early-instar larvae were numerous in these samples because the Surber-sampling technique collects animals from the hyporheos in addition to the substrate surface. Moreover, it is a quantitative technique that collects all animals within the area of the frame. Smaller animals such as the early instars may be more likely to be swept away in eddies of the current in sampling techniques such as kick sampling, where the net is a considerable distance away from the disturbance of the substrate. Although early-instar larvae are commonly discarded from qualitative samples in other studies, I considered that accurate numbers of the assemblage components were important to this study. Immature larvae are more time consuming to identify and cannot always be identified to species, but these are not persuasive arguments for exclusion in my opinion.

2.3.5.3 Taxonomic level

Specimens were identified to the lowest possible taxonomic level using current keys (Hynes, 1974; Hawking, 1986; Dean & Suter, 1996; Cartwright, 1997; St Clair, 1997; Suter, 1997; Wells, 1997; Cartwright, 1998; Davis, 1998; Harvey & Growns, 1998; Jackson, 1998; Dean, 1999a,b; Glaister, 1999; Hawking & Theischinger, 1999; Suter, 1999). This level varied among taxa due mainly to incomplete knowledge of the Australian fauna. In addition, immature or damaged larvae frequently do not exhibit diagnostic characters so that not all individuals of a taxonomic group were identified to the same level. Many of the keys used widely in Australia include recognisable taxonomic units that have not been described and do not necessarily correspond to species or genus.

All arthropods (insects and mites) were identified at least to genus, with the majority of specimens identified to species. Exceptions were the dipteran families of Tipulidae, Empididae and Simuliidae. Only oligochaetes, platyhelminths and nematodes were not identified -these taxa comprised a minor component of the samples.

2.4 Analysis

2.4.1 Autocorrelation analysis

Spatial autocorrelation may be defined as "the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations" (Legendre,1993, p. 1659).

Autocorrelation-analysis was performed on assemblage data by using the Mantel-test (Mantel, 1967). The Mantel-test is useful for testing a linear relationship between two sets of data. The test has no assumptions regarding the distribution of variables measured, so it can be used on non-normally distributed data. A Bray-Curtis dissimilarity index was calculated between every possible pair of sites. Sixteen sites resulted in ${}^{16}C_2$=120 site-pair combinations. The Bray-Curtis dissimilarity index can be interpreted as a measurement of the ecological distance between sites (Clarke, 1993). This index has been found to be sensitive to community differences and robust to noise (Hruby, 1987; Pontasch & Brusven, 1988; Faith *et al.*, 1991).

Each of the distances was represented in a matrix of sites. Two matrices were formed: (1) geographic distances between each pair of sites (see section 2.3.5); and (2) ecological distances (as measured by Bray-Curtis dissimilarity index).

The normalised Mantel-test statistic was calculated by using the following formula:

$$r = [1/(n-1)] \sum_i \sum_j [(x_{ij} - \bar{x})/S_x] [(y_{ij} - \bar{y})/S_y]$$

for $i \neq j$, where i and j are row and column indices of matrices x and y and n= number of distances in each matrix.

This statistic was then tested for significance by comparing it to a distribution obtained by randomly permuting the data and recalculating the test statistic many times. If the null hypothesis of no correlation between the two sets of distance values is correct, then the original calculation of the test statistic using the data in the observed order would be

in the middle of the possible values for R calculated from the randomly permuted data (Legendre, 1993).

Although the Mantel-test has no assumptions regarding the distribution of the variables tested, the test does assume the relationship between the two variables is linear. Scatterplots were used to check whether the relationship appeared linear. Analyses of different scales of inter-site distance were used in addition to Mantel-tests.

2.4.1.1 Correlograms

Mantel-correlograms are commonly used to investigate the scales at which autocorrelation occurs in multivariate data. Correlograms have been used to describe spatial structures and to identify the approximate point at which autocorrelation ceases to be significant. The Mantel-test assumes a linear relationship between ecological and geographic distances. However, this assumption may not always hold true; the relationship between geographic distance and ecological difference may reach a plateau (see Fig. 2.5). This would occur if increasing distance (past a certain point) does not produce a corresponding increase in ecological difference.

A correlogram is a graph of an autocorrelation coefficient at distance classes. The distance classes are geographic distances grouped into classes. The distance classes may be grouped to contain site pairs with approximately equal distances between them or equal numbers of site pairs.

Correlograms are used in spatial analysis with univariate (e.g. Moran's I, Legendre & Fortin,1989) and multivariate data (Mantel-correlogram). The Mantel-correlogram was devised by Sokal (Sokal, 1986). Like the Mantel-test, it requires two distance matrices. In this study, the first matrix was that of ecological distance. The second matrix, instead of a second measure of distance, as in the Mantel-test, is a model in which sites within each distance class are given the same value. From this second matrix, a matrix is created for each distance class whereby all site pairs that are members of a particular distance class are allocated a value of one, while all non-members are allocated a value of zero (Sokal, 1986). The normalised Mantel-coefficient (R) is then calculated separately for each distance class. Each coefficient is tested for significant deviation from zero with the same randomisation method as in the Mantel-test (see section 2.4.1). A global test of the correlogram is performed before interpretation of the spatial structure can proceed. If at least one autocorrelation coefficient displays significant deviation from zero, with the type-I error rate (α) corrected to compensate for multiple tests (Legendre & Fortin, 1989), then interpretation of each coefficient can be attempted by using correlogram shape.

Characteristic correlogram shapes have been related to underlying mechanisms (Sokal, 1979). Legendre & Fortin (1989) have produced correlograms for a number of distributions, such as gradients, random data and patchy distributions.

The large number of sites needed to detect a significant relationship is a limitation of this technique. The assumption of linearity in the Mantel-test is reduced in the Mantel-correlogram (Burgman & Williams, 1995). However, this technique does rely on the assumption that a single dominant spatial structure is present (Legendre & Fortin, 1989).

2.4.1.2 Extensions of the Mantel-test

Extensions of the Mantel-test were used to investigate the influence of the habitat superimposed on the autocorrelation pattern. The Mantel-test can be extended to include three matrices in an analogous method to multiple regression (Smouse *et al.*, 1986). The two matrices used to explain the variation in the variable of interest need not be independent (Smouse *et al.*, 1986). The partial correlation coefficient is calculated in several steps. The three matrices are standardised. A new matrix is created by regressing the values of one explanatory-variable matrix (e.g. geographic distance matrix) against the other (e.g. environmental matrix). The residuals of the regression comprise a new 'residual matrix'. A second residual matrix is calculated in the same way by regressing the values of the third original matrix (e.g. ecological distance matrix) against the values of the environmental matrix. The two residual matrices are then tested using the standard Mantel-test described in (see section 2.4.1) (Legendre & Vaudor, 1991).

This method effectively holds the covariate, in this case environmental dissimilarity, constant so that the relationship between ecological distance and geographic distance can be tested in the absence of an effect of environmental variables. The matrix of environmental dissimilarity was calculated by finding Canberra metric dissimilarity indices between each pair of sites for most environmental variables recorded in the field.

2.4.2 The SIGNAL statistic

Because spatial patterns of invertebrates may be affected by environmental impacts, the AUStralian RIVer Assessment System (AUSRIVAS, see below) and Stream Invertebrate Grade Number Average Level (SIGNAL) bioassessment summary statistics were calculted for each sampling site. The SIGNAL statistic is a rapid bioassessment technique that summarises the water quality of a site by taking into account the presence of particular macroinvertebrates (Chessman, 1995). It is a calculation of the average of

the 'pollution sensitivity grade' for all macroinvertebrate families sampled at a particular site (Chessman *et al.*, 1997). The pollution sensitivities account for known tolerance to organic and inorganic contaminants (Chessman *et al.*, 1997). The 1997 version of this index provides good discrimination between sites of varying environmental quality, and is highly correlated with habitat variables such as water conductivity (Chessman *et al.*, 1997). This metric has been found to be sensitive, cost efficient and robust to variations in sampling (Chessman *et al.*, 1997). The statistic is used to rate sites for environmental quality (Table 2.7).

2.4.3 AUSRIVAS

The AUStralian RIVer Assessment System (AUSRIVAS) is a modelling technique for rapid assessment of biological impairment of rivers in Australia. This method has been adopted by the Australian EPA (Environmental Protection Agency). The AUSRIVAS model was used in this study to obtain univariate summary scores for each site sampled.

The AUSRIVAS model is based on the River InVertebrate Prediction and Classification System (RIVPACS) used in the United Kingdom (Wright *et al.*, 1984; Moss *et al.*, 1987; Wright *et al.*, 1993, 1996). The model predicts the taxa that should be found at a site if no environmental degradation has occurred, based on the values of habitat variables at the site. The ratio of taxa predicted to those observed gives a measure of environmental impairment. The invertebrates expected at a site are predicted by comparing the habitat at the site with the habitat of reference sites by using quantities such as physico-chemical, substrate and riparian variables.

Reference sites are indentified *a priori* and the habitat and invertebrates are then sampled. Reference sites are selected on the basis of being in a 'least disturbed' state according to documentation of pollution, either from water quality data or information regarding point source and diffuse pollution and land-use (Coysh *et al.*, 2000). The invertebrate data from these sites are used to form site groups. Bray-Curtis dissimilarity indices, calculated from presence/absence family data, are used in Unweighted Paired-Group arithMetic Averaging (UPGMA) -an agglomerative clustering technique -to produce the site groups.

The habitat variables used in the model are those unlikely to change with anthropogenic impact, such as distance from source, latitude, longitude, river width, etc. A subset of all the possible habitat variables that best places the reference sites into their site groups (based on invertebrate data) is determined using stepwise Multiple Discriminant Function Analysis (MDFA). This subset of habitat variables is used as a predictor

for putative impact sites. The habitat variables used in the model for Victorian rivers include water chemistry, physical, biotic and geographic variables (Table 2.8). The habitat variables have been tested for error in assigning reference sites to their site groups using MDFA. This model is available to researchers and government agencies to determine ecological impairment of rivers or sites. Standard protocols for invertebrate and habitat sampling have been prescribed (Coysh *et al.*, 2000). The sampling technique for invertebrates is a 'standardised kick sample', incorporating all representative habitats. The sample is then 'ive-picked in the field for 30 min (Coysh *et al.*, 2000).

To test sites for environmental impairment, habitat and invertebrate data are entered into the model. Sites are validated to ensure they fit within the range of the model. The values of the habitat variables are used to predict the probability of the test site grouping with each of the reference site groups. The frequency of occurrence for each taxon sampled at the reference sites is calculated for each group of reference sites. The probability of a test site falling within a reference site group is multiplied by the frequency of occurrence for each taxon present in that group. This estimates the probability that each taxon should be found at the test site. Taxa thought to have $P>0.5$ of occurring at the test site form a list of **predicted** families. The number of **expected** taxa (E) is calculated by summing the probabilities of occurrence of each taxa on the list of **predicted** families. This value is less than the number of taxa in the list of **predicted** families as all $P<1$. Families sampled at the test site that are on the list of **predicted** families comprise **observed** families (O). The ratio of the number of **observed** families to **expected** families (O/E) is the diagnostic summary statistic. This is placed into bands for interpretation (Table 2.9).

2.4.4 Inferential statistics

Standard t-tests were employed to test differences between sampling seasons in taxonomic richness and abundance. Normality and similar variance were visually checked before tests were conducted. The SYSTAT statistical package was used to perform t-tests (Wilkinson, 1992).

2.4.5 Analysis of Similarity

Analysis of Similarity (ANOSIM) was used for a number of multivariate comparisons. ANOSIM may be regarded as a multivariate analogue of Analysis of Variance (ANOVA), in that it compares the within-site similarity to the between-site similarity. ANOSIM

is a non-parametric method that uses the rank similarities of site pairs (Clarke, 1993). Bray-Curtis similarity coefficients, calculated from faunal abundances, are used to rank the site pairs in order of similarity. There is no requirement of normal distributions of the similarity coefficients (Clarke, 1993) because the test of the null hypothesis of no difference between the fauna of different sites is a permutation test (Hope, 1968). The statistic tested (R-value) incorporates the difference between the mean of rank similarities among replicates within sites and the mean rank of similarities among samples between different sites (Clarke, 1993). A distribution of possible R-values is generated by permuting the sample labels, such that similarity coefficients do not correspond with their a priori groups (sites), and then calculating an R-value for each permutation. If there were no differences in the fauna between sites then the sample R-value would lie in the middle of the distribution of possible R-values calculated from permutations of the sample labels. Sites with similar faunas will have an R-value close to zero. The p-value is the number of permutations that generated an R-value less than, or equal to, the sample R-value.

ANOSIM comparisons were performed by using the PRIMER Package (Carr *et al.*, 1994).

Table 2.1: Discharge (ML/day) of Macalister and Wonnangatta Rivers in spring versus summer (mean ± SE).

Season	Macalister River	Wonnangatta River
Spring 1996	2720 ± 346	2030 ± 230
Summer 1996- 1997	106 ± 1	200 ± 2
Spring 1997	649 ± 73	547 ± 60
Summer 1997- 1998	24 ± 3	91 ± 6

Data provided by Theiss Environmental Services

Table 2.2: Vegetation of the Wellington and Wonnangatta River catchments.

Vegetation class	Wellington River	Wonnangatta River
Catchment Vegetation	Open forest	Open forest
Upper story	*Eucalyptus polyanthemos*	*E. polyanthemos*
	E. macrorhyncha	*E. macrorhyncha*
	E. bridgesiana	
	E. viminalis	
	E. rubida	
Middle story	*Acacia mearnsii*	
	A. melanoxylon	
Under story	*Bursaria spinosa*	*Cassinia longifolia*
	Xanthorrhoea australis	*Bursaria spinosa*
Valley vegetation	Tall open forest	Tall Open Forest
Upper story	*E. polyanthemos*	*E. viminalis*
	E macrorhyncha	*E. rubida*
	E. bridgesiana	
	E. viminalis	
	E. rubida	
Middle story	*Acacia mearnsii*	*A. mearnsii*
	A. melanoxylon	*A. melanoxylon*
	Exocarpus cupressiformis	
Under story	*Bursaria spinosa*	*Pteridium esculentum*
	Pomaderris aspera	Pasture grasses*
	Pteridium esculentum	
	Coprosma quadrifida	
	Cassinia longifolia	
	Lomatia myricoides	
	Callitris endlicheri	
	Hakea eriantha	
	Leptospermum lanigerum	
Riparian vegetation†	*Leptospermum obovatum*	*Leptospermum obovatum*
	Sedges	*Salix babylonica**
	Lamandra sp.	*Rubus fructicosus**
	*Rubus fructicosus**	
	Phragmites australis	

The most com mon plants are listed for the slope, valley and riparian zones of the Wellington and Wonnangatta Rivers

† Plants found in the valley vegetation also extend into the riparian zone. Only plants specific to the riparian zone are listed.

* Introduced species

Table 2.3: Water quality in the Wellington and Wonnangatta Rivers in comparison to ANZECC guidelines.

Water quality parameter	Wellington River (mean ± se of monthly records for 1995, 1996, 1997)	Wonnangatta River (mean ± se of monthly records for 1995, 1996, 1997)	ANZECC guidelines (1992)
Conductivity (Adjusted to 25°C)	52.2 ± 5.4 μS/cm	45.5 ± 4.4 μS/cm	<1500 μS/cm
Turbidity	3.2 ± 0.4 NTU	3.1 ± 0.4 NTU	See optical guidelines
pH	7.1 ± 0.1	7.0 ± 0.1	6.5-9.0
Dissolved Oxygen	10.3 ± 0.3 mg/L	9.5 ± 0.9 mg/L	>6.0 mg/L
Total Kjeldahl Nitrogen	0.173 ± 0.018 mg/L	0.134 ± 0.015 mg/L	No global guidelines
Total Phosphorus	0.016 ± 0.003 mg/L	0.015 ± 0.002 mg/L	No global guidelines

Data provided by Australian Water Technologies (Water EcoScience)
All parameters for which ANZECC (1992) has global guidelines were within suggested limits.

Table 2.4: Differences between the Wellington and Wonnangatta Rivers.

Character along studied length	Wellington River	Wonnangatta River
Altitude	480m -240m above sea level*	340m - 260m above sea level*
Stream Order	2-6*	7
Stream width	4-30 m*	11-35 m*
Catchment Area	97 km^2 -324 km^2*	972 km^2- 1138 km^2*
Mean daily discharge (January 1996)	204 ML/day†	581 ML/day
Distance from source	17-51 km*	54-87 km*
Runoff/catchment area	0.630 ML/day/ km^2	0.5105 ML/day/ km^2
Slope	0.68-0.79m/100m*	0.29-0.23m/100m
Number of tributaries		
Third order	7	11
Fourth order	4	5
Fifth order	1	1
Catchment Geology	Silurian siltstone and mudstone, Upper Devonian-Lower Carboniferous siltstone and sandstone	Ordovician siltstone and sandstone
Riverbed Geology	Quarternary alluvium and Silurian siltstone and mudstone	Quarternary alluvium
Catchment vegetation	Native open forest	Native open forest
Riparian vegetation	Native with limited *Rubus fructicosus* invasion	Predominantly native with moderate *R. fructicosus* invasion, limited *Salix babylonica* and pasture grasses planted

Discharge data provided by Theiss Environmental Services
* Range is from uppermost site to lowermost site
† at Licola downstream of the Wellington and Macalister confluence

Table 2.5: ANOSIM results for faunal differences between sites within a sampling event.

Test	River and year	Number of sites	ANOSIM R statistic	*P* value
One-way ANOSIM	Wellington River 1996	16	0.611	<0.001
One-way ANOSIM	Wellington River 1997	16	0.618	<0.001
One-way ANOSIM	Wonnangatta River 1996	16	0.678	<0.001

Table 2.6: Habitat variables measured or estimated in the field.

Variable	Definition (units)
Width of riparian zone of woody vegetation*	Categorical: -more than 30 m -more than 30 m -between 5 and 30 m -less than 5 m -no woody vegetation
Bank structure*	Categorical: -banks fully stabilised trees, shrubs etc -banks firm but held mainly by grass and herbs -banks loose, partly held by grass -banks unstable, mainly loose sand or soil
Riffle/pool sequence*	Categorical: -frequent alteration of riffles and pools -long pools with infrequent short riffles -natural channel without riffle/pool sequence -artificial channel, no riffle/pool sequence
Sediment*	Categorical: -little or no accumulation of loose sediments -some gravel bars but little sand or silt -bars of sand and silt common -braiding by loose sediment
Retention*	Categorical: -many large boulders and/or debris dams -rocks/logs present; limited damming effect -rocks/logs present, but unstable; no damming -stream with few or no rocks or logs
Bed roughness†	Categorical: -mean stone height >4 cm -mean stone height 3-4 cm

continued

∗ Estimated in field

† Measured in field

Note that all categorical variables comprise original categories

Table 2.6: (continued from previous page)

Variable	Definition (units)
	-mean stone height 2-3 cm
	-mean stone height <2 cm
Substrate composition*	Mean of phi values for composition of reach (no units)
Substrate heterogeneity*	Number of categories of substrate size with >10% abundance
Land use*	Categorical:
	-undisturbed native vegetation
	-native forest with some modification
	-intensive modification of native vegetation
	-urban land use
Macrophyte richness*	Number of species of macrophytes
Macrophyte cover*	Categorical:
	-<10%
	-10-35%
	-35-65%
	-65-90%
	->90%
Stream bottom*	Categorical:
	-mainly clean stones with obvious interstices
	-mainly stones with some cover of algae/silt
	-bottom heavily silted but stable
	-bottom mainly loose and mobile sediment
Percent shading*	Categorical:
	-None
	-low
	-medium
	-high
Stream width†	Mean width of water at site (m)

continued

∗ Estimated in field

† Measured in field

Note that all categorical variables comprise original categories

Table 2.6: (continued from previous page)

Variable	Definition (units)
Water temperature†	°C
Air temperature†	°C
Current speed†	m/s
Water depth†	cm
Turbidity*	Categorical:
	-clear
	-slight
	-turbid
	-opaque
Bank height†	m
Bank width†	m
Riparian vegetation*	Categorical:
	-native tree and shrub spp.
	-mixed native and exotic trees and shrubs
	-exotic trees and shrubs
	-exotic grasses/weeds

∗ Estimated in field

† Measured in field

Note that all categorical variables comprise original categories

Table 2.7: Interpretation of SIGNAL (97) values.

Environmental rating	Mean value of SIGNAL (97)
Excellent	>7
Good	6-7
Fair	5-6
Poor	4-5
Very poor	<4

SIGNAL (97) values and their environmental quality interpretation from Chessman *et al.* (1997).

Table 2.8: Habitat variables used in the AusRivAS model for Victoria.

Variable	Definition (units)
Distance from source	(kms)
Stream slope	Slope of reach (m/km)
Altitude	Height above sea level (m)
Latitude	(° ′)
Longitude	(° ′)
Catchment area	Area of catchment above sampled site (km^2)
Stream width	Mean width of water at site (m)
Substrate composition	Mean of phi values for composition of reach (no units)
Substrate heterogeneity	Number of categories of substrate size with >10% abundance
Riparian vegetation and land use	Categorical: -undisturbed native vegetation -native forest with some modification -intensive modification of native vegetation -urban land use
Macrophyte richness	Number of species of macrophytes
Macrophyte cover	Categorical: -<10% -10-35% -35-65% -65-90% ->90%
Annual air temperature	Mean annual air temperature (°C)
Range in annual air temperature	Mean range in annual air temperature (°C)
Alkalinity	Total carbonates (mg/L)
pH	(no units)

Source: Coysh *et al.* (2000)

Table 2.9: AusRivAS band widths and their interpretations.

Band	Label	Interpretation	Band width determinant
X	Very high occurrence of expected families	Biodiversity 'hot-spot' OR mild organic enrichment	Top 10% of reference sites (according to O/E value)
A	Number of families found similar to that expected	Water and habitat quality equivalent to that at reference site OR impact on water or habitat quality that does not result in the loss of families	Central 80% of reference sites (according to O/E value)
B	Several expected families not found	Impairment of either water and/or habitat quality	Band width (O/E values) same width as band A
C	Many expected families not found	Substantial impairment of water and/or habitat quality	Band width (O/E values) same width as band A
D	Very few of the expected families found	Severe impairment of water and/or habitat quality	Any sites with O/E value below that of band C

Source: Coysh *et al.* (2000)

Figure 2.1: Map of Victoria showing the location of Wellington and Wonnangatta Rivers. Shaded boxes represent the section of the Wellington and Wonnangatta Rivers enlarged in Figs. 2.2 and 2.3 respectively

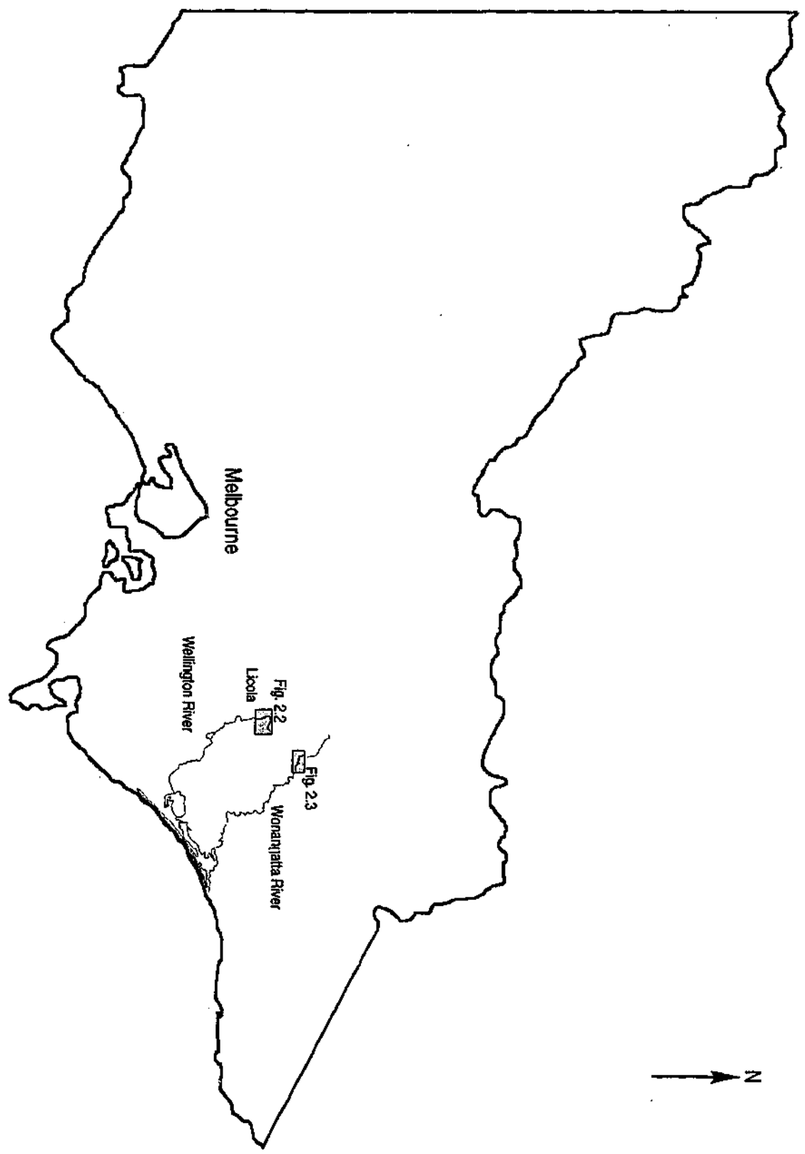


Figure 2.2: Map of Wellington River showing section locations, sampling sites for 1996 (△) and 1997 (○) and the location of water quality and discharge monitoring sites (?).

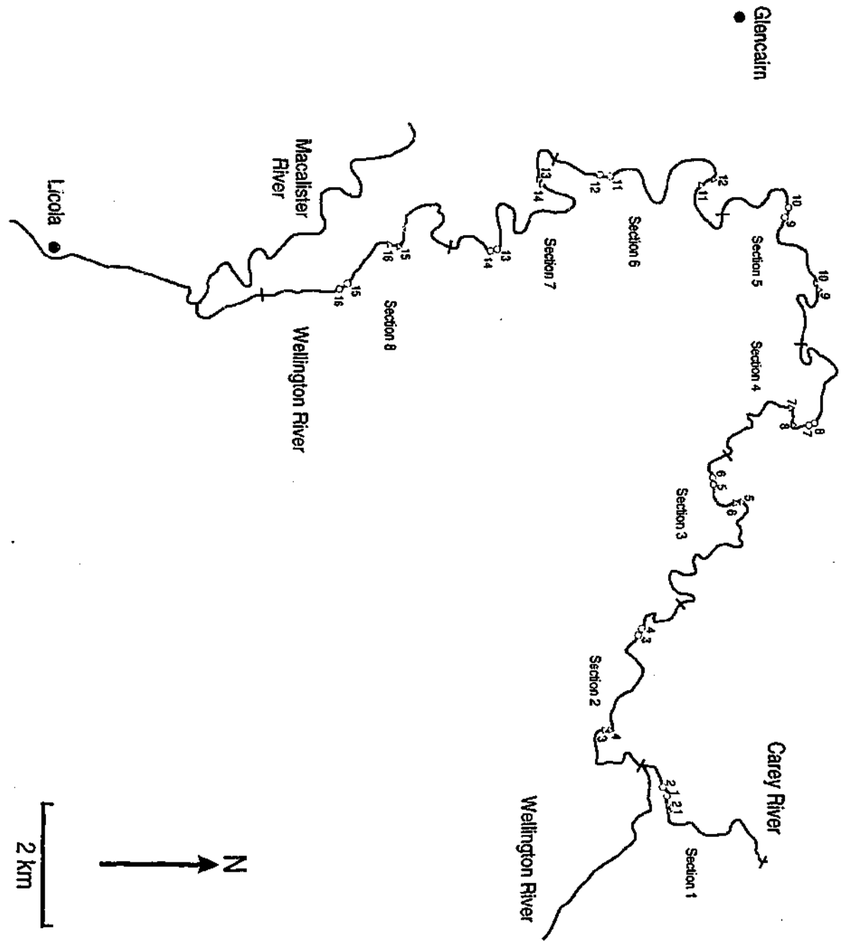


Figure 2.3: Map of the studied length of the Wonnangatta River showing section locations, site locations (○) and the location of water quality and discharge monitoring sites (?).

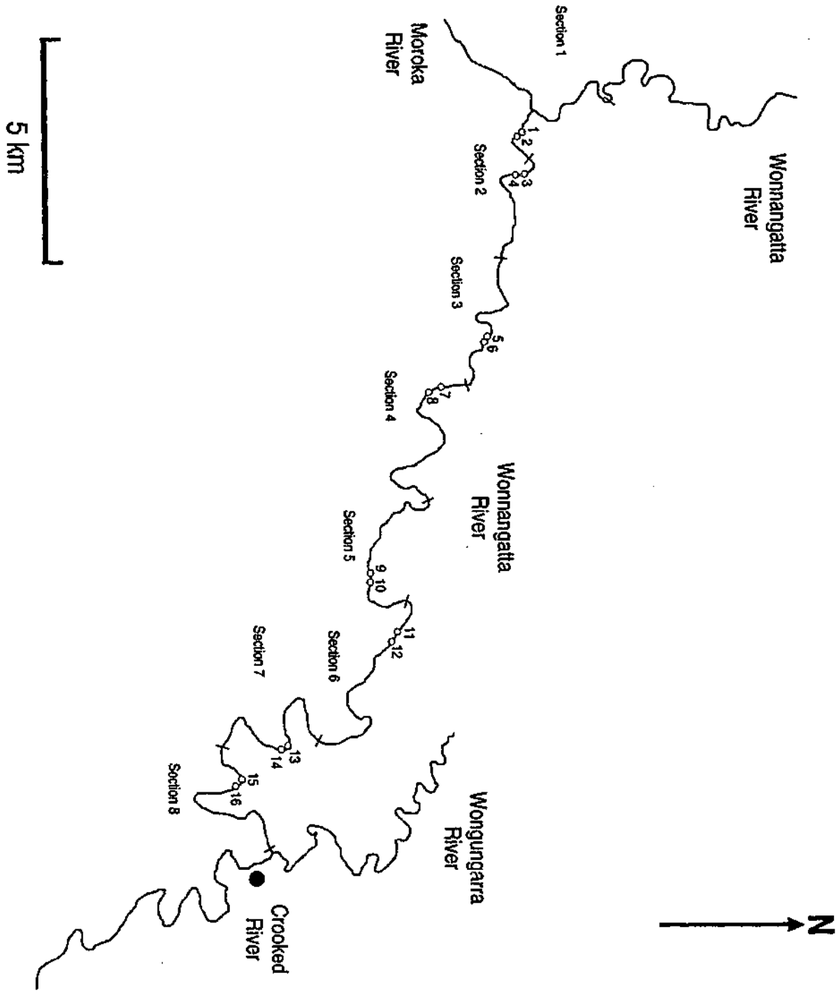


Figure 2.4: The cumulative number of taxa found in samples from selected sites in the Wellington and Wonnangatta Rivers. Five samples accounted for 86%, 73% and 90% of the taxa found in 10 samples from the Wellington River 1996, 1997 and Wonnangatta River 1996 sampling programs respectively.

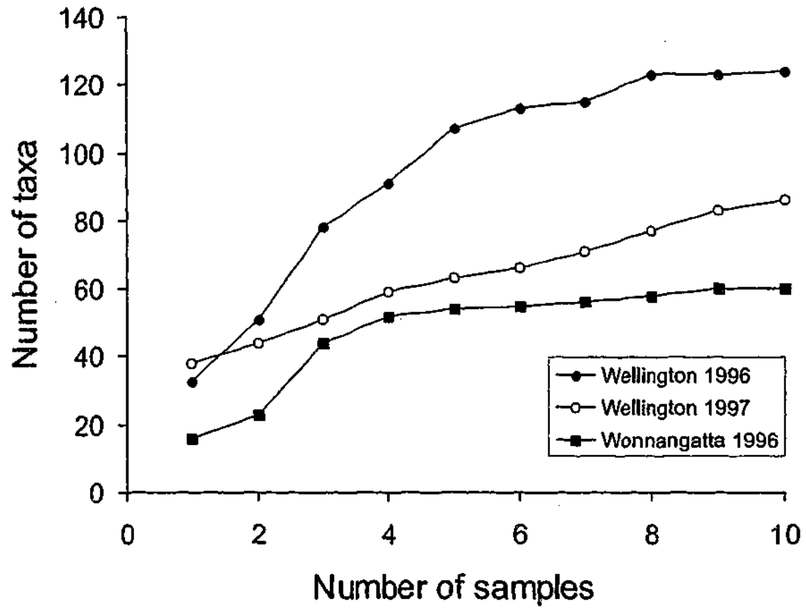
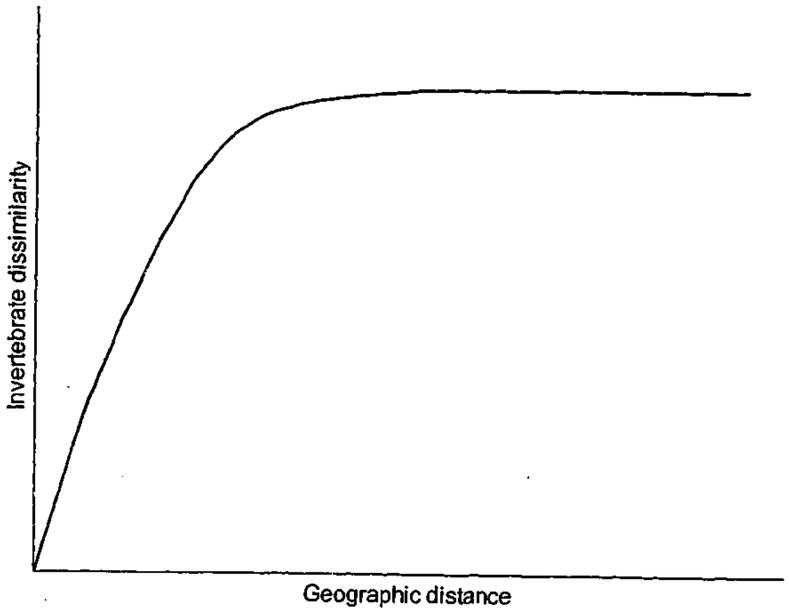


Figure 2.5: Hypothetical pattern of invertebrate dissimilarity over increasing geographic distance between sites. Spatially autocorrelated data shows an increase in dissimilarity over increasing geographic distance between sites. This relationship between geographic distance and ecological difference may reach a plateau if increasing intersite geographic distance (past a certain point) does not produce a corresponding increase in ecological difference between sites.



Chapter 3

Autocorrelation of invertebrate assemblages in the Wellington and Wonnangatta Rivers

3.1 Introduction

The primary aim of this chapter is to document spatial autocorrelation of the macroinvertebrate assemblages in the Wellington and Wonnangatta Rivers and compare the two rivers and sampling years. However, before these analyses were performed, the assumption that these rivers were unaffected by anthropogenic impacts was checked. Both rivers were assumed to be relatively pristine, although they experience some disturbance in the form of recreation, riparian zone and catchment clearing and cattle grazing. If these disturbances were causing impacts on the riverine fauna, then spatial patterns may have been affected.

Independence between sampling sites is often a major issue for study design. However, it is not the only one, nor will it operate in isolation. If different components of invertebrate assemblages exhibit different spatial patterns, the pattern of spatial autocorrelation detected may depend on which components of the fauna are examined. Therefore, factors important in the design of impact studies such as taxonomic resolution, rare species and surrogates for entire assemblages may influence spatial autocorrelation. If these do affect the detection of spatial autocorrelation or the scales at which spatial autocorrelation is significant, then these aspects of study design may alter assumptions regarding site dependence made by the researcher. For example, if EPT (Ephemeroptera, Plecoptera and Trichoptera) taxa are autocorrelated at a particular scale but entire

assemblages are not, the appropriate placement of replicate sites will be affected by the decision regarding which invertebrates are studied. In this way inconsistencies in rare-species protocols, taxonomic resolution and limited taxon suites may alter the influence of spatial autocorrelation on experimental or sampling design. Therefore, additional aims of this chapter were to investigate whether species show the same spatial autocorrelation pattern as genera and as families, whether rare and common taxa follow the same pattern and whether limited taxon suites behave in accordance with the entire data-set in relation to spatial autocorrelation. Because this project has a methodological perspective, common protocols within published literature have been applied.

Lower taxonomic resolution and limited taxon suites are two techniques of rapid biological assessment aimed at finding information quickly and cheaply. However, these two factors may influence the detection of spatial autocorrelation. For example, patterns of variation within macroinvertebrate assemblages on stones were not consistent over taxonomically or functionally related groups in one study in south-eastern Australia (Downes *et al.*, 1993).

The level of taxonomic resolution that should be employed is a contentious issue in Australia (New, 1996). Identification of invertebrates to species is difficult, time consuming and expensive. In many cases, it cannot be achieved because taxonomic knowledge is incomplete. Taxonomic focus is often determined by the state of taxonomic knowledge (Resh & McElravy, 1993): the well-known groups are enumerated at lower taxonomic level and consequently have greater influence in statistical multivariate analysis. The quality of identification is related to taxonomic level, and errors are more common at the species level than at higher taxonomic levels (New, 1996).

Several researchers have argued that identification to family is adequate for many studies, such as the detection of moderate or gross anthropogenic impacts in streams, and that finer resolution is unnecessary. New (1996) suggested that appropriate occasions for identification of taxa to a level higher than species are:

- detecting gross pollution, dramatic effects on benthos;
- early warning of changes, indicating need for more detailed study;
- when using indices insensitive to information loss to simplify presentation of results; and
- when taxa in a higher taxonomic group are consistent in their response to a given environmental change.

There are also valid reasons for enumeration to species. Many orders, families and

even genera contain species that occupy different trophic levels, different functional feeding groups, or have differing levels of sensitivity to contaminants (Beattie *et al.*, 1994). The Hydracarina, for example, contain parasitic and free-living species, predators and detritivores. Their sensitivities to pollution vary widely within families (Harvey & Growns, 1998).

Studies of taxonomic resolution have provided mixed results. In a study of ten data-sets from published work, Bowman & Bailey (1997) found that genus-level data did not provide considerably different descriptions of assemblage structure to those based on higher-level data. Faith *et al.* (1995) found little difference in sensitivity between family and species-level data in detecting the impact of mining in the Alligator Rivers Region, Northern Territory. Similarly, Wright *et al.* (1995) found that quantitative family-level data are sufficient to detect the impact of organic pollution in the Wentworth Falls area, New South Wales. However, the site groups from ordination were more distinct at species level than at family level (Wright *et al.*, 1995). In a study of the LaTrobe River basin, (Marchant, 1990) found that family-level data did not clearly show the seasonal patterns evident in species data. A classification of 49 undisturbed sites from six Victorian river basins on species-level and family-level data yielded different results, i.e. three and four site groups, respectively (Marchant *et al.*, 1997).

As with taxonomic level, the usefulness of limited taxon suites has not been resolved. Chironomids are sometimes excluded from identification beyond family (e.g. Lindegaard, 1994; Cao *et al.*, 1998) or excluded from the data-set altogether (e.g. Tikkanen *et al.*, 1994) due to the necessity of preparing individual slides and using the compound microscope to identify them. However, the Chironomidae is an extremely diverse family whose members live in a variety of habitats, belong to various functional feeding groups and have very different sensitivities to a number of pollutants (Smith & Cranston, 1994).

The EPT suite of insects has been used extensively as a surrogate for all invertebrates (e.g. Eaton & Lenat, 1991; Loch *et al.*, 1996; Diniz *et al.*, 1998). This is because these orders generally have high sensitivity to pollutants compared to most other insect groups (Harman, 1997). Several studies have found the EPT suite of invertebrates useful for detecting impacts (e.g. Quinn & Hickey, 1990; Eaton & Lenat, 1991; Poulton *et al.*, 1995). However, Statzner & Resh (1993) found this group was not successful in describing the patterns for all benthic invertebrates in a re-analysis of a number of published data-sets. In addition, both EPT assemblages (Brown *et al.*, 1997) and EPT richness (Stone & Wallace, 1998) can show different sensitivities to those of entire faunal assemblages and richness in detecting impacts.

Rare species are commonly excluded from data before analysis to reduce 'noise'.

Because some species are so rare, the probability of capturing them in a sample is so low that their presence may be effectively random. However, there are many definitions of rare species and the use of these definitions is inconsistent. The method of exclusion of rare species or whether any were excluded is frequently not reported (e.g. Richardson, 1985; Webber *et al.*, 1989; Harris *et al.*, 1992). There are two main types of definitions. The first is based on the number of samples in which a taxon is found. For example, Barmuta (1989) defined a rare taxon as one found in less than four samples out of 150. The second type of definition is based on the abundance of a taxon in a sample or the entire set of samples. Leland *et al.* (1989) defined a rare taxon as one that comprised less than 0.1% of the total individuals. Bunn *et al.*, (1986, p.71) only included taxa "comprising more than 5% of the total fauna collected at any of the twelve sites, or comprising more than 5% on at least one sampling occasion". Some definitions include components of both types of definition. Brooks & Boulton (1991) included only taxa that occurred in more than 75% of the replicates of any one treatment with a density greater than five individuals per sample. Studies into the effect of excluding rare taxa have produced mixed results. Austin & Grieg-Smith (1968) and Smith *et al.* (1988) suggest that inclusion of rare taxa is redundant and that adequate results may be obtained using only common taxa. However, Cao *et al.* (1998) found that different rare-species protocols produced different patterns of species richness between three sites with different levels of water quality. The different protocols would have lead to different conclusions regarding the impact on the macroinvertebrates at the three sites, if they had been interpreted in isolation (Cao *et al.*, 1998). Similarly, Faith & Norris (1989) found that inclusion of rare taxa exposed additional relationships with environmental variables in comparison to a subset of common taxa.

Given these inconsistencies in the use of rare taxa, limited taxon suites and level of taxonomic resolution and the growing use of rapid bioassessment techniques it is important to investigate the influence of these methodologies in the spatial characterisation of invertebrate assemblages.

3.2 Analytical methods

3.2.1 Taxonomic level

Separate Mantel-tests were computed for data arranged using three taxonomic protocols (Fig. 3.1).

- the 'species-level' protocol had all taxa that were identified to species enumerated separately. Taxa that were not identified to species-level, such as chironomids, were enumerated at the lowest taxonomic level to which they were identified.
- the 'genus-level' protocol combined data for all species within genera.
- the 'family-level' protocol contained the combined data for all genera within each family present.

These three protocols were applied separately to data from each sampling event.

3.2.2 Exclusion of taxa

3.2.2.1 Rarity protocols

Autocorrelation analyses were performed on the species-level, genus-level and family-level databases with three rarity protocols, making nine analyses in all (Fig. 3.1). The 'raw' protocol had no rare taxa excluded. This protocol is commonly used in macroinvertebrate studies (e.g. Weatherley & Ormerod, 1990; Burt *et al.*, 1991; Growns & Davis, 1991; Storey *et al.*, 1991; Quinn *et al.*, 1992; Metzeling, 1993; Stanley *et al.*, 1994).

The second-most inclusive rarity protocol, the 'non-unique' protocol, excluded taxa that were only found at one site. The exclusions were made separately for each sampling event because the data-sets were analysed separately. Therefore, a particular taxon may have been excluded from the Wellington River 1997 database but not the Wellington River 1996 database because it was sampled at more than one site in the Wellington River in 1996, but not 1997. Although this exclusion protocol is infrequently used (but see Downes *et al.*, 1993), its use can be justified on the basis that only very rare taxa are excluded. If these taxa were to remain in the data-set they would provide no additional information in terms of site discrimination. This is because a site containing a rare species will differ from every other site with respect to the species in question because the site is the only one at which the rare species was found. Inclusion of such a species therefore produces noise within the data-set. This protocol, although moderate, excluded a large number of taxa (up to 33% of taxa) from all data-sets (Table 3.1).

The third protocol used ('common') was more exclusive. In this protocol, a rare species was defined as one comprising less than 1% of the total individuals sampled in each sampling regime. Many taxa were excluded from autocorrelation analysis- up to 89% of taxa (Table 3.1). However, this protocol, and others even more exclusive, are common within published studies (e.g. Campbell, 1978; Bunn *et al.*, 1986; Chessman & Robinson, 1987; Leland *et al.*, 1989; Tikkanen *et al.*, 1994). The exclusion of taxa

comprising less than five percent of total individuals (e.g. Bunn *et al.*, 1986; Tikkanen *et al.*, 1994) resulted in the exclusion of all taxa from all data-sets in this study.

3.2.2.2 Chironomid removals

Species-level and genus-level data-sets excluding all chironomids were created for each sampling event and used in autocorrelation analysis (Fig. 3.2). There was no family-level data-set created without chironomids because all chironomids are within one family (Chironomidae). Only the non-unique rarity protocol was used to produce the data-sets for chironomid-excluded analyses because this protocol is moderate and justifiable (section 3.2.2.1). The numbers of taxa excluded from these data-sets were great (Table 3.2) because the Chironomidae is a diverse family and forms a significant proportion of the fauna from the Wellington and Wonnangatta Rivers.

3.2.2.3 EPT only

Subsets of the complete data-set, consisting of only the Ephemeroptera, Plecoptera, and Trichoptera were created for family, genus and species data-sets and tested for autocorrelation using Mantel-tests (Fig. 3.2). Taxa were excluded if found at only one site (non-unique rarity protocol). As both the Ephemeroptera and the Trichoptera sampled in the two rivers were diverse groups (Table 3.3), approximately half of the original taxa remained in the EPT data-sets (Table 3.4).

3.3 Results

3.3.1 Macroinvertebrate fauna of the Wellington and Wonnangatta Rivers

Taxa collected were predominantly insects within the orders of Ephemeroptera, Trichoptera, Coleoptera, Diptera, Plecoptera, Odonata and Megaloptera. Other significant components of the fauna included the orders Hydracarina and Oligochaeta. Ephemeropterans, trichopterans and dipterans were the most abundant taxa, while the trichopterans and dipterans were the most diverse groups collected (Table 3.3). Thus, the proportion of EPT taxa was high for both abundance and taxonomic richness. Individuals of the phyla Platyhelminthes and Nematoda were rarely collected.

3.3.1.1 Species richness and diversity

The Wellington River 1996 samples yielded 209 morphospecies, comprising 156 genera and 50 families. Similarly, 180 morphospecies from 141 genera and 49 families were collected from the Wellington River in the 1997 sampling season. The Wonnanngatta samples yielded a total of 150 morphospecies from 116 genera and 43 families (Table 3.5).

The majority of taxa (128 morphospecies) were found in every sampling event. However, six taxa were unique to the Wonnanngatta River, 36 taxa were collected only from the Wellington River, a further 45 taxa in 1996 sampling season alone and 16 taxa (including 1 family) only in the 1997 field season (Table 3.6).

Of the 95 morphospecies found only in one sampling season, 29 were rare taxa; these were only found in one site. Therefore, the remaining 66 unique taxa were moderately common, yet were exclusive to a particular sampling event. This indicates that the sampling events comprised distinct assemblages.

3.3.1.2 Univariate summary measures of 'river health'

SIGNAL scores obtained for all sites were consistently high, with most sites scoring above six (Table 3.7), therefore achieving a rating of good environmental quality (Table 2.7).

The Victorian AUSRIVAS model placed the majority of sites for all sampling events in Band A (Table 3.8), suggesting little anthropogenic impact (Table 2.9). Several sites were grouped in band B, indicating mild impact, and a few were placed in bands X and C. Placement in band X relates to higher O/E ratios than the reference sites, indicating either no anthropogenic impact or slight organic enrichment. Classification in band C suggests moderate impact because the O/E ratio was considerably lower than that of the reference sites.

3.3.1.3 Differences between rivers

Despite the occurrence of most taxa in both rivers, the Wonnangatta River had lower taxonomic richness per sample (mean $\pm$ SD) (Wonnangatta River 1996 6.7 $\pm$ 1.1, Wellington River 1996 7.9 $\pm$ 1.1) (t-test t=3.014 (square root transformed), df = 30, P=0.005) than the Wellington River fauna sampled in 1996. In addition, the mean ($\pm$ SD) number of individuals found in samples from the Wonnangatta River was lower than samples from the Wellington River (Wonnangatta River 1996 5.5 $\pm$ 0.7; Wellington River

1996 6.0 ± 0.6) (*t*-test *t*=2.073 (natural log transformed), *df* = 30, *P*=0.047).

It is not surprising in the light of the differences in abundances, richness, and the large number of taxa unique to each river, that the faunas from the two rivers were statistically different (Fig. 3.3a). The differences in fauna between the two rivers were much greater than those within each river (one-way ANOSIM, *R*=0.592 *P*<0.001, *N*=16).

3.3.1.4 Differences between years

There was no difference in the mean (± SD) taxonomic richness (1996: 7.9 ± 1.1; 1997: 7.9 ± 0.8) or abundance (1996: 6.0 ± 0.6; 1997: 6.3 ± 0.3)per sample of animals collected from the Wellington River in 1996 compared to 1997 (*t*-test richness (square root transformed): *t*=-0.070, *df* = 30, NS; *t*-test density (natural log transformed): *t*=-1.663, *df* = 30, NS).

The assemblages of the Wellington River differed between 1996 and 1997 (one-way ANOSIM *R*=0.326, *P*<0.001, *N*=16) (Fig. 3.3b). There were many non-rare taxa unique to either the 1996 (18 taxa) or the 1997 sampling seasons (12 taxa) (Table 3.6).

The summer of 1996-1997 was drier than the previous summer for the region (The Meteorological Board of Victoria, 1996; 1997) (Table 3.9). Therefore the discharge and water quality were markedly lower in 1997 than in 1996 (Table 3.10). Dissolved oxygen was lower and water temperatures and conductivity were higher in 1997 compared to the previous summer. Water-chemistry variables in the Wellington River were different in the sampling seasons of 1996 and 1997. In the summer of 1997, discharge and dissolved oxygen were lower while water temperatures and conductivity were higher than 1996 values (Table 3.10).

3.3.2 Multivariate autocorrelation analysis

There was significant positive spatial autocorrelation in the macroinvertebrate assemblages of the Wellington River in both 1996 and 1997 (Table 3.11, Fig. 3.4a-b). Scatterplots of data from both years indicated that a linear model, although not ideal, was adequate to test the statistical relationship. However, the fauna of the Wonnangatta River did not show an autocorrelated pattern- the ecological distance appeared to bear no relationship with geographic distance (Table 3.11, Fig. 3.4c). There were no differences in the pattern of autocorrelation detected by using the data-sets of differing taxonomic resolution or differing rarity protocols (Table 3.11). Nor was there any effect of reducing the non-unique data-set by removing either chironomids or the non-EPT taxa (Table 3.12).

The patterns of highly significant autocorrelation in the Wellington River and non-significant data in the Wonnangatta River were found in all combinations of data considered here.

3.4 Discussion

3.4.1 Are these unimpacted rivers?

The high species richness and SIGNAL scores obtained in the Wellington and Wonnangatta Rivers suggest that these rivers were relatively 'pristine'. The high proportion of EPT families is consistent with this result. However, the AUSRIVAS O/E ratios did not entirely agree-many sites were classed in bands A and X, indicating no anthropogenic impact, but a substantial number were assigned to bands B or C, indicating mild or moderate impact (see section 2.4.3). The sites that had low O/E scores had few of the families that were expected to be present. However, there was a large number of families, including those with high scores in SIGNAL, that were present but not 'expected', so these were not included in the 'observed' families. Many of the variables in the Victorian AUSRIVAS model have relatively coarse resolution, so that all sites within the one river were allocated the same or very similar values for latitude, longitude and climatic factors. In addition, the water-chemistry data were the same for all sites within one river because data were not available for each site. Therefore, only a few variables played an important role in determining which families were to be expected. The sites were distinguished only on the basis of substrate composition, substrate heterogeneity, distance from source, catchment area, stream width, altitude, riparian vegetation and land use.

Invertebrates respond to a large number of habitat variables other than those in the Victorian AUSRIVAS model (Collier, 1995), including current speed (Degani *et al.*, 1993), hydraulic flow (Wetmore & Mackay, 1990; Fruget *et al.*, 1996), food abundance (Williams & Levens, 1988; Kerby *et al.*, 1995) microhabitat characteristics (Erman & Erman, 1984; Downes *et al.*, 1995, 1998a) and disturbance events (Lake, 1995). Biotic interactions can also be important in determining distributions at a small scale (Peckarsky, 1985; Scrimgeour *et al.*, 1994; Anholt, 1995). Therefore, the variables in the AUSRIVAS model are unlikely to be able predict the families present at a fine grain. The results indicate that AUSRIVAS results may not be reliable for distinguishing sites within the Wellington and Wonnangatta Rivers with respect to detection of anthropogenic impacts.

These considerations led me to conclude that the Wellington and Wonnangatta Rivers were suitable to investigate spatial autocorrelation as the confounding influences of human disturbance were minimal.

3.4.2 Multivariate Autocorrelation

Significant spatial autocorrelation was found in the Wellington River in both 1996 and 1997. This result is consistent with the only published study to investigate spatial autocorrelation in freshwater invertebrates. Diniz *et al.* (1998) found a marginal geographic effect for EPT assemblages in Cerrado streams of Brazil during the wet season. However, there was no effect of geographic distance in the dry season, perhaps due to increased habitat heterogeneity. A number of studies have discussed spatial patterns without specifically investigating spatial autocorrelation. A study of the chironomid fauna of the Rockhole Mine Creek, Northern Territory found assemblages to show a strong spatial pattern that overrode seasonal effects (Smith & Cranston, 1994).

Many studies of spatial pattern have focussed on longitudinal spatial patterns in invertebrate assemblages (Hawkins & Sedell, 1981; Culp & Davies, 1982; Marchant *et al.*, 1985; Growns & Davis, 1994; Ramirez & Pringle, 2001). Invertebrate assemblages showing longitudinal spatial patterns are also likely to be spatially autocorrelated, if autocorrelation analysis were to be performed, because fauna at sites closely situated are more similar than those at more distant separations. Danehy *et al.* (1999) found a longitudinal spatial pattern in invertebrate functional groups over distances less than 10 km in riffles of headwater streams of the Onondaga catchment, New York. This spatial pattern may have been caused by the underlying spatial pattern of environmental variables. Functional groups responded to a narrow range of physical conditions of geomorphological variables, including stream slope, mean Froude number and Froude variability. A longitudinal spatial pattern in community composition, functional groups and individual taxa was also detected over 65 km in the pristine Jacks Fork River, Missouri, USA (Doisy & Rabeni, 2001). This study also documented strong correlations between invertebrate spatial patterns and hydrological variables including current velocity, Froude number and Reynolds number (Doisy & Rabeni, 2001). In her very large-scale study of five sites at each of nine rivers within three biomes of northern USA, Corkum (1992) noted that although longitudinal patterns were detected, macroinvertebrate composition was more closely related to site-specific environmental variables than distance from source.

Spatial autocorrelation was significant in both years the Wellington River was sampled, despite differences in the composition of assemblages between years. The

faunal differences may be due to the summer of 1996-7 being hotter and drier than that of 1995-6. A number of the taxa unique to the 1997 sampling season, such as *Diphlebia* sp. and *Garinjuga* sp. also occupy pools. These taxa are tolerant of slow currents and low dissolved oxygen concentrations, such as may have been present in the riffles of the Wellington River in 1997.

It is not surprising that the fauna of the Wellington River was spatially autocorrelated because many processes occurring within the benthos of streams were expected to be spatially autocorrelated. The contagious processes likely to produce spatial autocorrelation include the dispersal of invertebrates: drift, benthic movements and flight; underlying patterns of environmental variables that influence colonization and survival of invertebrates and biotic interactions, such as competition, predation and parasitism (see section 1.1).

Unexpectedly, significant spatial autocorrelation was not found in the Wonnangatta River. There are two possible reasons for this finding: (i) the benthic faunal assemblages do show spatial autocorrelation but this pattern was not detected or (ii) there was no spatial autocorrelation of the invertebrates within the Wonnangatta River in 1996 at the scales sampled.

Lower densities of animals in samples from the Wonnangatta River contributed to more variable results than those from the Wellington River. Increased variation decreases the power of an analysis to detect a relationship. However, the scatterplots of Wonnangatta sites indicate that there is little evidence of a relationship between spatial separation and distinctness of invertebrate faunas.

Therefore, significant spatial autocorrelation was most likely not present in the Wonnangatta River in 1996 at the scales measured. The detection of spatial autocorrelation has been the common result in published studies of investigations into autocorrelation, for example Thrush *et al.* (1989) documented spatial autocorrelation in several species of benthic marine invertebrates. However, there are also some exceptions to this general trend. Although there are no published studies of communities showing a lack of spatial dependence, a number of examples of single species showing no significant spatial autocorrelation have been reported. Underwood & Chapman (1996) reported spatially autocorrelated distributions for most, but not all, of the rocky intertidal invertebrates sampled. Several populations of acorn woodpeckers (*Melanerpes formicivorus*) throughout the USA showed no spatial autocorrelation (Koenig, 1999a). Woodpecker densities were instead related strongly to acorn production and the number of species of acorn trees.

It is possible that the invertebrate fauna may show significant spatially autocorrelated distributions at smaller or larger scales than those sampled. For example, a smaller

sampling grain, e.g. within riffles, may reflect spatial patterns influenced by small spatial and temporal scale contagious processes such as competition, microhabitat choice and stone-turnover disturbances. A larger extent of sampling may have revealed distributions determined by large-scale biotic and abiotic processes relating to rainfall and soil types.

Contagious processes may not have a strong influence on the patterns of invertebrate distribution and abundance in the Wonnangatta River. Some of the contagious processes expected to cause patterns of spatial autocorrelation may not be applicable to this river. The three groups of contagious processes suggested comprise dispersal processes, biotic interactions and underlying environmental variables. Dispersal processes are unlikely to differ between the two rivers. Although the Wonnangatta River fauna was distinct from the Wellington River fauna, there were enough taxa present in both rivers to expect similar trends of dispersal. The taxa unique to either river were not the most abundant, the taxa unique to the Wellington River comprised 4.6% of total abundance and the taxa unique to the Wonnangatta River comprise less than 0.1% of the total number of invertebrates sampled from the Wonnangatta River. Nor is there any evidence to suggest that the taxa unique to the Wellington River are particularly prone to dispersal. Schreiber (1995) found the most common animals in the drift of a low order, unimpacted stream in Victoria included *Zavreliella* sp. (Chironomidae), *Austrosimulium* sp. (Simuliidae) and *Nousia* sp. (Leptophlebiidae), none of which were unique to the Wellington River, although all were found in both the Wellington River and the Wonnangatta River. Similarly, she also reported that the most common invertebrates of the Wellington River (*Notalina* sp., *Riethia* sp., *Rheotanytarsus* sp. and *Cheumatopsyche* sp.) were underrepresented in the drift (Schreiber, 1988). Other forms of dispersal have not been well studied in Australian freshwater invertebrates, but there is no intuitive reason to suspect that there may be differences in benthic movement or flight between the two rivers when the majority of animals were species found in both rivers.

It was beyond the scope of this study to examine the second group of contagious processes, the biotic interactions between invertebrates sampled and other organisms that may effect their patterns of dispersal, recruitment and survival. Therefore, it is not possible to suggest whether there may be differences in these processes between the two rivers.

The third suggested group of contagious processes was responses by invertebrates to underlying spatial patterns of environmental variables. There may be differences in the spatial patterns of environmental variables that influence the distribution and abundance of benthic invertebrates in the two rivers. The Wonnangatta River catchment has a greater diversity of land-uses than the Wellington River catchment. Some sites were located in cleared farmland or areas with modified riparian zones. Modifications to riparian zones

included clearing or reduction of the vegetation and/or the introduction of exotic species such as weeping willow (*Salix babylonica*) or pasture grasses. Cows had access to the water's edge at some sites. If the invertebrate fauna responded to habitat variables affected by land-use, such as shade, riparian-carbon inputs or nutrient enrichment, the pattern of spatial autocorrelation may have been overridden by these influences.

Another suite of environmental variables that may affect invertebrate fauna are hydrologic and geomorphological variables. Both the Wellington River and the Wonnangatta River have been classified in the same group of Victorian rivers by Hughes & James (1989). The characteristics of both rivers are a relatively low coefficient of variation of annual flow and high constancy of flow on a monthly basis and can be classified as 'early spring rivers' in Haines *et al.*'s (1988) river classification scheme (Hughes & James, 1989). Despite falling in the same category within Victorian rivers, some differences in the natural disturbance regimes of the sections sampled in the Wonnangatta and Wellington Rivers would be expected because the stream order, catchment area and distances from source are much larger in the Wonnangatta River that those in the Wellington River (Table 2.4, Fig. 3.5). A corollary of the size difference between the two rivers is that, although a similar geographic distance was studied in each river, the relative change in values for altitude, stream order, catchment area, distance from source and slope over the section sampled is much greater in the Wellington River than the Wonnangatta River (Table 2.4, Fig. 3.5). The implication of the greater range in environmental variables for the Wellington River is that the contagious processes created by the spatial pattern of environmental variables may be stronger in the Wellington River compared to the Wonnangatta River. If the spatial pattern of the invertebrates is determined by the underlying spatial pattern of the environmental variables, then this may explain why the distribution of the Wellington River invertebrates showed significant autocorrelation whereas that of the Wonnangatta River invertebrates did not. The role of the environmental variables measured (comprising some components of the habitat experienced by invertebrates) on the pattern of spatial autocorrelation of the benthic macroinvertebrate assemblages of the Wellington and Wonnangatta Rivers is considered in Chapter 5.

An alternative explanation for the lack of autocorrelation in the fauna of the Wonnangatta River may be a greater role for stochastic events in this river. Benthic macroinvertebrate assemblages frequently exhibit high variability, much of which cannot be ascribed to deterministic biotic and abiotic influences. For example, black fly assemblages among similar streams in the USA were largely unpredictable in terms of species co-occurrence (McCreadie *et al.*, 1997). Li *et al.* (2001) apportioned variation in common metrics (including taxonomic richness, density, % EPT and Shannon diversity)

between seven spatial scales in streams in Oregon, USA. Residual variance, i.e. sample to sample variance not attributable to any spatial factors in the design, was very high, accounting for 20-40% of total variance and 60-70% of within-stream variance. Hawkins *et al.* (1997, p. 728) found that variation in the assemblage structure of 45 Californian upland streams was random with respect to latitude or elevation "because of the strong dependency of assemblage structure on temperature and the lack of strong geographic trends in temperature among these streams". Bunn & Hughes (1997, p. 338) argued that the fauna present in particular riffles is due to "stochastic effects of recruitment" in addition to the dispersal ability of the taxa present. There are several theories of community ecology that place high importance on the role of stochastic events in determining community structure. These include the non-equilibrium theory advocated by Reice (1985, 1994), Sale's equal chance hypothesis (Sale, 1980) and the group of patch dynamics theories including founder controlled, relict controlled, and competitive lottery models (Townsend, 1989). These theories may be applicable to benthic stream assemblages in some cases (Lake, 1986; Townsend, 1989; Reice, 1994). Cooper *et al.* (1998) suggested that open stream systems are analagous to the coral reef fish to which Sale's equal chance hypothesis (Sale, 1980) was applied. That is, at small scales, the structure of assemblages is controlled by limited, stochastic recruitment, whereas as at large scales populations are essentially closed and are controlled by demographic processes (Cooper *et al.*, 1998). Therefore, the important difference between the Wellington and Wonnangatta Rivers with respect to autocorrelation may be the role played by chance.

The role of chance may be more important in the Wonnangatta River than the Wellington River because the Wonnangatta River has more tributaries than does the Wellington River (Table 2.4). Tributaries may influence the availability of drifting invertebrates and alter physicochemical and hydraulic environmental variables in the main channel. The possibly disruptive role of tributaries may have been more pronounced in the Wonnangatta River than the Wellington due to the section of each river sampled. The Wonnangatta River was sampled along a flatter portion of its longitudinal profile than was the Wellington River (Fig 3.5). This may mean that spatial patterns of near-bed hydraulic variables, which are influenced by the average slope of a river section (Statzner & Higler, 1986) and have been very important in influencing invertebrate fauna in other studies (?Doisy & Rabeni, 2001), were more affected by the incoming tributaries of the Wonnangatta River than the Wellington River.

The contradictory results from the two rivers throws into question the generality of spatial autocorrelation of macroinvertebrate assemblages and the scales at which it occurs. The ramifications of this lack of generality of the presence of significant spatial

autocorrelation may be critical. This result implies that the assumption that sites a small distance apart will be independent may or may not hold true. If the river sampled follows the pattern of the Wonnangatta River, this assumption would be valid. However, if the river in question is more similar to the Wellington River, then the distance between sites will partially determine the difference in faunal assemblages. This means that inferential statistics should not be applied without checking this critical assumption. If spatially autocorrelated data are tested using statistics that require independent replicates, then the risk of a false significant result (i.e. a type I error) is increased as the degrees of freedom are overestimated. Indeed, when Drinkwater & Myers (1987) re-analysed results from previous studies of fisheries catches in the Gulfs of St Lawrence and Maine, USA taking autocorrelation into account, they found that correlations that had been thought to be significant were not. Inferential tests can be applied to spatially autocorrelated data if the error terms are corrected (Legendre, 1993). Alternatively, spatial analysis is a useful tool and can be used to test alternative models in the context of the underlying spatial patterns (see section 6.7).

The different patterns found between the two rivers also invalidate the assumption that one can predict the fauna at one site based on the fauna at another site in close proximity. This model is used in studies that employ upstream 'reference' sites. In rivers like the Wellington River, this assumption is valid. However, the distance between the reference and treatment or impacted sites would be very important. The reference site(s) would ideally be situated as close as possible to the site(s) to be tested. The further away the sites are from each other, the greater the faunal differences would be, even if there is no effect of the treatment or impact. Therefore, a design such as that used by Quinn *et al.* (1992), in which control sites were situated between 0.5 km and 3 km upstream of the impacted sites may be spatially confounded. If the site-pairs that were separated by a greater distance had greater faunal differences, the effects of spatial autocorrelation and the impact tested cannot be separated. Quinn *et al.* (1992) assumed that the differences between the upstream controls and the downstream impacted sites was due to disturbance, and it may be that the effect of the disturbance was so great as to override underlying spatial patterns. However, in the absence of pre-impact data from these sites it is not possible to confirm this assumption and ascribe the cause of invertebrate change to the disturbance studied. Alternatively, if some or all of the rivers did not have significantly autocorrelated faunas, then the variable distances between the controls and treatment sites would not matter, but the model of using upstream sites as controls and predicting the fauna that should be found at the downstream sites would be inappropriate, because the two faunas would not necessarily be similar in the absence of an impact. The consequence of using this model in the absence of spatial autocorrelation is that some rivers may have been assigned impacted status due to a variety of differences, including purely stochastic

ones, between the sites.

Ultimately, before the model of spatial pattern against which a test will be performed is chosen for each study, an investigation into autocorrelation should be conducted, particularly if more than one river is involved in the design, or if the use of inferential statistics is planned. Alternatively, because impact studies are often complicated by a spatially biased pattern of anthropogenic disturbance, it would be sensible to incorporate spatial analysis rather than relying on space free designs such as the upstream - downstream site or BACI designs.

3.4.3 Different data representations

In contrast to the differences between the Wellington and Wonnangatta Rivers, spatial autocorrelation patterns within each river were consistent. Both sampling seasons showed the same results, as did the different data-sets. The lack of difference between the protocols indicates that all components of the fauna are driving the pattern of significant autocorrelation seen in the Wellington River, and that all faunal elements are responding to the factors producing the random pattern with respect to geographic distance in the Wonnangatta River. This at first appears surprising because the contagious processes likely to be responsible for spatial autocorrelation are unlikely to be the same for different taxa. Dispersal abilities, habitat preferences and biotic interactions all vary between taxa. Therefore subsets of the entire fauna sampled might be expected to behave differently. Indeed, the EPT suite has been found to show different patterns to the complete insect fauna in an analysis of 12 emergence studies of unimpacted sites (Statzner & Resh, 1993) and two studies testing the impact of logging (Brown *et al.*, 1997; Stone & Wallace, 1998). Chironomids also have shown different spatial patterns to the complete macroinvertebrate suite. In a tropical Australian stream, chironomids showed patterns of spatial zonation while the entire faunal assemblage was dominated by a spatial structure relating to an environmental impact (discharge from an abandoned uranium mine) between groups of sites (Smith & Cranston, 1994). Similarly, Brown *et al.* (1997) found the chironomid subset of taxa showed different spatial patterns to the entire faunal assemblage when testing the impact of different logging practices. Cao *et al.* (1998) investigated the effect of different rarity protocols on impact assessment. They found that the species-sample size curves for three sites with differing water quality varied depending on the rarity protocol used. They argued that this result was due to the different patterns of frequency of occurrence at sites (Cao *et al.*, 1998). For example, the assemblages at the least-impacted site contained a higher frequency of rare species.

Conversely, Marchant *et al.* (1995) found that there was little difference in the

ordinations of EPT taxa compared to the entire data-set. Correlations between ordination data and environmental variables such as altitude, temperature and substrate were as easily detected in the EPT sub-set as the entire data-set in a broad-scale analysis of several existing data-sets across Victoria (Marchant *et al.*, 1995). In a similar study of the unimpacted LaTrobe River upper catchment by Faith & Norris (1989), the sub-set of common taxa was less successful than the entire data-set in the detection of correlations with environmental variables. Comparisons of the common taxa subset with random rare taxa subsets containing the same number of taxa suggested that this result was primarily due to the increased sample size in the complete data-set, rather than different responses to environmental variables by rare taxa compared to common taxa (Faith & Norris, 1989).

The discrepancies between these results may be related to differences between individual taxa. Individual taxa are more likely to show clearly distinct spatial patterns than large groups that include a suite of animals influenced by different environmental variables and biotic interactions. Once a collection of taxa is studied-whether it be based on taxonomic groups, rarity or a microhabitat location (e.g. stone surfaces and hyporheos)-a mixture of responses will be obtained and an overall trend may be difficult to elucidate as the trends of different taxa cancel each other out. However, in this study, all taxa were predicted to display an autocorrelated spatial pattern. The scales over which autocorrelation is significant and the ultimate causes of this pattern may well be different, but the overall trend should not be confounded by alternative patterns shown by individual taxa.

3.4.3.1 Taxonomic level

The similarity of results for all taxonomic levels in both the Wellington and Wonnangatta Rivers is consistent with the findings of Faith *et al.* (1995), Marchant *et al.* (1995) and Bowman & Bailey (1997). Faith *et al.* (1995) found little difference in sensitivity between family and species-level data for mining impact detection. Bowman & Bailey (1997) found high correlations using Mantel-tests between species and family abundance data. Marchant *et al.* (1995) found no difference in ordination patterns for family and species data in a compilation of several Victorian data-sets. Although taxonomic resolution may be important in detailed studies (Marchant, 1990; Wright *et al.*, 1995), where different species show different behaviours and requirements, the broad pattern of spatial autocorrelation was as easily detected at family-level as at species-level in the two rivers studied. This may be useful for pilot studies of the suitability of different spatial models.

3.5 Summary

The Wellington and Wonnangatta Rivers appeared to be relatively pristine and therefore suitable rivers in which to investigate natural spatial patterns. The benthic invertebrate assemblages of the Wellington River showed a strongly autocorrelated pattern, whereas those of the Wonnangatta River showed a distance-independent pattern, at least at the scales sampled. The implication of this result for the design of ecological studies in such rivers is that no assumptions should be made regarding patterns of autocorrelation. There appeared to be no effect of taxonomic resolution, rarity protocols or assemblage surrogates on the detection of autocorrelation patterns.

Table 3.1: The number of taxa removed from each taxonomic level data-set for each rarity protocol.

River	Year	Rarity protocol	Taxonomic level	No. of taxa removed	No. of taxa remaining
Wellington	1996	Raw	Species	0	209
Wellington	1996	Raw	Genus	0	156
Wellington	1996	Raw	Family	0	50
Wellington	1996	Non-unique	Species	56	153
Wellington	1996	Non-unique	Genus	35	121
Wellington	1996	Non-unique	Family	6	44
Wellington	1996	Common	Species	185	24
Wellington	1996	Common	Genus	130	26
Wellington	1996	Common	Family	32	18
Wellington	1997	Raw	Species	0	180
Wellington	1997	Raw	Genus	0	141
Wellington	1997	Raw	Family	0	49
Wellington	1997	Non-unique	Species	40	140
Wellington	1997	Non-unique	Genus	28	113
Wellington	1997	Non-unique	Family	4	45
Wellington	1997	Common	Species	152	28
Wellington	1997	Common	Genus	114	27
Wellington	1997	Common	Family	27	22
Wonnangatta	1996	Raw	Species	0	150
Wonnangatta	1996	Raw	Genus	0	116
Wonnangatta	1996	Raw	Family	0	44
Wonnangatta	1996	Non-unique	Species	45	105
Wonnangatta	1996	Non-unique	Genus	34	82
Wonnangatta	1996	Non-unique	Family	4	40
Wonnangatta	1996	Common	Species	129	21
Wonnangatta	1996	Common	Genus	95	21
Wonnangatta	1996	Common	Family	25	19

Raw protocol: all taxa were retained in the analysis.
Non-unique protocol: taxa unique to a site were removed.
Common protocol: taxa comprising less than 1% of total individuals were removed

Table 3.2: Number of chironomid taxa removed from species and genus data-sets for each sampling event.

Sampling event	Taxonomic level	Number of taxa removed	Number of taxa remaining
Wellington 1996	Species	20	133
Wellington 1996	Genus	20	101
Wellington 1997	Species	19	121
Wellington 1997	Genus	19	94
Wonnangatta 1996	Species	14	91
Wonnangatta 1996	Genus	14	69

Rare taxa were removed according to the non-unique rarity protocol (see Table. 3.1). The same number of taxa were removed from species and genus data-sets as chironomids were identified to genus only.

Table 3.3: Relative abundances of major taxa sampled in the Wellington and Wonnangatta Rivers

Taxon	No. of families*	No. of genera*	No. of morpo-species*	Relative Abundance (% of total)		
				Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
Ephemeroptera	5	21	26	29	31	33
Plecoptera	4	9	12	1	<1	<1
Trichoptera	15	36	54	33	28	36
Diptera	7	35	54	15	22	11
Odonata	3	7	10	<1	1	<1
Coleoptera	6	10	23	10	8	14
Hydracarina	8	15	26	3	1	1
Oligochaeta	1	1	1	3	2	<1

*Figures are combined for all sampling events.

Table 3.4: The number of taxa excluded from, and remaining in, the EPT (Ephemeroptera, Plecoptera Trichoptera) only data-sets for each sampling event.

Sampling event	Taxonomic level	Number of taxa removed	Number of taxa remaining
Wellington 1996	Species	84	69
Wellington 1996	Genus	68	53
Wellington 1996	Family	22	22
Wellington 1997	Species	70	70
Wellington 1997	Genus	60	53
Wellington 1997	Family	23	22
Wonnangatta 1996	Species	59	46
Wonnangatta 1996	Genus	45	37
Wonnangatta 1996	Family	19	21

Rare taxa, those found only at one site during a particular a sampling event, were excluded before this data-set was created.

Table 3.5: List of taxa collected from the Wellington and Wonnanngatta Rivers during sampling events of 1996 and 1997.

Taxa	Family	Identified to...
Order Ephemeroptera		
Jappa kutera	Leptophlebiidae	Species
Ulmerophlebia pipinna	Leptophlebiidae	Species
Austrophlebioides sp.	Leptophlebiidae	Genus
A. pusillus	Leptophlebiidae	Species
A. marchanti	Leptophlebiidae	Species
Kirrara procera	Leptophlebiidae	Species
Koorrnonga sp.	Leptophlebiidae	Genus
Garinjuga sp.	Leptophlebiidae	Genus
Noussia sp.*	Leptophlebiidae	Genus
Atalophlebia sp.*	Leptophlebiidae	Genus
Unidentified Baetidae	Baetidae	Family
Baetid genus 2 spMV 3†	Baetidae	Species
Baetid genus 2 spMV 1†	Baetidae	Species
Baetid genus 2 spMV 6†	Baetidae	Species
Baetid genus 2 spMV 2†	Baetidae	Species
Baetid genus 2 sp.†	Baetidae	Genus
Bungona sp.	Baetidae	Genus
Baetid genus 1 sp.†	Baetidae	Genus
Baetid genus 1 spMV 4†	Baetidae	Species
Baetid genus 1 SWB5N†	Baetidae	Species
Cloeon sp.*	Baetidae	Genus
Unidentified Caenidae	Caenidae	Family
Caenid genus C sp.†	Caenidae	Genus
Caenid genus D sp.†	Caenidae	Genus
Caenid genus B sp.†	Caenidae	Genus
Tasmanocoenis sp.*	Caenidae	Genus
Coloburiscoides sp.*	Coloburiscidae	Genus
Mirawara aapta	Ameletopsidae	Species
Order Plecoptera		
Cosmioperla kuna	Eusthinidae	Species

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
Unidentified Gripopterygidae	Gripopterygidae	Family
Dinotoperla sp.	Gripopterygidae	Genus
Dinotoperla christinae	Gripopterygidae	Species
Dinotoperla brevipennis	Gripopterygidae	Species
Illiesoperla sp.	Gripopterygidae	Genus
Illiesoperla mayi	Gripopterygidae	Species
Illiesoperla brevicauda	Gripopterygidae	Species
Leptoperla sp.‡	Gripopterygidae	Genus
Reikoperla sp.	Gripopterygidae	Genus
Acruroperla atra	Austroperlidae	Species
Austropentura victoria	Austroperlidae	Species
Austroheptura neboissi	Austroperlidae	Species
Austrocercella marianne	Notonemouridae	Species
Order Coleoptera		
Austrolimnius sp.	Elmidae	Genus
Austrolimnius L36E†	Elmidae	Species
Austrolimnius L32E(A)†	Elmidae	Species
Austrolimnius L32E†	Elmidae	Species
Austrolimnius L37E†	Elmidae	Species
Austrolimnius L40E†	Elmidae	Species
Austrolimnius L39E†	Elmidae	Species
Austrolimnius L10E†	Elmidae	Species
Austrolimnius waterhousei	Elmidae	Species
Austrolimnius L35E†	Elmidae	Species
Kingolus sp.	Elmidae	Genus
Kingolus aeratus	Elmidae	Species
Kingolus yarrensis	Elmidae	Species
Kingolus tinctus	Elmidae	Species
Kingolus metallicus	Elmidae	Species
Kingolus flavoplagiatus	Elmidae	Species
Simsonia L3E(F)†	Elmidae	Species
Simsonia L12†	Elmidae	Species
Notriolus setosus	Elmidae	Species
Notriolus L57E†	Elmidae	Species

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
Adult *Kingolus* sp.*	Elmidae	Genus
Adult *Austrolimnius* sp.*	Elmidae	Genus
Adult *Notriolus* sp.*	Elmidae	Genus
Adult *Simsonia* sp.*	Elmidae	Genus
Berosus sp.	Hydrophilidae	Genus
Unidentified Hydrophilidae	Hydrophilidae	Family
Unidentified Gyrinidae	Gyrinidae	Family
Scleroscyphon sp.†	Psephenidae	Genus
Unidentified Scirtidae††	Scirtidae	Family
Unidentified Ptilodactylidae	Ptilodactylidae	Family
Nectoroscma sp.	Dityscidae	Genus
Order Odonata		
Unidentified Gomphidae	Gomphidae	Family
Hemigomphus heterocly[illegible]gouldii§	Gomphidae	Species
Austrogomphus ochraceus	Gomphidae	Species
Austrogomphus guerini	Gomphidae	Species
Austrogomphus cornutus	Gomphidae	Species
Unidentified Aeschnidae	Aeschnidae	Family
Austroaeschna inermis	Aeschnidae	Species
Austroaeschna pulchra	Aeschnidae	Species
Notoaeschna sagittatus	Aeschnidae	Species
Spinaeschna tripunctata	Aeschnidae	Species
Aeschna brevistyla	Aeschnidae	Species
Diphlebia lestoides	Amphipterygidae	Species
Order Diptera		
Pentaneura sp nov†	Chironomidae	Species
Paramerina levidensis	Chironomidae	Species
Pentaneurini genus D sp†	Chironomidae	Genus
Pentaneurini genus A sp†	Chironomidae	Genus
Pentaneurini genus ST1 sp†	Chironomidae	Genus
Cardiocladius sp.	Chironomidae	Genus
Cricotopus sp.	Chironomidae	Genus
'grape th' sp.†	Chironomidae	Genus
Stictocladius sp.	Chironomidae	Genus

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
Eukiefferiella sp.	Chironomidae	Genus
Ablesmayia sp.	Chironomidae	Genus
genus Australia A*	Chironomidae	Genus
Thienemanniella sp.	Chironomidae	Genus
Parakiefferiella sp.	Chironomidae	Genus
Dicrotendipes sp.	Chironomidae	Genus
Tanytarsus sp.	Chironomidae	Genus
Riethia sp.	Chironomidae	Genus
Rheotanytarsus sp.	Chironomidae	Genus
Zavreliella sp.	Chironomidae	Genus
Paratanytarsus sp.	Chironomidae	Genus
Polypedilum sp.	Chironomidae	Genus
Parachironomus sp.	Chironomidae	Genus
Unidentified tanypod	Chironomidae	Subfamily
Stictochironomus sp.	Chironomidae	Genus
Austrobrillia sp.	Chironomidae	Genus
Paracladopelma sp.	Chironomidae	Genus
Podonominae	Chironomidae	Subfamily
Omisus sp.	Chironomidae	Genus
Nilothauma sp.	Chironomidae	Genus
Djalmabatista sp.	Chironomidae	Genus
Cladotanytarsus sp.	Chironomidae	Genus
Nanocladius sp.	Chironomidae	Genus
Conochironomus sp.	Chironomidae	Genus
Nilotanypus sp.	Chironomidae	Genus
Harrisius sp.	Chironomidae	Genus
Compterosmittia sp.	Chironomidae	Genus
Paracladopelma sp.	Chironomidae	Genus
Unidentified Ceratopogonidae	Ceratopogonidae	Family
empidid 1*	Empididae	Morphospecies¶
empidid 2*	Empididae	Morphospecies
empidid 4*	Empididae	Morphospecies
empidid 5*	Empididae	Morphospecies
empidid 5a*	Empididae	Morphospecies

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
empidid 6*	Empididae	Morphospecies
Unidentified Tabanidae	Tabanidae	Family
tipulid 1*	Tipulidae	Morphospecies
tipulid 2*	Tipulidae	Morphospecies
tipulid 3*	Tipulidae	Morphospecies
tipulid 4*	Tipulidae	Morphospecies
tipulid 5*	Tipulidae	Morphospecies
tipulid 6*	Tipulidae	Morphospecies
tipulid 7*	Tipulidae	Morphospecies
tipulid 8a*	Tipulidae	Morphospecies
tipulid 8*	Tipulidae	Morphospecies
tipulid 9*	Tipulidae	Morphospecies
tipulid 10*	Tipulidae	Morphospecies
Simulium sp.	Simuliidae	Genus
Dasyoma tonnoira	Athericidae	Species
Order Trichoptera		
Cheumatopsyche sp 6†	Hydropsychidae	Species
Cheumatopsyche sp 4†	Hydropsychidae	Species
Cheumatopsyche sp 3†	Hydropsychidae	Species
Cheumatopsyche sp 5†	Hydropsychidae	Species
Cheumatopsyche sp 2†	Hydropsychidae	Species
Cheumatopsyche sp 1†	Hydropsychidae	Species
Asmicridea sp 1†	Hydropsychidae	Species
Asmicridea sp 2†	Hydropsychidae	Species
Baliomorpha sp 2	Hydropsychidae	Species
Unidentified Conoesucidae	Conoesucidae	Family
Conoesucus sp.	Conoesucidae	Genus
Conoesucus fromus	Conoesucidae	Species
Costora sp.	Conoesucidae	Genus
Matasia sp.	Conoesucidae	Genus
Calocid/Helicophid spAV1†	Calocidae/Helicophidae	Species
Calocid/Helicophid C sp.§	Calocidae/Helicophidae	Species
Tamasia sp.	Calocidae	Species
Oxyethira columba	Hydroptilidae	Species

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
Hellyethira sp.	Hydroptilidae	Genus
Hellyethira simplex	Hydroptilidae	Species
Hellyethira exserta	Hydroptilidae	Species
Hellyethira basicolla/basilobata	Hydroptilidae	Species
Hydroptila sp.	Hydroptilidae	Genus
Hydroptila scamandra	Hydroptilidae	Species
Hydroptila obscura	Hydroptilidae	Species
Hydroptila losida	Hydroptilidae	Species
Hydroptila calcara	Hydroptilidae	Species
Othotrichia sp.	Hydroptilidae	Genus
Orthotrichia tortuosa	Hydroptilidae	Species
Unidentified Odontoceridae	Odontoceridae	Family
Genus P sp.	Odontoceridae	Genus
Caenota sp.	Calocidae	Genus
Unidentified Calamoceratidae	Calamoceratidae	Family
Tasimia spAV1†	Tasimiidae	Species
Tasiagma ciliata	Tasimiidae	Species
Unidentified Leptoceridae	Leptoceridae	Family
Notalina sp.Leptoceridae	Genus	
Helicopsyche sp.§	Helicopsychidae	Genus
Unidentified Ecnomidae	Ecnomidae	Family
Ecnomina D sp1†	Ecnomidae	Species
Ecnomina F sp.†	Ecnomidae	Genus
Ecnomina F sp9†	Ecnomidae	Species
Ecnomina batyle	Ecnomidae	Species
Ecnomina E sp.†	Ecnomidae	Genus
Ecnomina E sp2†	Ecnomidae	Species
Ecnomus sp.	Ecnomidae	Genus
Ecnomus continentalis	Ecnomidae	Species
Ecnomus cygnitus	Ecnomidae	Species
Unidentified Polycentropodidae	Polycentropodidae	Family
Neureclipsis napeae	Polycentropodidae	Species
Genus G sp.†	Polycentropodidae	Genus
Genus I sp.†	Polycentropodidae	Genus

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
Paranyctiophylax spAV6†	Polycentropodidae	Species
Paranyctiophylax spAV5†	Polycentropodidae	Species
Paranyctiophylax sp6†	Polycentropodidae	Species
Plectrocnemia sp.	Polycentropodidae	Genus
Agapetus spAV1†	Glossosomatidae	Species
Megogata necopina	Hydrobiosidae	Species
Taschorema spAV2†	Hydrobiosidae	Species
Ethochorema turbidum	Hydrobiosidae	Species
Apsilochorema obliquum	Hydrobiosidae	Species
Unidentified Hydrobiosidae	Hydrobiosidae	Family
Ulmerochorema lentum	Hydrobiosidae	Species
Ulmerochorema rubiconum group	Hydrobiosidae	Species group
Psyllobetina locula	Hydrobiosidae	Species
Philorheithrus sp.§	Philorheithridae	Genus
Kosrheithrus sp.§	Philorheithridae	Genus
Austrheithrus sp.§	Philorheithridae	Genus
Chimarra australica	Philopotamidae	Species
Hydrobiosella sp.	Philopotamidae	Genus
Order Megaloptera		
Archichauloides sp.	Corydalidae	Genus
Austrosialis sp.	Sialidae	Genus
Order Hydracarina		
Flabellifrontipoda sp.	Oxidae	Genus
Frontipodopsis sp.	Frontipodopsidae	Genus
Australiobates sp.	Hygrobatidae	Genus
Procorticacarus 3	Hygrobatidae	Species
Procorticacarus 2	Hygrobatidae	Species
Barwontius sp.	Aturidae	Genus
Monactractrides sp.	Torrenticolidae	Genus
Kallimobates sp.	Hygrobatidae	Genus
Procorticacarus 1	Hygrobatidae	Morphospecies
Tubophorella australiasis	Limnesiidae	Morphospecies
Gondwanabates 1	Hygrobatidae	Morphospecies
Gondwanabates 3	Hygrobatidae	Morphospecies

continued

Table 3.5: (continued from previous page)

Taxa	Family	Identified to...
Limnesia 1	Limnesiidae	Morphospecies
Procorticacarus 8	Hygrobatidae	Morphospecies
Procorticacarus 9	Hygrobatidae	Morphospecies
Procorticacarus 7	Hygrobatidae	Morphospecies
Procorticacarus 4	Hygrobatidae	Morphospecies
Rhynchaustrobates sp.	Hygrobatidae	Genus
Procorticacarus 6	Hygrobatidae	Morphospecies
Limnesia 2	Limnesiidae	Morphospecies
Tobelobates confusus	Hygrobatidae	Species
Anisitsiellides sp.	Anisitsiellidae	Genus
Procorticacarus 5	Hygrobatidae	Morphospecies
Gondwanabates 4	Hygrobatidae	Morphospecies
Albia sp.	Aturidae	Genus
Australorivaricus sp.	Hygrobatidae	Genus
Gondwanabates 2	Hygrobatidae	Morphospecies
Class Oligochaeta		Class
Class Bivalvia		
Pisidium sp.	Sphaeridae	Genus
Class Gastropoda		Class
Ferrissia sp.**	Ancylidae	Genus
Phylum Nematoda		Phylum
Phylum Platyhelminthes		
Unidentified Dugesiidae	Dugesiidae	Family
Phylum Hirudinea		
Alboglossophonia sp.	Glossophoniidae	Genus

† taxa without formal taxonomic description, informal names are widely published in guides

¶ taxa comprising recognisable taxonomic units, not published in keys

§ mature larvae indistinguishable

‡ immature larvae indistinguishable

∗ no key available

** spp. indistinguishable due to preservation technique

†† mature nymphs indistinguishable

Table 3.6: Taxa unique to a single sampling event or river and the sampling event(s) and number of sites they were collected from.

Unique taxa	Sampling event(s)	No of sites
Ulmerophlebia pipinna	Wellington River	2
Koorrnonga sp.	Wellington River 1997	4
Garinjuga sp.	Wellington River 1997	1
Baetid genus 2 spMV 2	Wellington River 1996	6
Cloeon sp.	Wellington River	3
Reikoperla sp.	Wellington River 1996	1
Acruroperla atra	Wellington River 1996	3
Austropentura victoria	Wellington River	3
Austroheptura neboissi	Wellington River 1997	2
Austrocercella marianne	Wellington River 1997	5
Austrolimnius L37E	Wellington River 1996	1
Austrolimnius L10E	Wellington River	2
Kingolus flavoplagiatus	Wellington River 1996	2
Adult *Notriolus*	Wellington River 1996	2
Gyrinidae	Wellington River 1996	1
Ptilodactylidae	Wellington River 1997	4
Austrogomphus ochraceus	Wellington River	17
Austrogomphus guerini	Wellington River 1996	1
Austrogomphus cornutus	Wellington River	6
Austroaeschna inermis	Wellington River 1996	2
Austroaeschna pulchra	Wellington River	6
Notoaeschna sagittatus	Wellington River 1996	1
Spinaeschna tripunctata	Wellington River	3
Aeschna brevistyla	Wellington River 1997	1
Diphlebia lestoides	Wellington River 1997	2
Paramerina levidensis	Wellington River	5
Pentaneurini genus D	Wellington River	3
Pentaneurini genus A	Wellington River 1997	1
Cardiocladius sp.	Wellington River 1996	2
Ablabesmayia sp.	Wellington River 1997	2
Thienemanniella sp.	Wellington River	8
Parakiefferiella sp.	Wellington River 1996	3
unidentified tanypod	Wellington River 1996	1

continued

Table 3.6: (continued from previous page)

Unique taxa	Sampling event(s)	No of sites
Zavreliella sp.	Wellington River	3
Paratanytarsus sp.	Wellington River 1996	2
Parachironomus sp.	Wellington River	3
Stictochironomus sp.	Wellington River 1997	2
Djalmabatista sp.	Wellington River	2
Cladotanytarsus sp.	Wellington River 1997	1
Nanocladius sp.	Wellington River 1997	3
Conochironomus sp.	Wellington River 1996	1
Compterosmittia sp.	Wellington River 1996	1
Tabanidae	Wellington River 1996	3
empidid 2	Wellington River 1996	2
empidid 6	Wellington River 1996	3
tipulid 3	Wellington River	5
tipulid 6	Wellington River	5
tipulid 7	Wellington River 1996	2
tipulid 10	Wonnangatta River	10
Cheumatopsyche sp. 3	Wellington River	6
Cheumatopsyche sp. 2	Wonnangatta River	1
Cheumatopsyche sp. 1	Wellington River	2
Baliomorpha sp. 2	Wellington River 1997	2
Matasia sp.	Wellington River	4
Calocid/Helicophid C	Wonnangatta River	1
Hellyethira simplex	Wellington River	4
Hellyethira exserta	Wellington River	9
Hydroptila scamandra	Wellington River 1996	1
Hydroptila obscura	Wellington River 1996	2
Hydroptila losida	Wellington River	7
Hydroptila calcara	Wellington River 1997	3
Tasimia spAV1	Wellington River	5
Tasiagma ciliata	Wellington River 1996	1
Ecnomina F sp9	Wellington River	2
Ecnomina batyle	Wellington River 1996	1
Ecnomus continentalis	Wellington River	4
Ecnomus cygnitus	Wellington River 1996	1
Genus I sp.	Wellington River	12

continued

Table 3.6: (continued from previous page)

Unique taxa	Sampling event(s)	No of sites
Paranyctiophylax spAV6	Wellington River	3
Paranyctiophylax spAV5	Wellington River 1996	1
Plectrocnemia sp.	Wellington River 1997	2
Ethochorema turbidum	Wellington River 1996	1
Ethochorema nesydrion	Wellington River 1997	1
Apsilochorema obliquum	Wellington River	6
Ulmerochorema rubiconum group	Wellington River 1996	3
Psyllobetina locula	Wellington River 1996	1
Hydrobiosella sp.	Wellington River	2
Frontipodopsis sp.	Wellington River 1996	1
Australiobates sp.	Wellington River	10
Procorticacarus 3	Wellington River 1996	1
Procorticacarus 2	Wellington River 1996	5
Gondwanabates 1	Wellington River 1996	2
Limnesia 1	Wellington River	14
Procorticacarus 9	Wonnangatta River	1
Procorticacarus 7	Wonnangatta River	2
Procorticacarus 4	Wellington River	11
*Limnesia*2	Wellington River 1996	4
Tobelobates confusus	Wellington River 1996	6
Anisitsiellides sp.	Wellington River 1996	1
Procorticacarus 5	Wellington River 1996	1
Albia sp.	Wellington River 1996	2
Ferrissia sp.	Wellington River	15
Alboglossophonia sp.	Wonnangatta River	1
Pisidium sp.	Wellington River	2
Dugesiidae	Wellington River 1997	3

∗ Estimated in field

† Measured in field

Table 3.7: SIGNAL scores for each site.

Site	Wellington River		Wonnangatta River
	1996	1997	1996
1	6.6	6.9	5.5
2	6.5	6.8	5.8
3	6.6	7.0	6.3
4	6.7	6.9	6.3
5	6.5	6.4	5.8
6	6.2	6.7	6.5
7	6.8	6.7	6.1
8	6.6	6.5	6.2
9	6.2	6.7	6.6
10	6.2	6.6	6.4
11	6.0	6.2	6.4
12	6.1	6.4	6.1
13	6.0	6.5	6.5
14	6.1	6.5	6.6
15	5.8	6.7	6.1
16	6.0	6.4	5.7

Note that site numbers do not correspond between sampling events. Site 1 is the uppermost site, site 16 the lowermost. See Figs. 2.2 and 2.3 for maps of site locations.

Table 3.8: Results from the AusRivAS model.

Site	Wellington River				Wonnangatta River	
	1996		1997		1996	
	O/E	Band	O/E	Band	O/E	Band
1	1.25	X	1.04	A	0.95	A
2	1.13	A	1.12	A	1.03	A
3	1.04	A	1.19	X	0.8	B
4	1.09	A	1.19	X	0.94	A
5	0.55	B	0.86	A	0.7	B
6	0.78	B	0.86	A	0.35	C
7	1.08	A	0.92	A	0.96	A
8	1.03	A	0.88	A	0.93	A
9	0.83	A	0.87	A	0.8	B
10	1.08	A	1.03	A	0.95	A
11	0.7	B	0.87	A	0.81	B
12	0.76	B	1.04	A	1.01	A
13	0.83	A	0.8	B	0.66	B
14	0.87	A	0.87	A	0.83	A
15	0.78	B	1.03	A	0.8	B
16	0.74	B	0.87	A	0.61	B

Note that site numbers do not correspond between sampling events. Site 1 is the uppermost site, site 16 the lowermost. See Figs. 2.2 and 2.3 for maps of site locations.

Table 3.9: Total monthly rainfall (mm) in the West Gippsland Region.

Month	Summer 1995-1996	Summer 1996-1997	Long term average
December	79	39	71
January	63	40	56
February	95	10	53

Source: The Meteorological Board of Victoria (1996, 1997)

Table 3.10: A comparison of water quality in the Wellington River in 1996 and 1997.

Water-quality variable	Wellington River 1996 (mean ± se for monthly records in summer 1996)	Wellington River 1997 (mean ± se for monthly records in summer 1997)
Maximum Temperature	22°C	26°C
Mean Temperature*	19.5 ± 1.0°C	23.9 ± 1.2°C
Conductivity† (adjusted to 25°C)	54.67 ± 5.36μS/cm	67.67 ± 17.07μS/cm
Dissolved Oxygen†	9.48 ± 0.41 mg/L	8.80 ± 0.60 mg/L
Discharge‡	271.7 ± 89.8 ML/day	214.7 ± 70.3 ML/day

Maximum temperature, conductivity, dissolved oxygen and discharge were measured at Licola (downstream of study section) every month.

* Mean temperature data was collected for each sampling site during sampling, not single monthly measurements at Licola.

† *Source:* Australian Water Technologies (Water EcoScience Pty Ltd).

‡ *Source:* Theiss Environmental Services.

In the summer of 1997 discharge and dissolved oxygen was lower while water temperatures and conductivity were higher than 1996 values.

Table 3.11: Mantel *R* values for species, genus and family and rarity protocol data-sets of the Wellington and Wonnangatta Rivers.

Taxonomic level	Rarity	Wellington River		Wonnangatta River
		1996	1997	1996
Species	Raw	0.52***	0.54***	0.11
Species	Non-unique	0.60***	0.56***	0.11
Species	Common	0.57***	0.33**	0.07
Genus	Raw	0.60***	0.61***	0.08
Genus	Non-unique	0.61***	0.61***	0.09
Genus	Common	0.55***	0.36**	0.07
Family	Raw	0.60***	0.58***	0.09
Family	Non-unique	0.61***	0.62***	0.09
Family	Common	0.55***	0.36**	0.09

Explanation of data-sets:-
- Raw: no taxa excluded
- Non-unique: taxa excluded if sampled at only one site within sampling event
- Common: taxa excluded if comprised <1% of total individuals at a site

*** P<0.001
** P<0.01

Table 3.12: Mantel *R* values for EPT and chironomid removed data-sets of the Wellington and Wonnangatta Rivers.

Data-set	Taxonomic level	Wellington River		Wonnangatta River
		1996	1997	1996
EPT only	Species	0.59***	0.68***	0.08
EPT only	Genus	0.57***	0.48***	0.07
EPT only	Family	0.58***	0.30***	0.05
Chironomids removed	Species	0.65***	0.56***	0.08
Chironomids removed	Genus	0.64***	0.56***	0.06

Non-unique data-set was used to create the EPT only and chironomid removed data-sets.
Non-unique data-set: taxa excluded if sampled at only one site within sampling event.
*** *P*<0.001

Figure 3.1: Schematic illustrating the production of taxanomic resolution and rarity protocol data-sets.

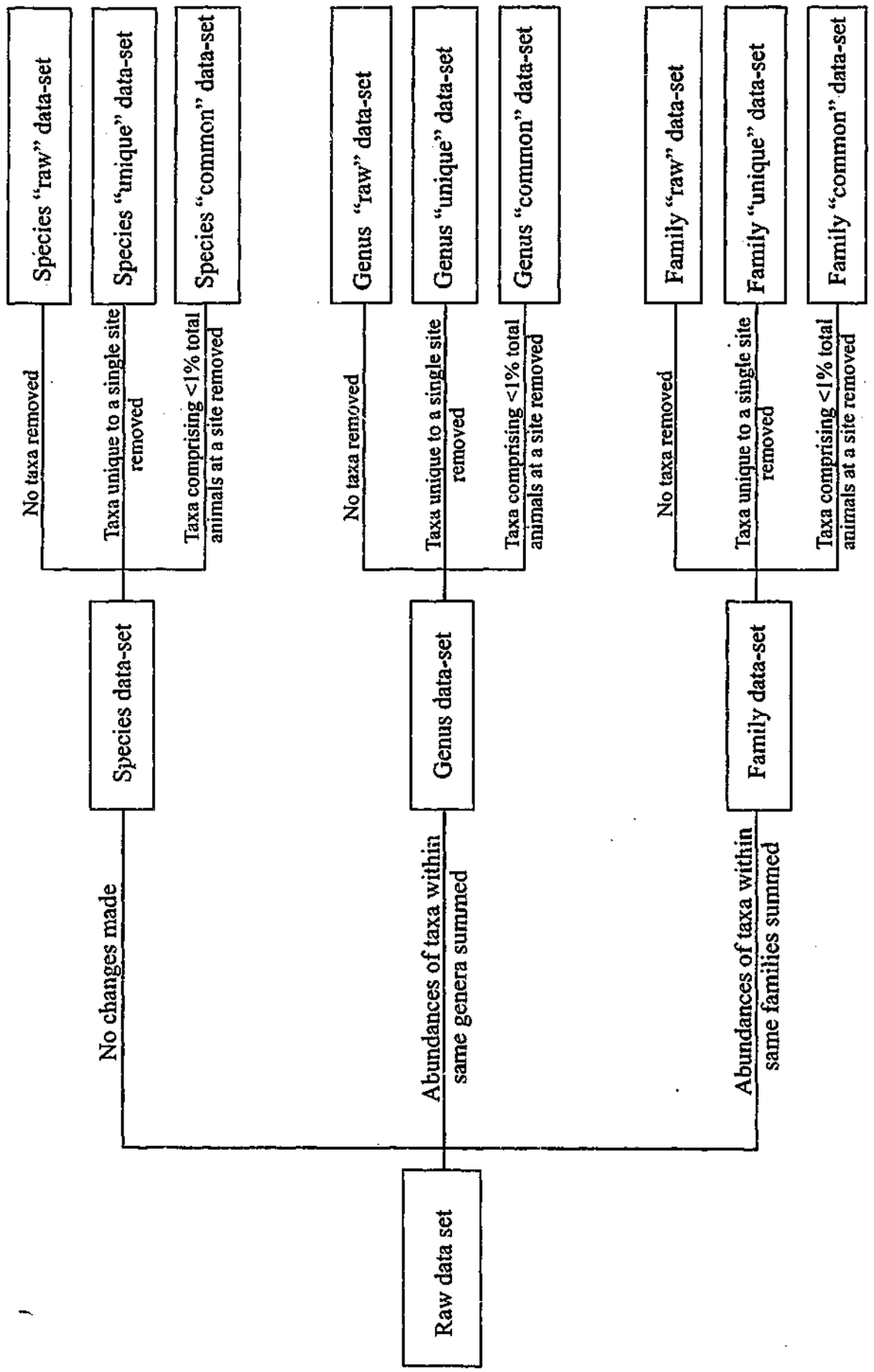


Figure 3.2: Schematic illustrating the production of limited-taxon data-sets.

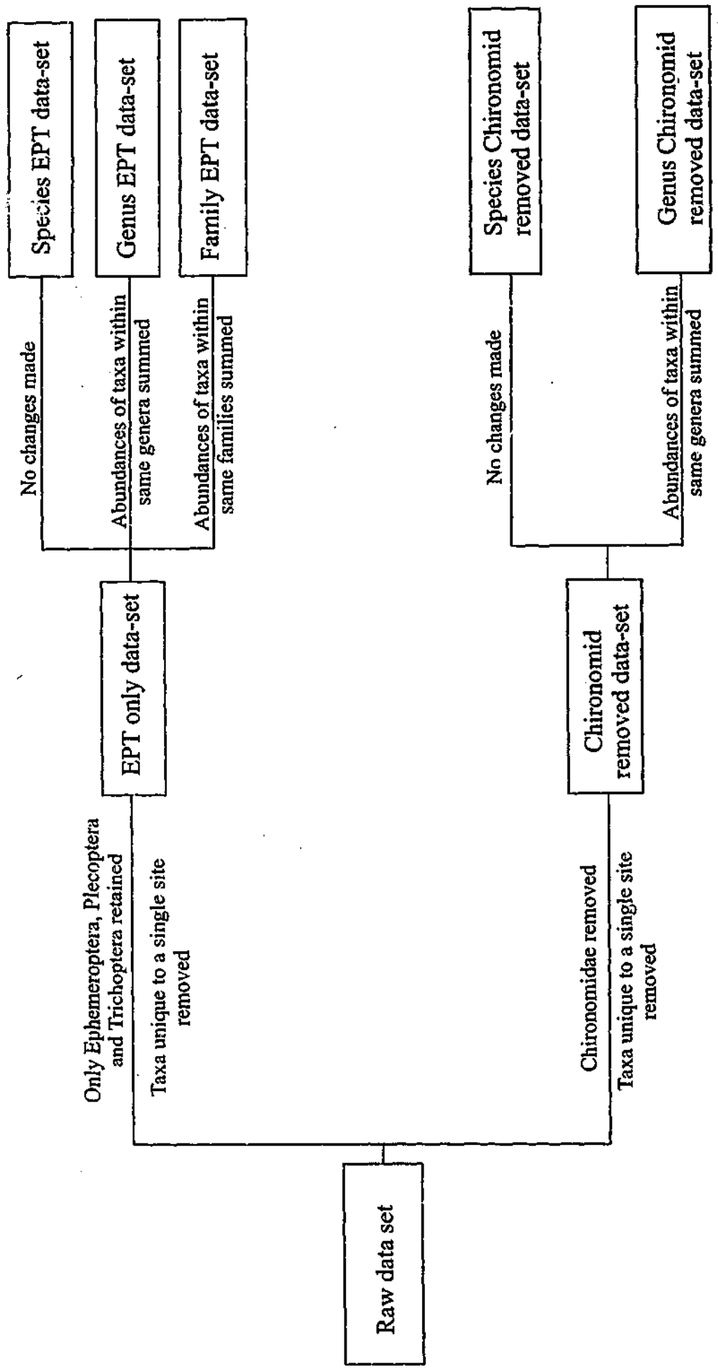
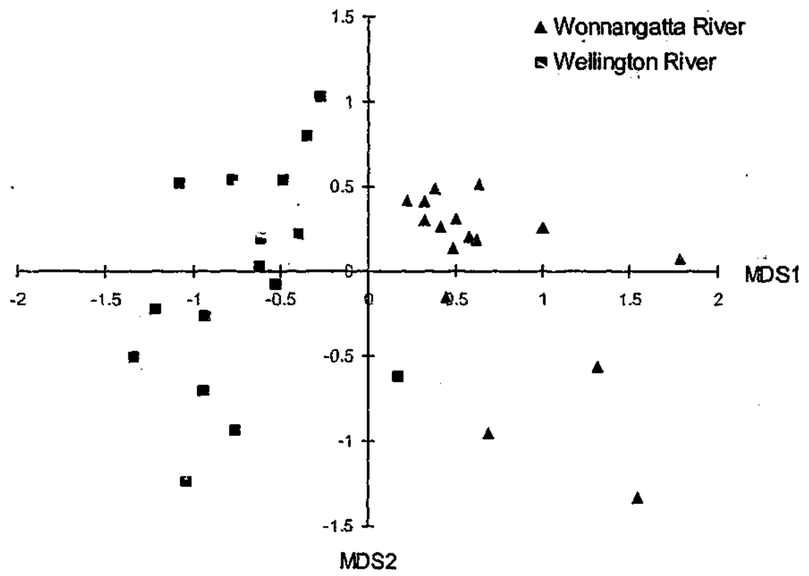


Figure 3.3: Ordination plot of invertebrate fauna at sites from a) Wellington (●) and Wonnangatta (■) Rivers in 1996 (stress = 0.16, n=16) and b) Wellington River sites in 1996 (open circles) and 1997 (closed circles). Numbers correspond to section numbers, each river was divided into eight, 5 km sections. Two randomly chosen sites were sampled in each section. Section 1 is the uppermost section in each river. See Fig. 2.2 for site locations. Stress = 0.19, n = 16.

a)



b)

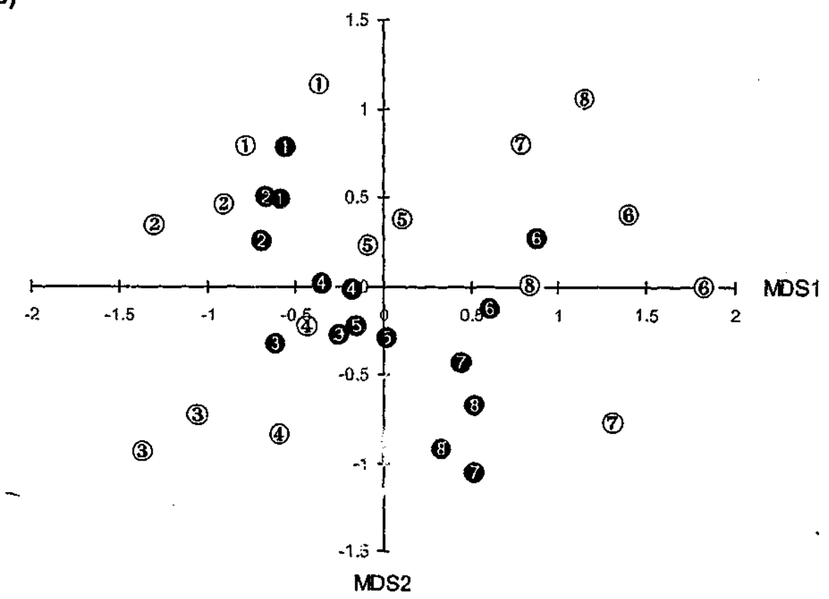
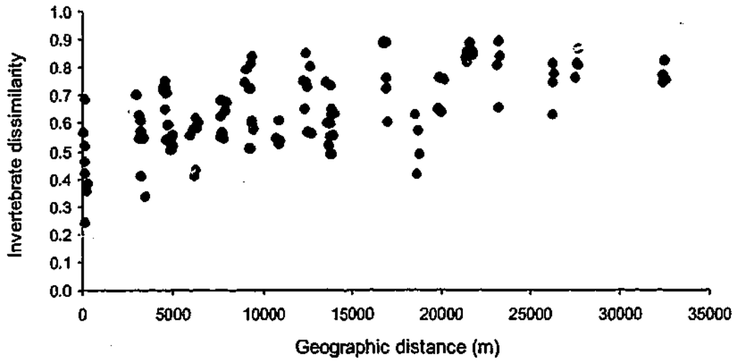
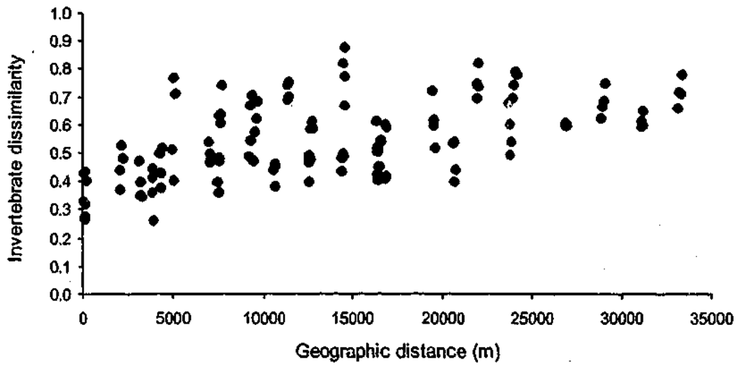


Figure 3.4: Correlation between invertebrate dissimilarity (Bray-Curtis dissimilarity index) and geographic distance (m) between sites from a) Wellington River 1996, b) Wellington River 1997 and c) Wonnangatta River 1996. Species-level, non-unique data-sets were used (see sections 2.3.5.2 and 2.3.5.3).

a)



b)



c)

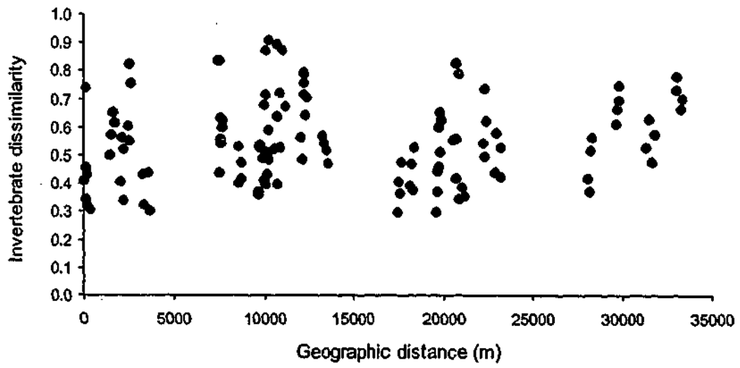
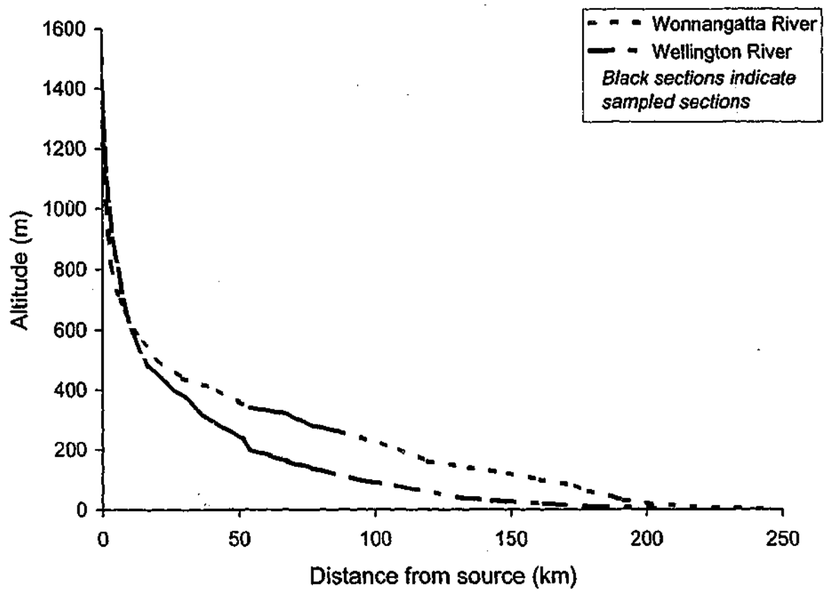


Figure 3.5: Profile of altitude (m above sea level) against distance from source (km) for Wellington and Wonnangatta Rivers.



Chapter 4

Scale and Autocorrelation

4.1 Introduction

Pattern and scale are the central issue in ecology (Levin, 1992). Patterns obvious at some scales may undetectable at others. The results of a study may be constrained by the scale the researcher has chosen. Both the extent (or range) and the grain (resolution due to experimental unit size) can influence study outcomes (Wiens, 1989). For these reasons it is important to investigate at which scales spatial patterns such as autocorrelation are occurring, both because of its inherent biological interest and because autocorrelation has important implications to the results of ecological studies. Therefore, the main aim of this chapter was to investigate the scales at which autocorrelation was significant in the Wellington and Wonnangatta Rivers. Because species- and family-level data may show different spatial patterns at some scales, a second objective was to investigate the spatial autocorrelation of the species- and family-level data-sets at different scales. Although the entire data-set for the Wellington River showed a significant relationship between inter-site distance and invertebrate dissimilarity in both 1996 and 1997, the scatterplots were more variable at larger scales. This may mean that the larger scales would not support a significant relationship if tested in isolation. As the biological processes causing autocorrelation are likely to be bounded in space, at some geographic distance between sites the macroinvertebrate fauna may become unrelated, thereby producing a plateau in the relationship between geographic distance and faunal difference. This would occur if increasing distance past a certain threshold does not produce a corresponding increase in faunal difference. The point beyond which the autocorrelation relationship becomes non-significant is the point at which sites become statistically independent. The approximate minimum distance between independent sites is a useful heuristic tool for both pure and applied freshwater ecology.

If the spatial autocorrelation seen in the Wellington River is due to dispersal by invertebrates, then the scales of the dispersal processes should dictate the scales at which spatial autocorrelation is occurring.

Most studies quantifying the distances travelled by aquatic invertebrates have found that only short distances are covered by a single drift or crawling event. For example, McLay (1970) found the mean distance drifted varied from 0.5-19.3 m. Similarly, *Plectrocnemia* sp. were recorded drifting only 5-25 cm at a time (Hildrew & Townsend, 1980). Under low flow conditions, many taxa may be relatively sedentary. Townsend & Hildrew (1976) found that 85% of the invertebrates in the drift originated from less than 2 m upstream. Similarly, Jackson *et al.* (1999) relocated 87-93% of marked *Gumaga nigricula* (Trichoptera) larvae within 4 m of their release location after 24 d. Söderström (1987) noted that most animals crawling upstream covered less than 10 m d^{-1}, however notable exceptions were three species of mayfly that covered between 130 m d^{-1} and 180 m d^{-1}. Self-marked individuals of *Chryandra centralis*, which had incorporated coloured plastics into their case, moved upstream before pupation: daily mean distances ranged from 1.8 to 22.6 m. Downstream daily mean movements ranged from 6.9 m to 37.0 m. The greatest distance travelled by a single larva was 56.9 m (Erman, 1986). Nymphs of *Pteronarcys californica* travelled maxima of 44 m downstream and 40 m upstream. The average time between captures for these nymphs was 16 days. Most single crawling movements were short (mean 1.8 m), although some individuals were consistently found to travel 6-22 m d^{-1} (Freilich, 1991). Ball *et al.* (1963, cited in Hynes, 1970) sampled invertebrates after introducing radioactively labelled *E. coli* into a Michigan stream. Radioactive invertebrates including *Simulium* spp. and *Isoperla* spp. were found 90 m upstream of the introduction site after a week. After two and five weeks radioactive invertebrates were sampled 180 m and 270 m upstream respectively. Waters (1965) deduced that *Baetis* nymphs were drifting 5060 m within a single night in a small Michigan stream after he constructed a barrier to drift and measured drift downstream of the barrier.

Drift distance is highly variable and differs with species, life stage, light intensity, current velocity and substrate composition (Elliot, 1971). Drifting distances may vary between day and night for the same species (Campbell, 1985). Drifting distances can vary between taxonomic groups due to behaviour (Otto & Sjöström, 1986) and morphology. Otto (1976) found that the first instar of *Potamophylax cingulatus* drifted more than ten times further than fifth instar larvae. Catastrophic drift after a heavy rainstorm transported *Pycnopsyche guttifer* nymphs up to 670 m downstream in one day (Neves, 1979). Spates transported *Gumaga nigricula*, an otherwise sedentary caddisfly, several 100 m, although mortality was high (Jackson *et al.*, 1999).

Despite short distances for single drift events, many species have been observed to disperse night after night. For example, in *Gammarus* sp., most drifters drifted again the following night, whereas individuals crawling upstream repeated that behaviour the following night (Goedmakers & Pinkster, 1981). Hemsworth & Brooker (1979) calculated that in the river Wye (Wales), some taxa could be transported 10 km downstream during a generation through drifting. Neves (1979) recovered marked trichopteran larvae (*Pycnopsyche guttifer*) 0.4-1.5 km downstream from their release location after 2-3 weeks in a second order Massachusetts stream. Mean drift distances were 400-700 m.

Therefore, most estimates of instream dispersal by macroinvertebrates indicate that autocorrelation should not occur at scales larger than a few km and the greatest estimates of the maximum distances travelled instream do not exceed 10 km within a generation.

Distances travelled in flight by adult insects are also usually limited to a few km. Bagge (1995) estimated flight distances of <0.2 km for one ephemeropteran and two trichopteran species, <0.6 km for several trichopteran species, including three hydropsychid species, a polycentropodid and a hydroptilid, and up to 3.7 km for several other trichopterans and *Baetis rhodani*. Similarly, a stable-isotope tracer experiment and mathematical models indicated that about one-third to one-half of the adult *Baetis* population of an arctic Alaskan stream flew 1.6-1.9 km upstream from where they emerged (Hershey *et al.*, 1993). Chironomids are known to fly distances of 500 m from streams (Delettre & Morvan, 2000). Crosskey (1990) reviewed research on the dispersal of simuliids. Mark and recapture studies indicated dispersal ranges of 3, 7, 8, 9, 13, 15.5, 17 and 35 km for a number of different species (Crosskey, 1990). However, presumed dispersal ranges, based on the distance to the nearest known breeding site included values up to 500 km (Crosskey, 1990). Crosskey (1990, p. 398) suggested that the mark and recapture studies focussed on "appetitive flight" distances, whereby the individual controls the length and direction of the flight, whereas the larger estimates of migration are due to flight above the boundary layer, whereby the prevailing wind patterns largely determine the distance and direction flown.

Biotic interactions may also affect the scales of dispersal, colonization and persistence of invertebrate assemblages. Biotic interactions are known to be important at very small scales. Interspecific and intraspecific competition can influence the immigration into, or emigration from, a particular patch, but are unlikely to regulate the distances travelled by migrating animals (section 1.1). Predators have the potential to influence the assemblages on which they prey, but this is likely to occur only at the spatial scale at which the predator forages, for most invertebrates this would be very small (Peckarsky, 1984, 1985; Cooper *et al.*, 1990). Predation by fish may also influence benthic assemblages

at the foraging scales of the predator in closed systems such as lakes (Healey, 1984). However, in open systems, such as rivers, the influence of predation by fish on invertebrate assemblages appears to be very localized (Cooper *et al.*, 1998), as prey animals emigrate in response to predator presence. Peckarsky *et al.* (1997) synthesised results of recent studies of competition and predation in an effort to extrapolate from small-scale studies to larger scales. Biotic interactions that produce strong effects in small-scale experiments sometimes influence assemblage patterns in larger scale field surveys, but more often do not (Peckarsky *et al.*, 1997). *In situ* studies predominantly found that biotic interactions became masked at larger scales because of increased complexity in environmental conditions or trophic webs. For example, the predatory dragonfly *Archilestes grandis* preferred baetid mayflies over other taxa including cased caddisfly and elmid beetles in a microcosm experiment. Reduced baetid densities in high density predator treatments allowed filamentous algae blooms. Field experiments in pools confirmed the dragonfly's prey preference and high-density predator treatments did yield reduced baetid densities, but the filamentous algae did not produce blooms. Other taxa present in pools (but absent in microcosm experiments) may have compensated for the reduced grazing pressure from the baetids (Peckarsky *et al.*, 1997). Parasitism may also affect spatial patterns of invertebrate assemblage composition. Parasitism of odonates by nematodes increases the distance flown by the adult odonate, due to effects on the nervous system of the host (Corbet, 1980). Parasitised animals comprise a disproportionate percentage of drifting invertebrates compared to benthic invertebrates (Wilzbach & Cummins, 1989). This may be due to parasitism increasing the likelihood of entry into the drift, or the increased susceptibility of drifting animals to parasitism (Wilzbach & Cummins, 1989). It is also possible the high proportion of parasitised drifting invertebrates may be related to increases in drifting distances as a result of parasitism. Because so little is known about large-scale effects of small-scale biotic interactions, it is not possible to suggest at which scales biotic interactions may influence the contagious processes of dispersal and persistence.

Genetic analysis has allowed a different approach to the study of dispersal by providing estimates of the effective dispersal (i.e. dispersal and colonization) of invertebrates rather than actual distances travelled, although Bossart & Prowell (1998) cautioned that results may be ambiguous. Jackson & Resh (1992) found genetic differences in sympatric populations of *Helicopsyche borealis* in three Californian steams, which indicated that these populations were not interbreeding extensively. Adjacent sites were between 7 and 11 km apart. Similarly, genetic distances in *Baetis* sp. and *Tasiagma ciliata* in tropical Australian streams appeared to show no relationship with geographic distances between sites (Schmidt *et al.*, 1995; Bunn & Hughes, 1997). The authors proposed that this pattern arose from limited instream movement and random

oviposition by a small number of females. Instream movement of invertebrates in these studies may have been hindered by waterfalls and intermittent flows. Gene frequencies in *Baetis tricaudatus* were similar between adjacent streams in Idaho, USA, indicating dispersal between the two streams (Robinson *et al.*, 1992).

Assemblages identified to species may be spatially autocorrelated at smaller scales than those identified to families because geographic ranges of most species are smaller than those of families. For example, the Hydropsychidae are widespread throughout Australia, occurring in all states and territories (Dean, 1999b). The distributions of some Australian hydropsychid genera are commonly observed to follow longitudinal gradients of rivers. *Diplectrona* spp. tend to occur in headwater streams only. *Asmicridea* spp. are distributed throughout upland stream sections, but below the range of *Diplectrona* spp. *Cheumatopsyche* spp., excepting *C. sp* AV3, are generally found below *Diplectrona* spp. (Dean & Cartwright, 1992). This difference in range size may be due to dispersal ability or to habitat requirements. Either cause of distribution would lead to autocorrelation of smaller taxonomic groups at scales smaller than those of larger taxonomic groups. In effect the total dispersal distances of families are equal to the dispersal abilities of the most mobile species or genera within each family. If habitat variables are autocorrelated and families have a broader range of habitat requirements than their constituent taxa, autocorrelation would be expected to occur at a larger scale for families.

4.2 Analytical methods

Mantel-correlograms (section 2.4.1.1) are commonly used to determine spatial autocorrelation at different scales. However, at least 30 sites are recommended for this analysis (Legendre & Fortin, 1989), whereas I sampled only 16 sites per river. In addition, the Mantel-correlogram does not test linear relationships between geographic distance and ecological distance *within* distance classes. The matrices tested are the ecological distance and a model matrix for each scale derived from the scale categories. All sites within each distance class are given the same value. A matrix is created for each distance class whereby all site-pairs that are members of a particular distance class are allocated a value of one, while all non-members are allocated a value of zero. Therefore, this test compares the ecological distances of site-pairs belonging to a particular scale with the distances of site pairs in other groups, not the linear relationship between geographic distance and ecological distance within a distance class as it does not have that information. Consequently, a different approach was used to investigate scales of autocorrelation.

The approach used to test autocorrelation at different spatial scales closely resembles

the Mantel-test (section 2.4.1). The site-pairs were grouped into distance classes and only the values of geographic distance and invertebrate dissimilarity within a particular distance class were used to calculate the Mantel R, which was tested for significance in the normal way for Mantel tests (Sokal, 1986). That is, subsets of the data were created and linear correlations were tested within these specified intervals. Because the data did not comprise full matrices, which are required for most software packages offering Mantel-tests, a purpose-built program (C++) was written for these tests. Type-I error rates (α) were adjusted for multiple tests (Legendre & Fortin, 1989) according to Holme's protocol (Holme, 1979). This method is less conservative than normal Bonferroni corrections. The value of α from the test associated with the most significant P value is $0.05/K$, where K tests are undertaken. The next most significant test has $\alpha = 0.05/(K-1)$ and so on, until non-significant P values are obtained (Holme, 1979).

Site-pairs for each sampling program were grouped into four scales according to geographic separation. The distance classes included sites with inter-site distances of 0-6 km, 6-12 km, 12-20 km and 20-40 km. These distances were chosen so that they contained approximately equal numbers of site pairs for all scales for all sampling seasons (Table 4.1). Therefore, all tests had approximately equal statistical power (Legendre & Fortin, 1989). The number of scales is arbitrary, so that the analysis was repeated with three intervals to check whether results were consistent over at least two interval sizes (Burgman & Williams, 1995). The three categories comprised site-pairs with inter-site distances of 0-8 km, 8-16 km and 16-40 km. The three distance classes had approximately equal numbers of site pairs for all scales and sampling seasons (Table 4.1). Both family-level and lowest taxonomic-level data-sets were used for these analyses to investigate whether similar patterns of spatial autocorrelation occurred for the different taxonomic levels. Only the non-unique data-set was used because there was no difference in the presence of spatial autocorrelation for different rarity protocols (section 3.3.2).

4.3 Results

4.3.1 Family-level data-set

Spatial autocorrelation of the benthic macroinvertebrate fauna was significant for the smallest scale (0-6 km) of geographic distance for the Wellington River in both 1996 and 1997 (Table 4.1, Fig. 4.1a-b) for the four interval analysis. The middle scales did not show significant relationships between geographic distance and invertebrate dissimilarity in either year. The macroinvertebrate assemblages separated by the largest

scale of geographic distances (20-40 km) were negatively autocorrelated in 1996 but not in 1997. In contrast, the invertebrate assemblages of the Wonnangatta River were not autocorrelated at any scale except the 12-20 km distance class (Table 4.1, Fig. 4.1c).

The three-interval analysis yielded different results. There was significant spatial autocorrelation at the smallest scale (0-8 km) of geographic distance for the Wellington River in both years. Wellington River invertebrate assemblages at inter-site distances within the middle scale (8-16 km) were not autocorrelated in either year (Table 4.1, Fig. 4.2a-b). In 1996, the invertebrate assemblages separated by the largest scale of geographic distances (16-40 km) were not autocorrelated. However, in 1997, there was pattern of autocorrelation at the largest scale. There was positive autocorrelation in macroinvertebrate assemblages at all three spatial scales in the Wonnangatta River samples (Table 4.1, Fig. 4.2c).

The results from the autocorrelation analyses with three distance classes were markedly different from those with four distance classes. The smallest scales (0-6 km and 0-8 km) were consistent for the Wellington River in both years-there was significant positive autocorrelation (Table 4.2). However, all other analyses provided inconsistent results between the two sets of intervals (Table 4.2). Thus, the significance of results appears to depend on the arbitrary scales of division.

4.3.2 Species-level data-set

The results of all Mantel-tests performed at species-level were the same as the results from the tests at family-level (Table 4.3). That is, positive spatial autocorrelation was detected in Wellington River assemblages at small scales for both years and both the three and four interval analyses. This was the only pattern consistent over the two analyses. As with the family-level tests, the middle- and large-scale intervals for the Wellington River were a mixture of non-significant, negative and positive autocorrelation. However, none of these tests were conclusive because the three and four interval analyses provided contradictory results.

The results for the Wonnangatta River were also the same for species- and family-level analyses. This was the case for all distance classes in both the three- and four-interval analyses (Table 4.3). The three-interval analysis suggested positive autocorrelation at all scales, yet the four-interval analysis provided non-significant results for all scales except the 12-20 km scale, which suggested negative autocorrelation.

4.4 Discussion

The inconsistencies between the three- and four-interval analyses at both family and species levels indicate that the locations of intervals are crucial to the results obtained. Burgman & Williams (1995) found the pattern of spatial autocorrelation in plant communities to be qualitatively consistent over different numbers of intervals. Other studies investigating spatial scales of autocorrelation have not examined more than one arbitrary set of intervals (Pinckney & Sandulli, 1990; Wildi, 1990; Koenig, 1999a). The dependence of results upon the scale of investigation is not unexpected, nor does it mean that the results are statistical artefacts. Nee *et al.* (1991) found a negative correlation between abundance and body size for all birds that breed in Britain. Within this overall negative relationship there were many positive or null relationships if smaller taxonomic groups (e.g. tribes or families) and, therefore, a narrower range of body sizes, were isolated from the entire data-set (Nee *et al.*, 1991). Consequently, the authors interpreted the different results from different sub-sets of the data according to phylogenetic relationships between taxa. Indeed, the frequency of different scales of study resulting in different conclusions is high, and this is why scale is considered to be a critical consideration in ecological studies (Wiens, 1989; Underwood & Chapman, 1996; Cooper *et al.*, 1998; Mac Nally & Quinn, 1998). In this study the argument for the biological relevance of one scale over another cannot be made because the numbers of intervals, and therefore the particular data points included in each interval, were arbitrary. Therefore, all conflicting results are likely to be artefacts of the particular data points included in each analysis, and so the evidence for the presence or absence of spatial autocorrelation at any particular scale is not conclusive. Therefore, I have disregarded all results that were not consistent between the two analyses. The only results to agree between the two analyses are those for the smallest scales of the Wellington River in both years.

Significant spatial autocorrelation was not observed consistently at any scale in the Wonnangatta River. I was therefore unable to conclude that spatial autocorrelation definitely was or was not occurring at any spatial scale. This is not surprising, given the generally asystematic appearance of the scatterplot of the complete set of data (see Fig. 3.4c). This lack of a clear spatial pattern indicates that dispersal processes are not an important mechanism for the distribution of invertebrate assemblages in this river because they are expected to act as contagious processes operating over small scales (section 4.1). The apparently low relative importance of dispersal processes in determining the faunal distributions within the Wonnangatta River may be due to other deterministic or stochastic forces overriding the contagious process of dispersal. Another suite of deterministic factors that influence the distribution of invertebrates are physical environmental factors. The Wonnangatta River may provide more heterogeneous habitat than the Wellington

River and this may explain the difference between the results from the two rivers; this possibility is examined in the following chapter.

Alternatively, the Wonnangatta River may be a case in which stochastic forces play an important role in determining invertebrate assemblage composition. It may be possible to discriminate between the two alternative explanations by investigating the spatial pattern of environmental variables. If environmental variables show little spatial pattern, but are closely correlated with the invertebrate fauna, there is some support for the argument that the heterogeneous environment of the Wonnangatta River is the reason for the lack of spatial structure in the invertebrate fauna. However, if the environmental variables do show a spatial structure, but are not closely correlated to the macroinvertebrate fauna, then there is no evidence to suggest that it is the spatial pattern of the environment of the Wonnangatta River determining the faunal distributions.

The autocorrelation seen at the smallest scales of the data-set for the Wellington River invertebrates in both 1996 and 1997 is consistent with the scales of dispersal documented for benthic invertebrates. Therefore, the contagious processes of drift, flight by adults and benthic movements may account for the pattern of spatial autocorrelation seen in these invertebrate assemblages. Although the measured environmental variables are expected to show spatial autocorrelation at larger scales than a few km, it is also possible that the spatial autocorrelation of habitat variables and their influence in determining assemblage composition may account for the observed autocorrelation pattern. This will be explored in the next chapter.

The implication of small-scale spatial autocorrelation in the Wellington River assemblages sampled is that sites further than ca 8 km apart are likely to be independent of each other with respect to macroinvertebrate assemblages. Therefore, such sites could be used in studies where the results are tested using classical inferential statistics. Conversely, if researchers wish to use the fauna present at one or more sites to 'predict' the fauna that should occur at a test site (in the absence of anthropogenic impacts), the sites should be situated closer than 8 km. However, these results may have little applicability to other rivers because this pattern of spatial autocorrelation is unlikely to be consistent between rivers, given the inconsistent results between the two rivers sampled in this study. This lack of generality implies that neither independence nor dependence should be assumed.

The consistency between family- and species-level analyses of scale may be the result of species and families showing similar dispersal distances and habitat requirements, contrary to expectations resulting from the broader distributions of families compared to species. No data are available for Australian taxa, but estimates of dispersal ability

for taxa for which there are reliable data from mark and recapture studies suggest that this is not the explanation. Crosskey (1990) reports that mark and recapture estimates of adult dispersal abilities for species within the Simuliidae vary widely, from 3 to 35 km. It is also unlikely that species have habitat preferences or requirements as broad as those of families. For example, the elmids *Kingolus yarrensis*, *K. tinctus* and *Simsonia wilsoni* occur in the stony substrate of riffles, whereas others in the same family including *Notriolus quadriplagiatus* and *N. victoriae* are only found on wood in streams (Glaister, 1999).

A more likely explanation for the similarity of scales of spatial autocorrelation between species and families may be that individual species do disperse and colonise over smaller scales than the family to which they belong, but this pattern is not obvious when entire assemblages are studied. The large variation in dispersal abilities between families may mask the differences between a particular family and its constituent species. For example, beetles of the subfamily Elminae comprised an important component of the fauna found in the Wellington River. These animals do not fly as adults (Glaister, 1999). In addition, this taxon is rarely encountered in drift samples (Schreiber, 1988). Therefore, they are unlikely to disperse far within a generation. In contrast, baetids, another important component of the fauna sampled in the Wellington River, show a high propensity to drift (Hynes, 1970; Brittain & Eikeland, 1988) and some species have been recorded drifting 50-60 m overnight (Waters, 1965). Northern hemisphere baetid adults have been recorded flying 1.9 km (Hershey *et al.*, 1993) and 3.7 km (Bagge, 1995) from emergence sites before ovipositing. Therefore, analysis on a family-by-family basis may highlight differences in dispersal ability as large as, or larger than, those between the least mobile and most mobile species within a family.

A final explanation for the similarity between species-level and family-level analyses may be that the dissimilarity index used in the analysis (Bray-Curtis index) is based upon abundances of taxa and extremely abundant taxa may dominate the dissimilarity values between different site-pairs.

The three given explanations: similar dispersal for families and their constituent species; assemblage patterns masking individual patterns; and abundant taxa dominating the analysis, for the consistency of spatial scales of autocorrelation between species and family data may be distinguished by further data and analysis. Data on the dispersal abilities of the taxa sampled in this study would allow the first explanation to be explored. Analysis of autocorrelation on a taxon-by-taxon basis, and the comparison of mobile taxa with more sedentary taxa may provide support for the second explanation. Re-analysis of the data using a presence/absence dissimilarity index would increase the influence of less abundant taxa and determine whether the abundant taxa were dominating the analysis.

The implication of the same trends at species and family level, both in the occurrence of spatial autocorrelation, and the scales at which it occurs in the Wellington River is that spatial autocorrelation should be considered paramount in the design of sampling programs or experimental protocols regardless of the level of taxonomic resolution planned. If only a few species are to be considered, the possibility of different scales of spatial autocorrelation among different taxa should be investigated during the pilot study, particularly if the taxa have different life histories. However, it may be sufficient to use family-level identification to detect spatial autocorrelation patterns in macroinvertebrate assemblages.

4.5 Summary

The spatial autocorrelation pattern of the Wellington River in both years is dominated by strong small-scale autocorrelation. This pattern is consistent with known dispersal abilities of taxa but may also be similar to the spatial pattern of environmental variables. The lack of autocorrelation in the Wonnangatta River may be due to environmental conditions or stochastic factors determining the spatial pattern of invertebrate assemblages in this river. These findings determine that sites become independent at approximately 8 km apart in the Wellington River but are independent at very small distances apart in the Wonnangatta River. The three- and four-interval analyses revealed different results. These data were sensitive to the arbitrary locations of the intervals. Therefore, the significance of middle or large-scale autocorrelation in the Wellington River was not conclusive. This result implies that autocorrelation analysis should be performed at more than one scale or set of intervals.

Table 4.1: Mantel R values for family level invertebrate data-sets of three and four geographic distance classes for the Wellington and Wonnangatta Rivers.

Geographic distance range	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
0-6 km	0.50* (30)	0.48* (28)	0.14 (24)
6-12 km	0.19 (30)	0.36 (28)	0.13 (36)
12-20 km	0.04 (35)	0.10 (32)	-0.53* (28)
20- 40 km	-0.46* (25)	0.24 (32)	0.34 (32)
0-8 km	0.42* (44)	0.57* (40)	0.39* (32)
8-16 km	-0.18 (36)	0.10 (32)	0.32* (40)
16-40 km	0.06 (40)	0.54* (48)	0.48* (48)

Family level, non-unique data were used to create the data-sets of different scales of geographic separation between sites.
Non-unique data-set: taxa excluded if sampled at only one site within sampling event.
* $P<0.05$

Table 4.2: Comparison of results from three and four interval Mantel-tests (family level).

Geographic distance range	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
0-6 km	+*	+*	n.s.
0-8 km	+*	+*	+*
6-12 km	n.s.	n.s.	n.s.
8-16 km	n.s.	n.s.	+*
12-20 km	n.s.	n.s.	-*
16-40 km	n.s.	+*	+*
20- 40 km	-*	n.s.	n.s.

* $P< \alpha$
Alpha was corrected for multiple tests using the sequential Bonferroni correction method advocated by Holme (1979)

Table 4.3: Comparison of Mantel-tests for family and species level invertebrate data-sets.

Geographic distance range	Wellington River 1996 Species	Wellington River 1996 Family	Wellington River 1997 Species	Wellington River 1997 Family	Wonnangatta River 1996 Species	Wonnangatta River 1996 Family
0-6 km	0.48* (30)	0.50* (30)	0.50* (28)	0.48* (28)	0.10 (24)	0.14 (24)
6-12 km	0.20 (30)	0.19 (30)	0.33 (28)	0.36 (28)	0.07 (36)	0.13 (36)
12-20 km	0.03 (35)	0.04 (35)	0.08 (32)	0.10 (32)	-0.53* (28)	-0.53* (28)
20- 40 km	-0.39* (25)	-0.46* (25)	0.16 (32)	0.24 (32)	0.32 (32)	0.34 (32)
0-8 km	0.40* (44)	0.42* (44)	0.54* (40)	0.57* (40)	0.38* (32)	0.39* (32)
8-16 km	-0.18 (36)	-0.18 (36)	0.06 (32)	0.10 (32)	0.36* (40)	0.32* (40)
16-40 km	0.13 (40)	0.06 (40)	0.50* (48)	0.54* (48)	0.46* (48)	0.48* (48)

Non-unique data were used to create the data-sets of different scales of geographic separation between sites. Non-unique data-set: taxa excluded if sampled at only one site within sampling event.

* $P<\alpha$

Alpha was corrected for multiple tests using the sequential Bonferroni correction method advocated by Holme (1979)

Figure 4.1: Familty-level invertebrate dissimilarity over four scales of geographic distances between sites from a) Wellington River 1996, b) Wellington River 1997 and c) Wonnangatta River 1996.

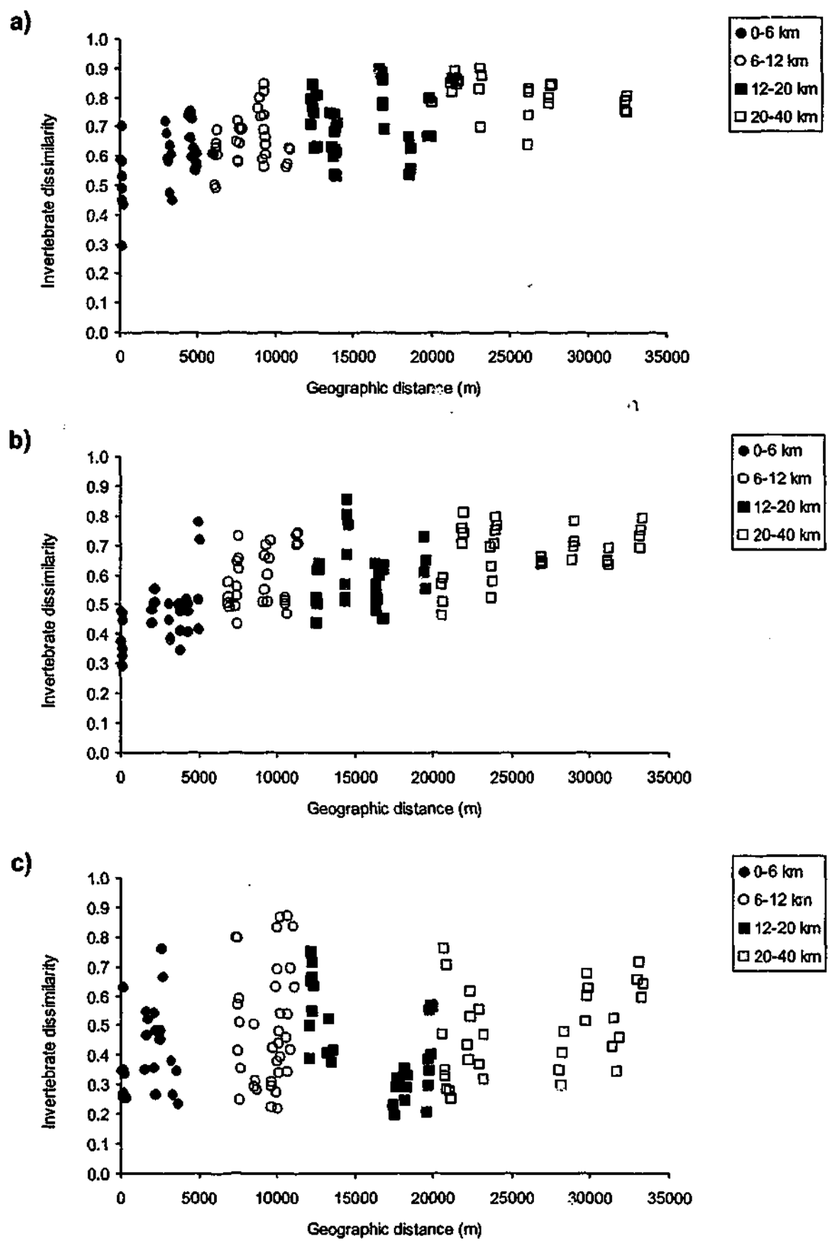
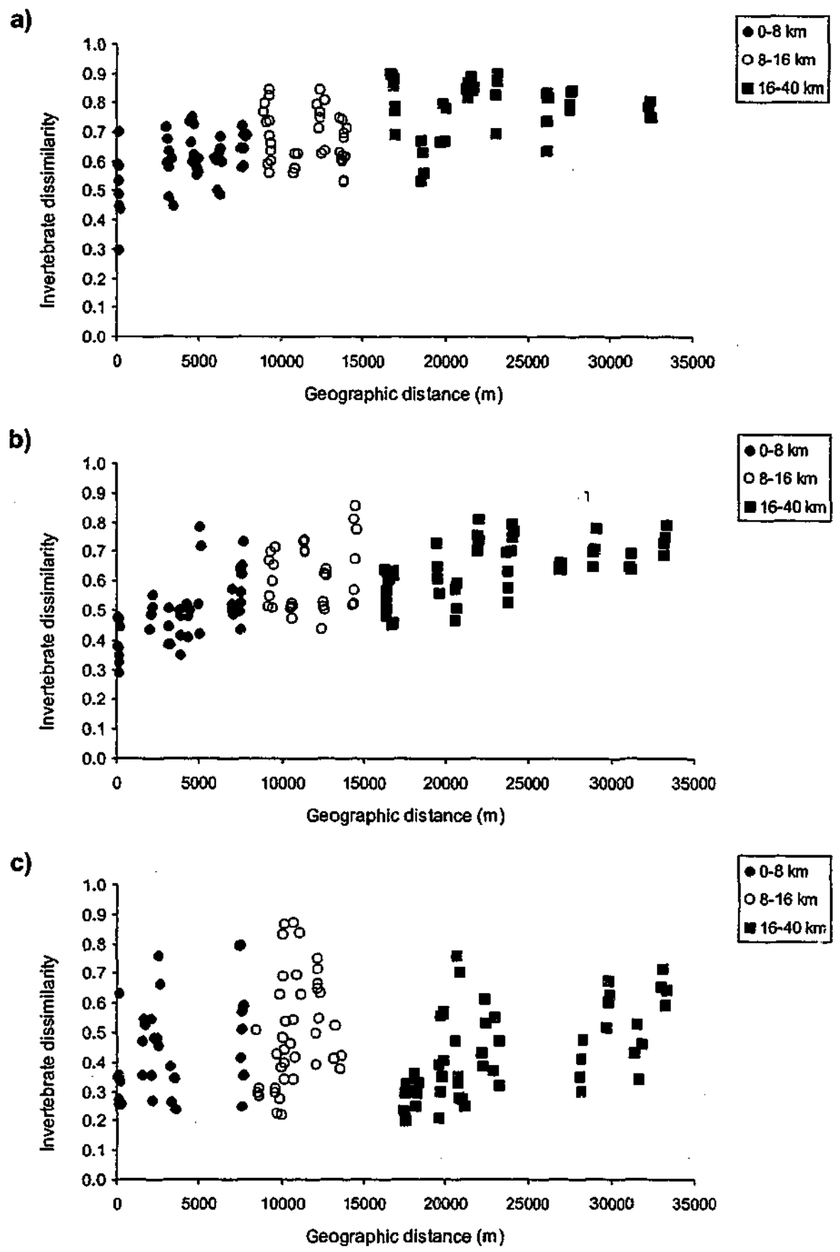


Figure 4.2: Family-level invertebrate dissimilarity over three scales of geographic distances between sites from a) Wellington River 1996, b) Wellington River 1997 and c) Wonnangatta River 1996.



Chapter 5

The potential influence of environmental variables on spatial autocorrelation of benthic invertebrates

5.1 Introduction

Much stream ecology and impact-detection literature has sought to explain the distribution and abundance of macroinvertebrates in relation to their abiotic environment. Many environmental variables may show non-random spatial patterns. The autocorrelation patterns of macroinvertebrate assemblages in the Wellington and Wonnangatta Rivers may be due to invertebrate responses to autocorrelated environmental variables, rather than to dispersal mechanisms *per se*. The aim of this chapter is to relate the spatial pattern of abiotic environmental variables to the spatial pattern of the invertebrate assemblages. This was done by determining whether environmental variables were autocorrelated and at which scales. The relationship between the environmental variables and the invertebrate assemblages was also explored. And last, the presence of autocorrelation in the invertebrate assemblages in the absence of an effect of environmental variables was tested.

The habitat of an organism can be defined as the place where it lives (Begon *et al.*, 1990). Habitat preferences by organisms can be made on the basis of environmental variables which may be abiotic (e.g. water temperature) or biotic (e.g. predator density), or they may comprise components of both (e.g. land use). The last example is a composite variable that is easy to measure (categorically at least), but its influence on other environmental variables and individual organisms may be quite complex.

There is ample evidence that benthic macroinvertebrates respond to a wide variety of environmental variables (Hynes, 1970). The type, particle size, heterogeneity and surface texture of the substratum can be important in influencing the density and composition of invertebrate assemblages (Hynes, 1970; Erman & Erman, 1984; Doeg *et al.*, 1989b; Arunachalam *et al.*, 1991; Downes *et al.*, 1995, 1998a). Depth, current velocity and hydraulic factors may be important in determining patterns of species abundance and distribution (Wetmore & Mackay, 1990; Georgian & Thorp, 1992; Hart, 1992; Degani *et al.*, 1993; Danehy *et al.*, 1999; Doisy & Rabeni, 2001). Water-quality variables, such as dissolved oxygen, temperature, turbidity, electrical conductivity, dissolved organic carbon, nitrogen, phosphorus and ammonia influence invertebrate communities (Tate & Heiny, 1995; Collier *et al.*, 1998). Food abundance, including epilithon, prey species, organic matter and woody debris affect the distribution of invertebrates (Dudley *et al.*, 1986; Mackay, 1992; Wallace *et al.*, 1996; France, 1997; Delong & Brusven, 1998). The state of the riparian zone and land use within the catchment (Campbell & Doeg, 1989; Davies & Nelson, 1994; Collier, 1995; Brown *et al.*, 1997) also have instream impacts. Many of these variables are interrelated, and frequently affect invertebrates in complex interactions (e.g. Hart, 1992).

Animals may become distributed according to habitat preferences either by preferential emigration or immigration, or differential mortality. Correlations between a number of biotic and abiotic environmental variables, including current, dissolved oxygen, pH, water temperature, periphyton densities, conspecific densities and predator presence and invertebrate drift densities have been documented (Sheldon, 1984; Wiley & Kohler, 1984; Brittain & Eikeland, 1988). Individuals of *Baetis tricaudata* actively enter the drift in response to habitat quality (Kohler, 1985). This suggests that optimal patches will not be deserted, but less suitable ones may be (Hildrew & Townsend, 1980). The direction and extent of crawling movements in *Baetis* have been related to periphyton abundance (Kohler, 1984, 1985). Unfavourable abiotic conditions such as increased current velocity appeared to trigger upstream movements in mayflies (Söderström, 1987).

Preferential immigration occurs when animals select patches based on environmental variables. For example, simuliid and some hydropsychid larvae prefer smooth rocks upon which to settle (Mackay, 1992). Some invertebrates crawl upstream in search of favourable sites for emergence, mating or pupation (Söderström, 1987). Robson & Barmuta (1998) found that substrate 'architecture' (i.e. pitted, creviced, moss-covered or plain artificial substrate) influenced colonisation by chironomids and *Conoesucus norelus*, a grazing caddisfly, in a small Tasmanian stream. Adults may select suitable habitat for offspring when they select clean surfaces for oviposition (Imhof & Smith, 1979; Deutsch, 1984). Female baetids show highly selective behaviour when locating rocks on which to

oviposit (Peckarsky *et al.*, 2000). Ten rocks, from over 600 suitable rocks, were selected for oviposition and 50% of the egg masses were deposited on only two rocks (Peckarsky *et al.*, 2000). This oviposition behaviour may have important influences on the resulting invertebrate assemblages. McCreadie (1991) argued that the occurrence of simuliid larvae at a particular site is largely the result of female oviposition behaviour. Similarly, Bunn & Hughes (1997) suggested that the populations of *Tasiagma ciliata* and *Baetis* sp. present in individual riffles or pools of a Queensland stream were the offspring of just a few females.

It is also possible that the mechanism causing the spatial pattern observed in the invertebrate fauna is spatial autocorrelation of abiotic variables. Certain environmental variables would be likely to be more similar for close site-pairs than distant ones. Assemblages of periphyton may be autocorrelated for the same reasons that invertebrate assemblages are: attenuated patterns for dispersal mechanisms, responses to spatially autocorrelated patterns for environmental variables or biotic interactions. Geomorphological variables typically change predictably downstream (Hynes, 1970; Petts & Foster, 1985):

- altitude decreases;
- slope decreases;
- the average size of substrate particles decreases;
- discharge increases;
- channel width and depth increase;
- average water temperature is elevated and temperature variation increases in the middle orders, then decreases again in large rivers due to the buffering capacity of the large discharge;
- the riparian zone shades less of the river and contributes less organic matter;
- and average current velocity may increase or remain constant.

The observation of these longitudinal patterns in abiotic variables, and longitudinal patterns of invertebrate composition changes led to the development of the River Continuum Concept (Vannote *et al.*, 1980). The scales at which the geomorphological patterns have been observed are typically much larger than those at which invertebrates disperse. For example, average particle-size decreases over tens of kms. Invertebrates are more likely to disperse over much shorter distances, from metres to kms (see section 4.1).

The biotic components of invertebrate habitat may show significant small-scale autocorrelation. Interactions between invertebrates, such as predation and competition, are likely to occur at similar scales to the dispersal abilities of the organisms involved. Interactions between macroinvertebrates and microinvertebrates or micro-organisms may occur at similar or smaller scales. The scales of dispersal of food organisms for scrapers, collector-gatherers and filter feeders, such as bacteria and algal taxa are not well documented. The dispersal propagules are most likely to be dispersed passively in the drift, and therefore to experience negative exponential distributions such as those noted for invertebrates (Sheldon, 1984), but perhaps on a smaller scale. Labelled bacteria were released in a second-order stream in North Carolina to investigate the rate of consumption by filter-feeding invertebrates and adhesion to the substrate. The bacteria were taken up within 78 and 83 m of the release point (Hall *et al.*, 1996). Bacterial assemblages on stones have patch sizes of less than 1 km (McArthur & Tuckfield, 1997). Algal communities are likely to differ on similar scales.

5.2 Analytical methods

Mantel-tests were used to investigate whether environmental variables were autocorrelated, and to test whether the relationship between environmental dissimilarity and invertebrate dissimilarity was significant. The matrix of environmental dissimilarity was estimated by calculating Canberra metric dissimilarity indices between each pair of sites for all environmental variables measured (Table 5.1), except distance from source, catchment area and altitude. These latter variables would explain no more variation than geographic distance due to intrinsic spatial autocorrelation. In addition, these variables are so strongly autocorrelated that they would have overridden any non-significant pattern in the other variables. The Canberra metric was used because variables are standardised to ameliorate the effects of differences in scales between variables (Clarke & Warwick, 1988). The autocorrelation of individual environmental variables was tested using univariate Mantel tests. This was done to investigate which environmental variables may be contributing to a pattern of spatial autocorrelation for the suite of environmental variables.

The scales of environmental autocorrelation were tested using the same methods as those used to determine scales of invertebrate autocorrelation in section 4.2. Both the four- and three-interval analyses were conducted because the number of intervals had bearing on the results for invertebrate autocorrelation. The same distance-classes were used as in the invertebrate-autocorrelation analysis. The four-scale analysis had intervals of 0-6 km, 6-12 km, 12-20 km and 20-40 km. The three categories comprised site pairs with inter-site distances of 0-8 km, 8-16 km and 16-40 km. Only the family-level, non-

unique data-set was used as there was no difference in the scales of spatial autocorrelation for the different levels of taxonomic resolution (see section 4.3).

The relationship between environmental dissimilarity and invertebrate dissimilarity was also tested by using the method outlined above. Site-pairs were divided into the same categories as above based on the geographic distance between the sites. These sub-sets of the complete data-set were then tested using Mantel-tests.

Three-matrix extensions of the Mantel-test were used to analyse autocorrelation of invertebrate assemblages with habitat variation held constant (Smouse *et al.*, 1986) (see section 2.4.1.2). This method tests the relationship between ecological distance and geographic distance in the absence of an effect of the environmental variables.

5.3 Results

5.3.1 Autocorrelation of environmental variables

The environmental variables measured in the Wellington and Wonnangatta Rivers were autocorrelated for the entire data-set. Environmental dissimilarity and geographic distance were related in the Wellington River in both years, and in the Wonnangatta River in 1996 (Table 5.2, Fig. 5.1).

The scale analyses of the environmental dissimilarity indicated that in 1996, environmental variables were autocorrelated in the Wellington and Wonnangatta Rivers at the smallest scales (0-6/8 km) only (Table 5.3). At all other scales, the environmental variables showed no autocorrelation. Results from the three- and four-interval analyses of the Wellington and Wonnangatta River data were consistent in 1996 (Table 5.3).

As with the scale analyses of invertebrate dissimilarity in Chapter 4, the scale analyses of environmental dissimilarity showed mixed results for Wellington River 1997 data. The results from the environmental autocorrelation analyses with three and four distance classes were not consistent for the smallest scale (Table 5.3). The 0-6km result indicated that small-scale autocorrelation was present, but the 0-8km autocorrelation test was non-significant. Consistent non-significant results were obtained for all larger scales (Table 5.3).

The Mantel tests of individual environmental variables indicated that landuse beyond the riparian zone, retention and the width of the riparian zone were spatially autocorrelated for all three sampling seasons (Table 5.4). Stream width and stream slope were

autocorrelated for the Wellington River in 1996 and 1997, but not for the Wonnangatta River (Table 5.4). Substrate composition and sediment were autocorrelated for the Wonnangatta River in 1996, but not for the Wellington River in either year. All remaining environmental variables did not appear to have a spatially autocorrelated pattern (Table 5.4).

5.3.2 Correlations between environmental and invertebrate dissimilarity

Environmental dissimilarity and invertebrate dissimilarity were correlated for the Wellington River in both 1996 and 1997 (Table 5.2, Fig. 5.2a-b). Although the faunal dissimilarity between sites shows a strong relationship with environmental dissimilarity, there is a stronger spatial correlation with geographic distance than with environmental dissimilarity (Table 5.2). There was no relationship between environmental dissimilarity and invertebrate dissimilarity in the Wonnangatta River samples (Table 5.2, Fig. 5.2c).

Unlike the autocorrelation analyses of invertebrate and environmental dissimilarity, the correlations between the environmental variables and invertebrates were consistent over the three- and four-interval analyses (Table 5.5). Only the three-interval analyses have been presented as figures because these figures are simpler to interpret.

Only the sites separated by the smallest geographic distances in the Wellington River in 1996 showed a positive correlation between habitat dissimilarity and invertebrate assemblage dissimilarity (Table 5.5, Fig. 5.3), all other results were non-significant.

5.3.3 Three-matrix Mantel tests

The correlation between invertebrate dissimilarity and geographic distance was significant when the effect of environment was eliminated for the Wellington River in 1996 and 1997 but not for the Wonnangatta River (Table 5.6). The Wonnangatta samples were also tested for a relationship between environmental dissimilarity and invertebrate dissimilarity in the absence of an effect of geographic distance. This relationship was also non-significant (Table 5.6).

5.3.4 Comparison between the Wellington and Wonnangatta Rivers

Environmental variables were autocorrelated for both rivers, however univariate Mantel tests indicated that the individual variables contributing to the overall spatial pattern may be slightly different. Sediment and substrate composition were autocorrelated in the Wonnangatta River but not the Wellington River whereas the reverse was true for stream width and stream slope.

The Wellington River invertebrate assemblages were correlated with both geographic distance and environmental variables, whereas the Wonnangatta River invertebrates were correlated with neither. The environmental variables were autocorrelated in both the Wellington River and the Wonnangatta River. The three-matrix Mantel tests, which separated the effects of geographic distance and environmental variables confirmed that the Wellington River invertebrate assemblages were related to both, whereas the Wonnangatta River invertebrate assemblages were related to neither.

5.4 Discussion

The patterns of autocorrelation of habitat variables for the Wellington River sites were consistent with the idea that several of the environmental variables, including land use, retention, width of the riparian zone, stream width, stream slope, sediment and substrate composition are subject to contagious processes. The differences in autocorrelation of individual environmental varaibles between the rivers were likely to be related to the difference in river sections studied. The Wellington River was sampled along a length that was closer to the river source than was the Wonnangattta River and consequently the section of the longitudinal profile studied was steeper for the Wellington River than the Wonnangatta River (Fig. 3.5).

The absence of substantial large-scale autocorrelation of environmental variables in all three sampling seasons was inconsistent with the longitudinal geomorphological patterns commonly noted (Hynes, 1970; Petts & Foster, 1985). Davies & Nelson (1994) also found no relationship between separation and a suite of habitat variables including water quality, and geomorphological, substratal and riparian variables in 45 site-pairs from 34 Tasmanian streams.

Significant large-scale autocorrelation of the environmental variables may not have been present because many of the variables that have longitudinal patterns, such as water temperature and current speed, vary widely from site to site. Many more than 16 sites

have been used to detect longitudinal patterns in geomorphological studies (e.g. Hack, 1972; Carter *et al.*, 1996). Perhaps the geomorphological patterns were masked by other habitat variables, such as shading and riparian vegetation, which were not autocorrelated at the scales studied.

Significant small-scale (0-6/8km) environmental autocorrelation, detected in the Wellington and Wonnangatta Rivers in 1996, may be due to instream aspects of habitat, such as the substrate variables, or land-use and riparian variables. Environmental variables may have been autocorrelated at small scales in 1997 for the Wellington River also, but results from the three- and four-scale analyses did not agree and are, therefore, inconclusive. This may be because the habitat variables used (from the AUSRIVAS protocol) were designed for detecting impaired habitat quality over large scales (Coysh *et al.*, 2000) rather than characterizing minor differences in closely situated high-quality habitats, and may therefore have been unsuitable for this study. Perhaps a larger suite of environmental variables, incorporating quantitative rather than categorical variables and including hydraulic variables (see Rempel *et al.*, 2000) and more physico-chemical variables (see Tate & Heiny, 1995) would allow a closer examination of the causes of small-scale autocorrelation. Such a sampling design would be more time consuming than the rapid habitat assessment approach taken here and would only be feasible for a study conducted at the smaller scales included in this research.

The correlations between invertebrate dissimilarity and environmental dissimilarity in the Wellington River samples in both 1996 and 1997 support the argument that invertebrate distributions are influenced by environmental variables. It is surprising that the correlations of invertebrate assemblages with environmental variables were less strong than those with geographic distance. Components of the invertebrates' habitat other than those measured may also be important in defining suitable patches. Biotic interactions, including the presence of predators and epilithon, and microhabitat factors, such as the depth of the hyporheic zone, stone roughness and crevices, have been shown to have strong relationships with invertebrate abundance and distribution at very small scales (i.e. within riffles) (e.g Boulton, 1993; Peckarsky *et al.*, 1997; Robson & Barmuta, 1998). In addition to microhabitat influences, larger-scale habitat factors such as the presence of large woody debris, or pool habitat compared to riffle habitat, may be important in controlling the invertebrate assemblages. However, suitable habitat patches at this scale are likely to be a few 100m, which is equivalent to the smallest geographic separtaions in the smallest scale of this study. Many studies that have indicated strong correlations between environmental variables and invertebrate fauna have compared reference sites to impacted sites, such as between forested sites and logged sites (e.g Davies & Nelson, 1994; Brown *et al.*, 1997), or sites with high water quality and polluted sites (e.g Tate

& Heiny, 1995; Collier *et al.*, 1998). These studies have examined wider extremes of environmental variables and, consequently, less subtle effects of environmental quality than in the current study, which investigated relatively unimpacted rivers.

The analysis that isolated the correlations between invertebrates and habitat at different scales suggests that the overall correlations may be driven by the relationship at the smaller scales for the Wellington River in 1996. This indicates that it is not the large-scale geomorphological variables causing autocorrelation patterns in invertebrates, contrary to the predictions of the River Continuum Concept and other large-scale models of invertebrate distribution (Vannote *et al.*, 1980; Statzner & Higler, 1986; Whittier *et al.*, 1988; Corkum, 1992). Other studies relating invertebrate distribution to environmental variables at similar scales to this study found that environmental variables have more influence on invertebrates at 'reach' and 'local' scales (equivalent to the small scales in this study) than at larger scales. Richards *et al.* (1997) found that invertebrate assemblages were more strongly correlated with reach-scale than with catchment-scale habitat properties in 58 catchments in Michigan, USA. Carter *et al.* (1996) found that segment- and reach-scale habitat variables discriminated well among species-defined groups in the Yakima River basin of the USA. Local hydraulic factors had a greater influence on macroinvertebrate assemblages of Jacks Fork River, Missouri USA, than stream-scale factors (Doisy & Rabeni, 2001).

The same analysis for 1997 did not verify whether small scale correlation between habitat and invertebrates was occuring; none of the scales showed significant relationships in either the three- or four-interval analyses. 1997 was a drier year than 1996, resulting in higher water temperatures, decreased current speeds and lower dissolved oxygen concentrations. Other water-quality variables may have been different between the two years. High temperatures, low dissolved oxygen and slow currents may be stressful conditions for many of the invertebrates that inhabit riffles (e.g Erman, 1986; Brown & Brussock, 1991). Therefore, the influence of these water-quality variables on the macroinvertebrate fauna may have overridden that of the other environmental variables, so the relationship with the suite of environmental variables measured was not as close as it was in 1996.

It is not possible to discriminate between environmental factors and geographic distance as the major factor influencing spatial autocorrelation in the distribution of Wellington River invertebrates, as both appear to be partially implicated. Some of the variation in invertebrate assemblages was due to the correlation between environmental variables and invertebrates. The autocorrelation of environmental variables, and the relationship between environmental variables and invertebrate assemblages was also likely to produce some degree of autocorrelation in the invertebrate fauna. Results

from the three-matrix Mantel-test indicated that the environmental variables (and their underlying spatial pattern) were not solely responsible. Once the effect of environment was removed, the fauna was still significantly autocorrelated. This is likely to be due to dispersal and subsequent colonization of invertebrates at small scales (<8 km) and perhaps the influence of biotic interactions at similar scales.

The distribution of the Wonnangatta River invertebrates appears to be related to neither geographic distance nor environmental variables. Both the two- and three-matrix analyses indicated no relationship between environmental variables and invertebrates at any scale, even when geographic distance was removed as an influence on the analysis. Therefore the suggestion (from Chapters 3 and 4) that the Wonnangatta River invertebrate assemblages were not autocorrelated due to the influence of patchy environmental variables is not supported. The difference between faunal patterns of the two rivers may relate to the different individual environmental variables that were autocorrelated. Perhaps stream width and stream slope, which were autocorrelated in the Wellington River but not the Wonnangatta River are more important in determining the community composition than are substrate composition and sedimentation of the substrate. These latter variables were autocorrelated in the Wonnangatta River but not the Wellington. Danehy *et al.* (1999) found that longitudinal patterns of macroinvertebrate distribution responded strongly to stream slope in second to fourth order streams in New York. In addition, Statzner & Higler (1986) suggested that major changes in stream slope cr ate areas of high in-stream hydraulic variability. Several recent studies of invertebrate spatial patterns have shown that hydraulic variables were very important in determining assemblage patterns (Statzner & Higler, 1986; Danehy *et al.*, 1999; Rempel *et al.*, 2000; Doisy & Rabeni, 2001). Perhaps, hydraulic variables were more patchy in the Wonnangatta River than the Wellington due to the differing spatial patterns of stream slope between the two rivers. Alternatively, the influence of an untested variable(s) on the patterns of invertebrate distribution may have been very importand in determining faunal patterns. The Hawkins *et al.* (1997) study of assemblage structure in 45 Californian upland streams is a case where one variable, water temperature, appeared to override geographic and geomorphic patterns. Partial clearing of riparian vegetation at some Wonnangatta River sites may have produced asystematic water temperature patterns. An additional possiblity is that the role of chance may have been more important in determining the fauna within the riffles of the Wonnangatta River than in the Wellington River. Perhaps because the Wonnangatta River receives more tributaries of third or higher order than the Wellington River along the sections studied (Table 2.4) the influence of drifting invertebrates from tributaries or larger increases in discharge may have been stronger in the Wonnangatta River than the Wellington River.

5.5 Summary

Both the invertebrate assemblages and environmental variables were autocorrelated at small scales in the Wellington River in 1996. Invertebrate assemblages were also correlated with environmental dissimilarity in both years in the Wellington River. It is therefore not possible to distinguish between environmental variables and dispersal processes as the principal determinants of the autocorrelated spatial pattern of the Wellington River invertebrate assemblages. The Wonnangatta River data showed very different patterns for invertebrate fauna, which was not autocorrelated at any scales studied. The suite of environmental variables was autocorrelated for Wonnangatta River sites, but individual environmental variables showed different spatial patterns between the two rivers. Factors other than contagious processes appear to be determining the spatial patterns of the fauna of the Wonnangatta River.

Table 5.1: Environmental variables used to calculate Canberra dissimilarity indices for environmental dissimilarity between each pair of sites.

Variable	Included in Bray-Curtis dissimilarity index of environmental dissimilarity between sites
Riparian vegetation	Yes
Width of riparian zone of woody vegetation	Yes
Bank structure	Yes
Riffle/pool sequence	Yes
Sediment	Yes
Retention	Yes
Bed roughness	Yes
Substrate composition	Yes
Substrate heterogeneity	Yes
Land use beyond riparian zone	Yes
Macrophyte richness	No†
Stream bottom	Yes
Percent shading	Yes
Stream width	Yes
Water temperature	No†
Air temperature	No†
Current speed	No†
Water depth	No†
Distance from source	No†
Stream slope	Yes
Altitude	No*
Latitude	No*
Longitude	No*
Catchment area	No*
Annual air temperature	No†
Range in annual air temperature	No†

See Table 2.6 for variable definitions
* excluded due to strong intrinsic spatial autocorrelation
† excluded due to lack of adequate estimates for each site

Table 5.2: Mantel R values for two matrix Mantel-tests between invertebrate fauna, habitat or geographic distance data-sets for the Wellington and Wonnangatta Rivers.

Data-sets tested distance range	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
Invertebrate dissimilarity and Habitat	0.41***	0.25***	0.14
Invertebrate dissimilarity and Geographic distance	0.61***	0.62***	0.09
Habitat and Geographic distance	0.36***	0.25**	0.26*

Family-level, non-unique data-sets only were used in the above analyses.
Non-unique data-set: taxa excluded if sampled at only one site within sampling event
*** $P<0.001$

Table 5.3: Mantel R values for habitat data-sets of three and four geographic distance scales for the Wellington and Wonnangatta Rivers Geographic distance range.

Geographic distance range	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
0-6 km	0.63* (30)	0.65* (28)	0.45* (24)
6-12 km	-0.23 (30)	0.40 (28)	-0.03 (36)
12-20 km	0.14 (35)	0.34 (32)	0.18 (28)
20- 40 km	0.09 (25)	-0.01 (32)	0.11 (32)
0-8 km	0.56* (44)	0.33 (40)	0.55* (32)
8-16 km	0.22 (36)	0.13 (32)	-0.08 (40)
16-40 km	0.13 (40)	0.03 (48)	-0.002 (48)

* $P < \alpha$
Alpha was corrected for multiple tests using the sequential Bonferroni correction method advocated by (Holme, 1979).

Table 5.4: Univariate Mantel R values for environmental variables for the Wellington and Wonnangatta Rivers.

Data-sets tested / Environmental variable	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
Landuse beyond riparian zone	0.46***	0.17***	0.18*
Width of riparian zone of woody vegetation	0.32***	0.17*	0.49***
Riparian vegetation	-0.03	-0.08	0.01
Bank structure	0.18	0.08	-0.04
Stream bottom	-0.03	0.13	-0.04
Detritus	-0.04	-0.002	0.07
Retention	0.29**	0.23**	0.39***
Percent shading	0.11	-0.12	0.07
Substrate heterogeneity	-0.15	-0.12	-0.09
Bed roughness	-0.03	-0.05	0.05
Substrate composition	0.18*	0.10	0.40***
Stream width	0.30***	0.27**	-0.04
Stream slope	0.40***	0.77***	0.04
Riffle/pool sequence†	-	-0.13	-0.10
Sediment†	-	-0.01	0.29**

See Table 2.6 for variable definitions.
† Analysis excluded for Wellington River 1996 dataset as all sites scored the same value
* $P<0.05$
** $P<0.01$
*** $P<0.001$

Table 5.5: Comparison of results from three and four interval Mantel-tests for correlations between habitat dissimilarity and invertebrate dissimilarity.

Geographic distance range	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
0-6 km	+*	n.s.	n.s.
0-8 km	+*	n.s.	n.s.
6-12 km	n.s.	n.s.	n.s.
8-16 km	n.s.	n.s.	n.s.
12-20 km	n.s.	n.s.	n.s.
16-40 km	n.s.	n.s.	n.s.
20- 40 km	n.s.	n.s.	n.s.

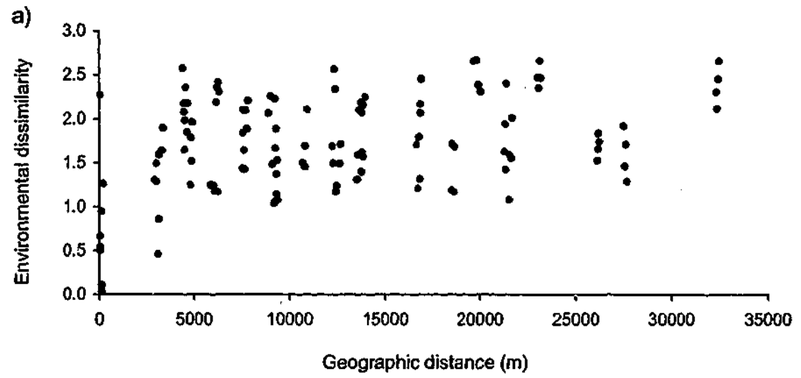
* $P < \alpha$
Alpha was corrected for multiple tests using the sequential Bonferroni correction method advocated by (Holme, 1979).

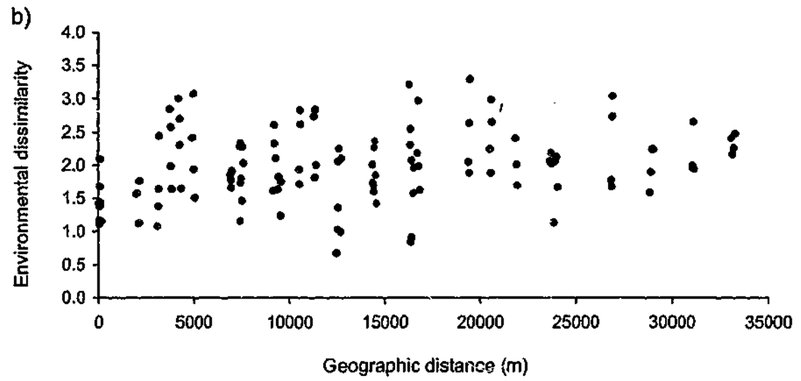
Table 5.6: Mantel R values for three matrix partial Mantel tests for the Wellington and Wonnangatta Rivers.

Data-sets tested distance range	Wellington River 1996	Wellington River 1997	Wonnangatta River 1996
Invertebrate dissimilarity and Geographic distance Habitat dissimilarity held constant	0.54***	0.59***	0.05
Invertebrate dissimilarity and Habitat distance Geographic dissimilarity held constant			0.14

Family-level, non-unique data-sets only were used in the above analyses.
Non-unique data-set: taxa excluded if sampled at only one site within sampling event.
*** $P<0.001$

Figure 5.1: Correlation between environmental dissimilarity (Bray-Curtis dissimilarity index) and geographic distance (m) between sites from a) Wellington River 1996, b) Wellington River 1997 and c) Wonnangatta River 1996.





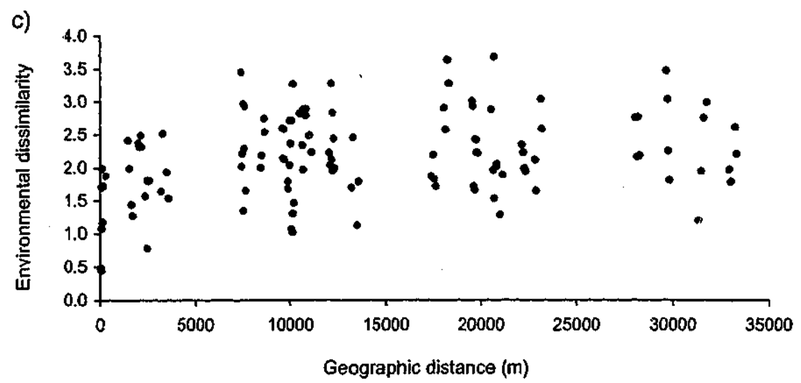
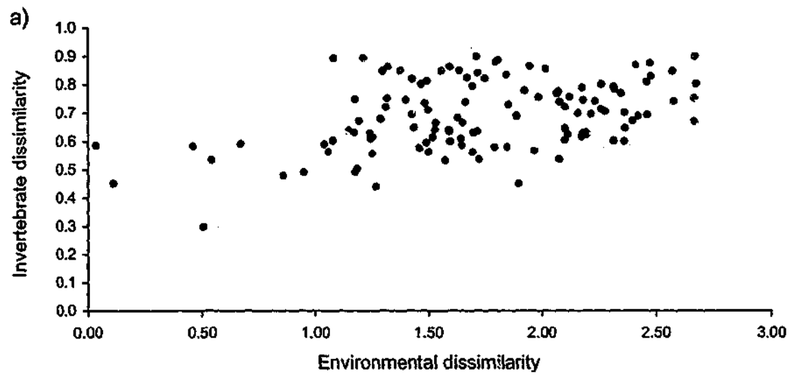
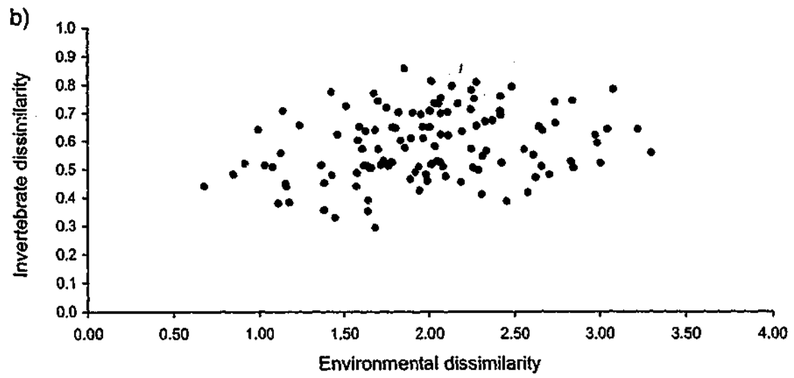


Figure 5.2: Correlation between family-level invertebrate dissimilarity and enviromental dissimilarity between sites from a) Wellington River 1996, b) Wellington River 1997 and c) Wonnangatta River 1996.





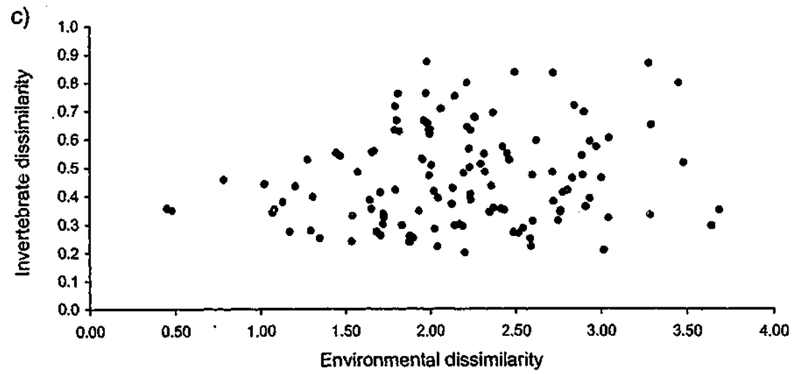
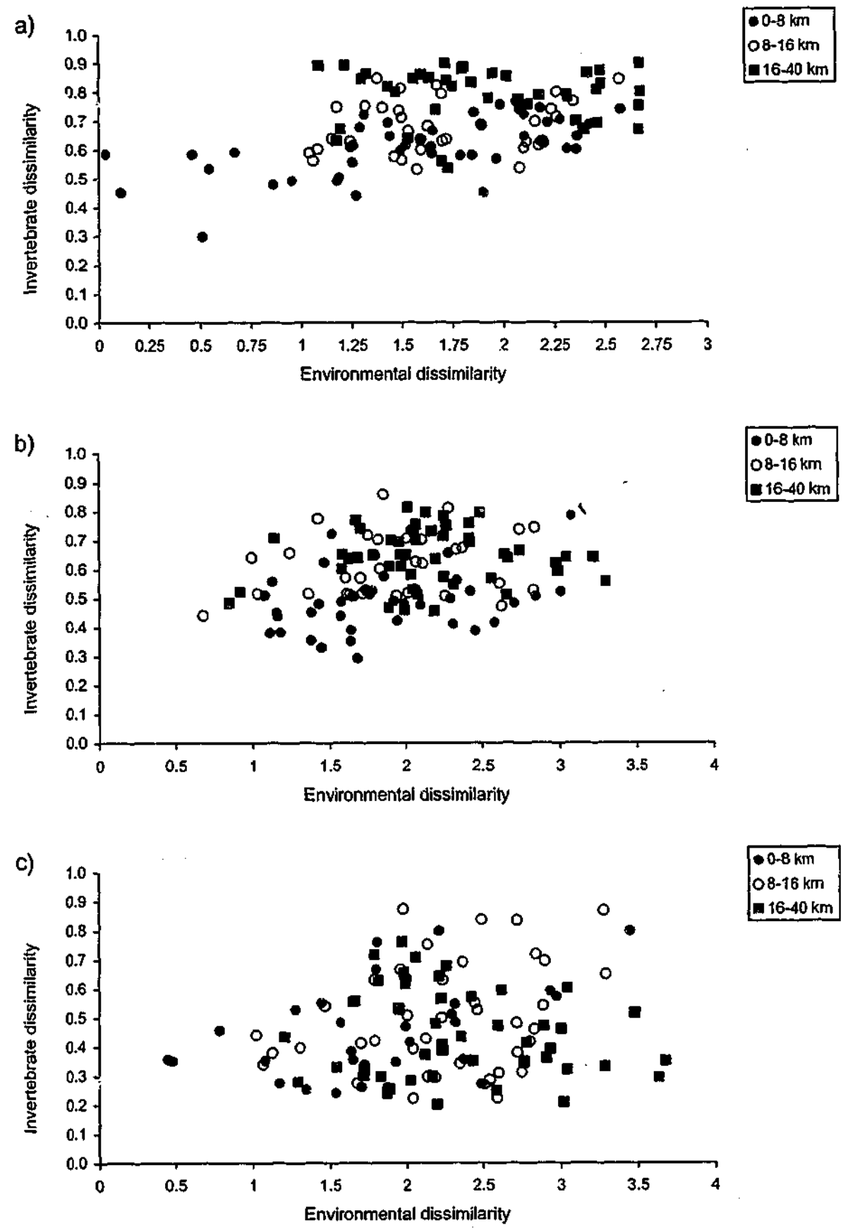


Figure 5.3: Correlation between family-level invertebrate dissimilarity and enviromental dissimilarity over three scales of geographic distances between sites from a) Wellington River 1996, b) Wellington River 1997 and c) Wonnangatta River 1996.



Chapter 6

Discussion and conclusions

The aim of this study was to describe the pattern and strength of autocorrelation in assemblages of benthic invertebrates of two upland rivers over a variety of spatial scales. Two components of autocorrelation patterns are likely to be important to ecologists- strength and scale. The strength of an autocorrelation pattern is given by the autocorrelation coefficient, which denotes the proportion of the variation of a variable that can be explained by the relationship between the variable and the inter-site distance. The strength of the autocorrelation pattern is indicative of the ecological importance of distance to the variable. A large coefficient value indicates that separation distance accounts for much of the variation and therefore that other factors have little influence on the distribution of the variable, whereas a small value of the autocorrelation coefficient could mean that contagious processes (e.g. migration) are weak or that the results of contagious processes are damped by other factors that have greater importance to the organism or assemblage in question. In either case, the distribution of the organism or assemblage structure is partially related to mechanisms other than the contagious process. It is therefore possible for an autocorrelation pattern to be statistically significant but of only minimal ecological importance. That is, an understanding of the autocorrelation pattern of an organism or assemblage may not assist in understanding its ecology. However, any statistically significant autocorrelation, even if the coefficient value is small, has important statistical ramifications and must be considered in the analysis and interpretation of the data.

Statistically, the scale of an autocorrelation pattern is the geographical or temporal extent over which autocorrelation is statistically significant. Diminishment of the autocorrelation coefficient with distance results from attenuation of the contagious process(es) or increases in effects of damping processes. If the contagious processes are based upon migration of organisms, then autocorrelation may diminish over the range

of the organisms' migration capabilities. Barriers to dispersal (e.g. weirs) may also limit the spatial scale of the autocorrelation. The extent of autocorrelation may also be affected by any ecological factor that operates as a contagious process, such as geomorphological patterns of environmental variables.

6.1 Wellington River results

Analyses including all separations showed that assemblages of invertebrates sampled in the Wellington River were autocorrelated in both 1996 and 1997, despite significant faunal differences (diversity, richness, abundance and composition) between the two years. Spatial autocorrelation was found using data-sets of different taxonomic resolution (species, genus, family), different rarity protocols (raw, non-unique, common) and the limited-taxon data-sets (only Ephemeroptera, Plecoptera, Trichoptera; no-chironomid data). Thus the autocorrelation patterns were robust with respect to all of these data representations.

At relatively small scales (0-6 km and 0-8 km), the Wellington River samples were autocorrelated in both years. There was no significant autocorrelation at larger scales that was consistent for both the three-interval and the four-interval analyses. The species- and family-level data-sets showed the same results. The Wellington River invertebrate fauna can therefore be described to have a pattern of strong autocorrelation at short range only in both 1996 and 1997.

Environmental variables were also autocorrelated in the Wellington River sites in both years. Scale analyses of the autocorrelation of environmental variables revealed significant small-scale autocorrelation in the Wellington River sites in 1996. Variables were not autocorrelated at larger scales. Therefore in 1996, the environmental variables also were autocorrelated at short ranges. The analysis of 1997 sampling sites provided inconsistent results for the smallest scales, but consistent non-significant resluts for the larger scales. Environmental variables in 1997 appeared to be weakly autocorrelated overall, but without any significant autocorrelation at any scale. The following individual environmental variables were autocorrelated for both 1996 and 1997 samples: landuse beyond the riparian zone; retention; width of riparian zone; stream width; stream slope.

Overall invertebrate dissimilarity was correlated with dissimilarity of environmental variables in both sampling seasons of the Wellington River. All scale analyses performed on the correlation between invertebrate fauna and environmental variables were consistent. Of all the analyses on the relationship between invertebrates and

environmental variables, only those at the smallest scales in the Wellington River 1996 were significant.

The three-matrix Mantel tests allowed the relationship between the invertebrates, environmental variables and geographic distance to be further explored. When autocorrelation in environmental variables between sites was accounted for, the invertebrate fauna of the Wellington River was autocorrelated in both 1996 and 1997. Therefore, the pattern of invertebrate assemblage autocorrelation was not solely related to the correlation between invertebrate dissimilarity and (autocorrelated) dissimilarity of environmental variables.

The patterns of autocorrelation documented in the Wellington River appear to have at least two main causes: (1) dispersal and subsequent survival of individual animals; and (2) autocorrelation of influential environmental variables.

(1) Instream dispersal by individuals and aerial dispersal of females before oviposition are likely to occur over the same scales as those at which the invertebrate assemblages were autocorrelated in the Wellington River (i.e. 0-8 km). Large numbers of animals are found in the drift (Brittain & Eikeland, 1988). Although some drifting animals do not survive the process or do not resettle successfully (Wilzbach & Cummins, 1989), enough animals drift and colonise new substrata (e.g. constructed riffles) to support the argument that this is an important dispersal mechanism (Gore, 1982). Although few data are available for Australian invertebrates, studies of drifting distances find that invertebrates drift for distances <10 km over one generation (see section 4.1). Flight by adults before oviposition is also likely to be within this range for all but the most mobile taxa, possibly including some Australian simuliids (see section 4.1). Survival of eggs and early-instar larvae has not been well studied, but Bunn & Hughes (1997) and Hughes *et al.* (1998) found, based on genetic differentiation, that recruitment of *Baetis* sp. and *Tasiagma ciliata* larvae within a reach may be due to the eggs of just a few females. Therefore, sufficient eggs may survive and remain in the area of egg deposition for aerial dispersal and location of egg deposition to be an important factor in the spatial patterns of mature nymphs. It is possible that the movement of individual animals and their subsequent settlement and survival in nearby locations is most likely to be contagious within the Wellington River. The importance of dispersal in determining scales of autocorrelation of benthic invertebrates would be further supported by comparisons between scales of autocorrelation among taxa with different known dispersal abilities.

(2) The influence of environmental variables on the autocorrelated spatial pattern of the Wellington River macroinvertebrates is suggested by two correlations. First, dissimilarity of invertebrates was correlated with dissimilarity of environmental variables in Wellington River samples. And second, environmental variables were themselves

autocorrelated. In 1996, both the environmental variables and the invertebrates showed a significant autocorrelation pattern at short range (<8 km) only. In 1997, the invertebrates showed a similar autocorrelation pattern, whereas the environmental variables were weakly autocorrelated for the entire data-set but not significantly autocorrelated at any particular scale.

6.2 Wonnangatta River results

The invertebrate fauna showed a distribution that was independent of geographic distance within the study section. This pattern was consistent for all data-sets, i.e. taxonomic level, rarity and limited-taxon suites. The Wonnangatta River scale analyses appeared to produce statistical artefacts. The four-interval analysis produced significant negative autocorrelation at the 12-20 km scale, yet the three-interval analysis resulted in positive significant autocorrelation at all three scales. These inconsistencies between the two scale analyses are inconclusive, although given the overall non-significant result and asystematic appearance of the scatterplot of invertebrate dissimilarity against geographic distance, the significant results in the three- and four-interval analyses appear unconvincing.

Environmental variables of Wonnangatta River sites showed a significant autocorrelation pattern overall. Like the Wellington River 1996 results, the scale analyses revealed significant autocorrelation at the small scales (0-6/8km) only. Individual environmental variables showing significant autocorrelation patterns were: landuse beyond the riparian zone; retention; width of riparian zone; substrate composition and sediment.

In contrast to the Wellington River invertebrates, the Wonnangatta River invertebrates were not correlated with environmental variables. Neither the overall relationship between dissimilarity of invertebrates and dissimilarity of environmental variables nor any of the scale analyses of that relationship were significant. Similarly, the three-matrix Mantel tests produced non-significant results. When differences in environmental variables between sites were accounted for, the invertebrate fauna of the Wonnangatta River was not autocorrelated in 1996. Invertebrate dissimilarity was not related to environmental variables, with geographic distance held constant.

Therefore, the lack of autocorrelation observed in the Wonnangatta River invertebrate samples cannot be ascribed to the influence of non-autocorrelated environmental variables because there was no relationship between the invertebrate dissimilarity and the environmental-variable dissimilarity.

6.3 Similarities and differences between the two rivers

The main difference between the two rivers was the pattern of autocorrelation detected in the macroinvertebrate fauna- Wellington River fauna showed a pattern of strong autocorrelation at short ranges, Wonnangatta River fauna showed a pattern that was independent of distance. This difference was robust, and found irrespective of the data representations used. The relationship between the invertebrate fauna and the environmental variables measured was very different between the rivers. The distribution of Wellington River fauna appeared to be strongly related to environmental variables, whereas there was no evidence for such a relationship in the Wonnangatta River. The determination of invertebrate distribution was clearly different between the two rivers. In the Wellington River, the invertebrate distribution was probably primarily determined by the contagious processes of invertebrate dispersal and colonisation and the underlying autocorrelated pattern of environmental variables. In contrast, the Wonnangatta River invertebrate distribution did not appear to be influenced by contagious processes. Either the same contagious processes did not occur, or, if they did, the pattern of autocorrelation was eroded by non-contagious processes.

Although the two rivers had different patterns of autocorrelation, there were similarities in the scale analyses. The samples from both rivers produced inconsistent results between the three-interval and the four-interval analyses. These inconsistent results highlight the difficulty in drawing conclusions from arbitrary decisions regarding the boundaries of different scales. Had the analysis been considered complete at the first set of intervals, the analysis may have appeared conclusive, but this may have been erroneous. Many studies use arbitrary intervals when computing correlograms and other scale analyses; perhaps this is unwise. If arbitrary choices of scale or interval cannot be avoided, then sensitivity analyses with different intervals or sub-sets of the complete data-set may be a useful approach.

There are several conclusions that can be drawn from these results: (1) the marked differences in autocorrelation among rivers and at different times make it potentially foolhardy to extrapolate to other rivers and times. The Wellington River and the Wonnangatta River are both stony upland rivers with minimal anthropogenic impacts and similar invertebrate faunas, yet the macroinvertebrate assemblages exhibited different spatial patterns. It is, therefore, potentially dangerous to assume that autocorrelation of benthic macroinvertebrate assemblages in rivers will show a particular pattern at any particular scale or time. (2) Spatial scale should be considered carefully because different scales may lead to divergent conclusions. In particular, where scales of analysis are arbitrary, more than one set of analyses should be conducted, to check whether results

are possibly an artefact of scale. Multiple scales of sampling are recommended (Wiens, 1989; Cooper *et al.*, 1998; Mac Nally & Quinn, 1998) and the data presented here support this argument. Furthermore, my data also suggest that different intervals (division of data-set into sub-sets based upon separations) can be important, and therefore more than one set of intervals should be tested. (3) Although these two rivers share a similar fauna, hydrological pattern, physical instream habitat, catchment soils and vegetation, and climate/geography, the underlying causes of faunal patterns of distribution and abundance are clearly different.

6.4 Spatial autocorrelation and the theory of lotic community ecology

The discipline of community ecology attempts to explain the diversity and distribution patterns of organisms. Freshwater ecologists have applied general community ecology theories to benthic invertebrate assemblages in rivers in an attempt to explain the high diversity and variability of assemblages seen in these habitats. Because many of these theories were developed without reference to spatially dependent processes, the following discussion explores the spatial assumptions and implications of each theory.

6.4.1 Deterministic models

Deterministic models of community structure are based on the premise that community structure is predictable and predetermined by interactions between organisms and their environment. Many of these models are equilibrium models whereby little change in overall community structure over time is assumed. The 'niche' concept of Cole (1960) and MacArthur & Levins (1967) directs that patterns of species composition and abundance are the result of interspecific competition. Superior competitors will gain access to high quality resources and inferior competitors will survive in marginal areas or on low quality resources. Specialisation and niche partitioning evolve and result in reduced competition and high diversity. The keystone predator hypothesis is a variant on this model that allows inferior competitors to persist by selective predation upon the strongest competitor(s) (Paine, 1969). These theories are based on competition for a single major resource, such as attachment space in the marine benthos or light in the ocean epilimnion. Although there is considerable evidence of competitive and predator-prey interactions in some stream invertebrate assemblages (see Wiley & Kohler, 1984; Cooper *et al.*, 1990, 1998), Tokeshi (1994) argued that species interactions are

unimportant in determining the structure of lotic communities. There is little evidence for niche partitioning in freshwater invertebrate communities (Tokeshi, 1994), perhaps because these organisms are mobile and the resources they require are complex (with the exception of net-spinning caddisflies) (Frid & Townsend, 1989). These theories suggest that community structure is determined locally by the availability of resources and small-scale intra- and inter-specific interactions (Table 6.1). Although the system is considered open, the only role for dispersal is in providing recruits. Because of this, there is little consideration for the role of autocorrelation in these theories.

A second group of deterministic community structure models are those in which the habitat is the template that determines the abundance and distribution of species. This view assumes that organisms will be found in a location if the environmental variables are within their tolerance values. This idea is based upon the Hutchinsonian niche concept (Hutchinson, 1957, 1961). There is ample evidence that benthic freshwater invertebrates respond to physical and chemical factors and many models of invertebrate community structure, including the River Continuum Concept (Vannote *et al.*, 1980), longitudinal patterns (see Statzner & Borchardt, 1994), impact assessment models such as RIVPACS (Wright *et al.*, 1984, 1993), AUSRIVAS (Coysh *et al.*, 2000) and models of biotic integrity (e.g Fore *et al.*, 1994; Kerans & Karr, 1994; Roth *et al.*, 1996), explicitly or implicitly use this assumption. Like the competition-based niche theories, these habitat template models assume local determination because species composition in a local area is determined by habitat variables. However, unlike in the competition-based niche theories, the importance of biotic interactions in structuring communities is considered to be relatively low. These models require an open system because dispersing propagules are thought to be widespread but to have little influence on the local community (Table 6.1). Therefore, there is no role for autocorrelation in influencing community structure by way of dispersal as a contagious process. However, habitat template theories dictate that autocorrelation patterns of communities should result if environmental variables are autocorrelated.

6.4.2 Non-equilibrium models

Many of the community ecology theories invoked to explain high species diversity in freshwater systems, including the intermediate disturbance hypothesis (Connell, 1978), dynamic equilibrium hypothesis (Huston, 1979), patch dynamics concept (Thompson, 1978; Townsend, 1989), disturbance-productivity-diversity model (Statzner & Resh, 1993) assume that inter-specific interactions and physical-habitat variables are the principal determinants of faunal composition and distribution only in the absence of

disturbance (Frid & Townsend, 1989; Townsend, 1989). Disturbance (hydrologic in the case of rivers) removes equilibrium conditions (Reice, 1994) and 'resets' succession processes (Townsend, 1989). Reice's (1994) non-equilibrium model suggests that disturbance is so frequent that it prevents the establishment of equilibrium conditions so that high diversity is maintained by stochastic recruitment. There is weak evidence from long-term emergence data-sets to support the intermediate disturbance hypothesis and disturbance-productivity-diversity model (Resh *et al.*, 1988). McAuliffe (1984) found that invertebrate community structure in Owl Creek, Montana, conformed to predictions of the intermediate disturbance hypothesis. Similarly, Townsend *et al.* (1997) suggested that the intermediate disturbance hypothesis explained species richness in the Taieri River catchment, New Zealand, but Doeg *et al.* (1989a) found no supportive evidence in the Acheron River of Victoria. Australian streams have higher variability in annual flows and peak discharges than streams of the same catchment area on other continents (except South Africa) (McMahon, 1982). Consequently, hydrological disturbance has been considered very important in determining stream fauna in Australia (e.g Lake *et al.*, 1985; Boulton *et al.*, 1988; Doeg *et al.*, 1989a; Lake *et al.*, 1989; Brooks & Boulton, 1991; Boulton & Lake, 1992; Lake, 1995; Downes *et al.*, 1998b; Bond & Downes, 2000; Lake, 2000). These non-equilibrium theories view disturbance as a stochastic factor, although the recolonisation process is still considered predictable/successional. Systems are considered open (Connell, 1979; Frid & Townsend, 1989), but the only influence of dispersal is to provide recruits to recolonise disturbed areas (Table 6.1). Autocorrelation of assemblages may be noted in these models if recolonisation is related to the supply of recruits. However, local control is implicitly assumed in most of these theories whereby interspecific interactions control succession of organisms.

Invertebrate composition has been commonly viewed as being determined by a combination of biotic and abiotic factors, including disturbance. However, species assemblages may not respond in a predictable manner to biotic and abiotic conditions, the role of chance may be significant (Lake, 1986). Models such as the competitive lottery model (Chesson, 1986), and equal-chance hypothesis (Sale, 1980) are founder-controlled communities (sensu Yodzis, 1986), which provide for the role of stochastic recruitment and other chance factors in the settlement of dispersing propagules. There is convincing evidence, in at least some cases, that stochastic factors may be of prime importance in influencing faunal assemblages. For example, Hart (1992) concluded that stochastic effects in combination with competition, predation and abiotic factors determine community composition in a small Michigan stream. McCreadie *et al.* (1997) found that black-fly assemblages in similar streams were largely unpredictable in terms of species co-occurrence. Tokeshi (1994) documented apparently random chironomid assemblages on *Myriophyllum* stalks. Similarly, Bunn & Hughes (1997) and McCreadie

(1991) argued that recruitment from eggs laid by only a few individuals determined the abundance of *Baetis* spp., *Paratya* spp. and *Tasiagma ciliata* and the composition of simuliid assemblages respectively. McCreadie (1991) suggested that in similar streams the species pool from which a potential assemblage for a single site is drawn is limited by habitat requirements, however the resulting assemblage is due to stochastic recruitment. Sheldon (1984, p. 419) suggested that "although colonization seems to be adaptive and explainable by natural selection there is a large random component". Due to the stochastic nature of recruitment, only weak autocorrelation of community structure as a result of attenuated dispersal patterns is expected because the composition of the drift is not strongly related to successful colonisation (Table 6.1). Weak autocorrelation may also result from strongly autocorrelated environmental variables, as the habitat of a patch provides a number of possible templates, from which stochastic recruitment determines ultimate community composition.

6.4.3 Dispersal

While the above theories all acknowledge that rivers are open systems and that the magnitude of dispersal is high, the influence of immigration and emigration on established communities may be more important than has been recognised. Cooper *et al.* (1998, p. 30) argued that "the smaller the study area, the larger the importance of exchange [immigration and emigration] to short-term population dynamics, relative to processes occurring within the study area" (see also Mac Nally, 2000). Rather than local control of communities either by biotic, abiotic, stochastic or a combination of factors, Palmer *et al.* (1996, p. 324) suggested that regional control may be widespread in stream benthic invertebrates because these systems experience "high levels of disturbance *and* extent of dispersal". Regional refers to "scales that are sufficiently large that fauna disperse in the water over distances that encompass more than one local assemblage" (Palmer *et al.*, 1996, p. 323). Furthermore, such regional control should result in a highly variable community structure, determined largely by stochastic recruitment. This model is similar to Reice's (1994) non-equilibrium model, but the role of dispersal is explicitly stated. Experimental and modelling evidence indicating the importance of immigration and emigration in structuring communities has been provided by (Cooper *et al.*, 1990) for predaceous stoneflies and (Sih & Wooster, 1994) for invertebrate predators in general. Sih & Wooster (1994) demonstrated that emigration as a result of predator presence is likely to influence community structure more strongly than predation *per se*. The importance of dispersal in influencing established communities, and not just recolonising disturbed substrate, distinguishes this model of community composition from the stochastic models discussed above (Table 6.1). As in the stochastic models only weak spatial autocorrelation

of community structure is expected for dispersal models because of high variability in community composition resulting from stochastic recruitment. If the assumption of highly stochastic recruitment and emigration is relaxed, strong autocorrelation as a result of a strong relationship between attentuated dispersal and community composition would be expected (see section 1.1).

6.4.4 Lotic community ecology theory and the spatial patterns of the Wellington and Wonnangatta River invertebrate fauna

The fauna of the Wonnangatta River did not appear to be regionally controlled by dispersal or contagious environmental conditions. Local control as a result of biotic interactions may have occurred. It is possible that local control resulting from habitat requirements exists. However, the environmental variables measured did not appear to be important in determining the assemblage structure of invertebrates in the Wonnangatta River. Reice's (1994) non-equilibrium theory may also provide a suggestion for the non-autocorrelated pattern seen in the Wonnangatta River invertebrate assemblages. This seems unlikely because the Wonnangatta River was not subject to large or frequent spates in the months prior to sampling. The absence of a spatial pattern was consistent with stochastic recruitment of invertebrates in the Wonnangatta River.

The spatial pattern of the Wellington River fauna seems most consistent with the regional control model of Palmer *et al.* (1996). Local control by (autocorrelated) environmental variables may also be occurring in the Wellington River macroinvertebrate assemblages. Local biotic control may influence assemblages to some extent, but this was not evaluated. The role of disturbance in preventing/resetting equilibrium conditions was not investigated, but the Wellington River, like the Wonnangatta River, was not subject to extreme hydrological disturbance prior to either sampling event. Stochastic recruitment may account for the high variability in the correlations between invertebrate dissimilarity and geographic distance and environmental variables.

6.5 Ecological implications of spatial autocorrelation in assemblages

The ecological implications of spatial autocorrelation patterns relate to the causative processes behind such patterns and will depend upon the strength and scale of the contagious process(es). Where autocorrelation results from 'biotic contagion' i.e.

dispersal and recruitment of organisms, then regional control of assemblages ensues. Autocorrelation can also result from 'abiotic contagion', in which environmentally similar sites are situated close together and assemblage structure is locally determined by the habitat at a location.

Where autocorrelation resulting from biotic contagion is strong, changes in assemblage structure in one location are more likely to affect assemblage structure in other locations. Thus, when the autocorrelation coefficient is large (approaching a value of 1 or -1), autocorrelation is most likely to be ecologically important because the contagious process(es) have a strong bearing on the end result of recipient assemblages. Such a pattern of autocorrelation would imply that the system is open, that some components of the assemblage are mobile and that their presence (influx/efflux) influences local assemblage dynamics (e.g Cooper *et al.*, 1990; Sih & Wooster, 1994). Such assemblages are more susceptible to detrimental contagious processes such as the transfer of disease or parasites which may lead to changes in species composition, ratios of functional groups or local extinctions. If the assemblage in question has a strong influence on the functioning of a system, such as bacteria involved in nutrient cycling or toxic planktonic algae, then the ecological ramifications of autocorrelation could be major, such as a toxic algal bloom. In addition to contagion of detrimental processes, strong autocorrelation could mean that the recovery from local impacts could be rapid, either by decreasing the time of recovery or increasing the scale over which recovery can quickly occur.

Abiotic contagion can result in highly autocorrelated assemblages when strongly autocorrelated abiotic variables, for example salinity gradients, function as contagious processes. Here, the system is open, with all potential taxonomic components of an assemblage being able to migrate. Recruitment and survival are determined by habitat suitability. Changes to the physical or chemical habitat will result in changes to the assemblage structure. Examples of detrimental abiotic contagious processes include floods, water-chemistry differences and water-borne or wind-borne pollution. Recovery of species abundances should be rapid once the environmental variables are returned to within tolerable ranges if the disturbance was not so widespread that migrant sources were also affected. Changes to assemblage structure should not affect nearby locations under this local control model, because assemblage structure is determined by the local habitat, not by immigration of individuals.

The difference between strong and weak autocorrelation (over the same scales) may relate to either (1) the ecological importance of the contagious process or (2) the degree of contagion. (1) In the case of strong autocorrelation, the variable is strongly influenced by the contagious process. Therefore, strongly autocorrelated assemblages may signify a deterministic community structure being driven by one or

a few spatially dependent process(es). Weakly autocorrelated assemblages could mean either a deterministic assemblage structure being driven by a **number** of processes with different spatial patterns, or a stochastic assemblage structure. Autocorrelation would be less ecologically significant if it is weak. One ramification of deterministic, compared to stochastic, assemblage structure is low plasticity (ability to survive under a range of physical conditions). Change in environmental conditions would have a larger impact in deterministic assemblages than in more stochastic assemblages. (2) It is also possible that a weakly autocorrelated pattern may result from a contagious process that is important ecologically but that has low contagion. Heavy-metal pollution may be an example because this type of pollution usually adheres to particle surfaces and is not quickly transported or easily bioavailable, but is extremely toxic if it does become available to organisms. Ecological ramifications of this type of contagious process are low unless some change occurs that modifies the 'infectiousness' of the contagious process. For example, eductor dredging of gold tailings with mercury contaminated sediments mobilises mercury and other toxicants, although the effects on biota have not been well quantified (Hall, 1988).

Autocorrelation occurring at medium or large scales in addition to smaller scales indicates that the processes are more contagious than in the other types of autocorrelation patterns. Neither the dispersal of organisms nor the influence of immigrating organisms on established assemblages is strongly limited. Therefore, there is a larger ripple effect if change occurs. If dispersal of organisms is the main contagious process it may be controlled by the mobility of the species or system characteristics.

A lack of autocorrelation could indicate sets of closed systems or sedentary taxa. Either there are barriers to the movement of animals or the animals are not inclined to move. Waterfalls and man-made structures such as dams can provide such barriers to some riverine fish (Mallen-Cooper, 1994). Hughes *et al.* (1996) documented extensive genetic differentiation between shrimp *Caridinia zebra* populations within a single catchment and suggested that waterfalls were limiting migration in a normally sedentary species. Decreased genetic exchange, as a result of closed systems, can lead to rapid speciation or low levels of community plasticity. Detrimental contagious factors (e.g. disease) may be less influential in such a system, but recovery from local extinctions, or other community impairment, may take longer or be less likely to occur.

No autocorrelation in assemblage structure need not necessarily signify a closed system- it may mean that contagious factors are not ecologically important. The assemblage may be locally determined, either by the physical and chemical habitat factors, which do not show an autocorrelated spatial pattern, by fauna present at a local site, or by a combination of the /o. Low levels of genetic exchange may result from this

community structure also. However unlike the previous situation, if local extinctions occur recolonisation is possible because the system is open and immigration occurs, generally, though immigration has little bearing on local assemblage structure.

No autocorrelation may also be a result of sampling within a homogeneous local patch, within which the organisms move freely and environmental variables are evenly distributed. Such a scenario is unlikely to occur in natural systems, but is not impossible if sampling is constrained to a small area, relative to the scale of the homogeneity. If sampling occurred at the scale less than that at which dispersal (or any other contagious process) begins to taper, then the variable may be expected to show no relationship with distance. If change occurs it will affect the entire patch.

6.6 Statistical ramifications of spatial autocorrelation

The presence of autocorrelation influences the conclusions of inferential statistical tests. The degrees of freedom (and hence precision) are overestimated even when autocorrelation is weak (Cressie, 1991) therefore artificially increasing the type I error rate. The standard error terms may also be affected by autocorrelated data, although the effect is not always consistent. For example, if two variables, both positively spatially autocorrelated, are correlated, the error terms will be artificially reduced, making the test more likely to be falsely significant (Legendre, 1993). However, if variables are negatively correlated, the error terms will be too large, resulting in a higher likelihood of a false non-significant result (Cressie, 1991). Drinkwater & Myers (1987) re-analysed data from previous studies of fisheries catches taking autocorrelation into account and found that correlations that had been thought to be statistically significant were not. Burgman & Williams (1995) re-analysed data using a Mantel-correlogram that had been analysed using inferential statistics. They found that the original analysis had erroneously inferred that there was no influence of spatial autocorrelation. Pinckney & Sandulli (1990) provided an example of autocorrelation analyses revealing links between marine meiofaunal and microalgal populations when conventional correlation analysis did not.

In addition to violating assumptions of independence, spatial autocorrelation can influence the interpretation of temporal sequences. Thrush *et al.* (1994) found that species with pronounced spatial autocorrelation were the most difficult to detect responses to anthropogenic impacts. They sampled assemblages of marine soft sediments in New Zealand and found that the temporal sequences of those animals which had highly patchy abundances, such as the polychaete *Heteromastus filiformis*, could remain undetected if too few spatial replicates were taken (Thrush *et al.*, 1994). The polychaete commonly

showed high densities in winter with a distinct decline in summer. They simulated less extensive spatial sampling regimes by randomly subsampling their data. The temporal pattern observed in the original data was detectable in only 28% of randomised subsamples.

The basic assumption of all sampling- experiments and models- is that replicates are sampled independently from a population about which we wish to draw conclusions (Hurlbert, 1984). Many questions in ecology and natural-resource management involve comparisons where spatial sampling points are treated as replicates. However, few such studies explicitly explore the potential implications of spatial autocorrelation on design and analysis. Three designs of particular interest in relation to management of freshwater systems are before-after-control-impact (BACI) and AUSRIVAS models and the upstream reference site design for determining impacted stream reaches. BACI-type designs require 'replicate' sites to be independent because researchers wish to draw conclusions about the populations, represented by samples from sites, not just the samples themselves (Underwood, 1992). This applies to the original BACI design, based on one 'before' and 'after' site (for both control and impact treatments) (Stewart-Oaten *et al.*, 1986) and the variations, including multiple sites and multiple sampling of each (Faith *et al.*, 1991; Underwood, 1992; Smith *et al.*, 1993; Faith *et al.*, 1995). If autocorrelated data are used in BACI designs then the analysis may be inaccurate as described above.

The main assumption of the AUSRIVAS and RIVPACS modelling approach is that the fauna at a site is determined by a few environmental variables, primarily geographic, geomorphological and chemical variables. This technique does not accommodate biological interactions or stochastic events influencing the fauna present at a particular location. This deterministic assumption may hold true, to a degree, in the absence of autocorrelation, but if the species sampled are autocorrelated at the scale of sampling then the presence of a particular species at one location will be related to its presence at another location. If a species presence is influenced by such autocorrelation, in addition to other biological factors, then the assumption upon which the model is built, that the environment determines the fauna, is undermined. Therefore autocorrelation may reduce the accuracy of the model predictions. However, if the autocorrelation pattern is primarily due to the underlying spatial pattern of ecologically important environmental variables, rather than dispersal *per se*, then the invertebrate assemblage is deterministic, the model's assumption holds and the autocorrelation of the invertebrates is not a problem.

The upstream reference site model, used extensively in impact testing (Reynoldson *et al.*, 1997) assumes that the fauna that should be found at a potentially impacted site, in the absence of any impact, can be predicted from the fauna at the upstream site due to strong longitudinal linkages in streams and the unidirectional flow of water. This model,

instead of being based on **estimation** of populations by the measurement of samples and the application of inferential techniques, is based on the **prediction** of one sample from the known results of another. In prediction, the assumption operating is that processes affecting one site will affect the other (Cressie, 1991). That is, strong autocorrelation is present. Spatial techniques such as kriging are used for such prediction. Therefore, the use of the upstream reference site model is valid for autocorrelated sites, but care must be taken in using inferential statistics on data produced from such a design.

Spatial autocorrelation does not necessarily preclude the use of the designs discussed above. However, care in the application of these methods, and consideration of underlying assumptions, is necessary. Below are some suggestions for safeguards and alternative approaches, valid in the presence of spatial autocorrelation.

6.7 Recommendations for studying spatially autocorrelated variables

A major conclusion from my work is that one cannot assume that autocorrelation of benthic invertebrate assemblages is very pronounced, even at small scales. Moreover, rivers are likely to be idiosyncratic, some having strongly autocorrelated fauna and others with fauna not autocorrelated at all. Given that the ramifications of autocorrelated data are the misinterpretation of results, I recommend that spatial autocorrelation should always be given serious consideration in the planning of ecological studies. It would also be desirable to answer questions regarding autocorrelation with less time and effort than was expended in this study. To this end, I include a section on useful tools for measuring autocorrelation and some suggestions for accessible literature that provide more detailed information.

6.7.1 Describing autocorrelation

The first step is to describe the nature of autocorrelation present in any system. The issue can then be approached by assigning independent replicates, using statistical techniques robust to non-independent replicates, or incorporating spatial questions into the study.

The Mantel-test (see section 2.4.1) is a linear, non-parametric test of matrix association (Mantel, 1967) (Table 6.2). Because it is a randomisation test, and therefore the test is distribution-free, it is very useful to test autocorrelation. The advantages of this test for the use in autocorrelation analysis is that the measures of distance between

site-pairs can be univariate (e.g. geographic distance) or multivariate (e.g. Bray-Curtis coefficient of dissimilarity).

Correlograms and Mantel-correlograms are graphs with the autocorrelation coefficient plotted against the spatial or temporal distance measure partitioned into classes (Table 6.2). Each distance class can then be tested for statistical significance (section 2.4.1.1). In correlograms the degree of autocorrelation exhibited by pairwise values within the categories is compared to the overall average autocorrelation between sites. This provides a test of autocorrelation relative to overall dataset (Koenig, 1999b). Burgman & Williams (1995) used correlograms to analyse the spatial distribution of arthropods in eucalypt forests of Western Australia. They were able to define the patch size over which the arthropod fauna was autocorrelated. Mantel-correlograms are similar to correlograms except that Mantel R value is used as the coefficient of autocorrelation instead of the univariate Moran's I or Geary's C coefficients (Sokal, 1986). Characteristic correlogram shapes have been related to underlying spatial distributions such as gradients, random data and patchy distributions (Legendre & Fortin, 1989). Correlograms are useful for analysing autocorrelation at a number of scales, although they require large numbers of sites. Legendre & Fortin (1989) recommended at least 30 sites for the successful use of correlograms.

Koenig & Knops (1998) developed modified correlograms in which the autocorrelation coefficients (e.g. Mantel R) are divided into distance categories and each set is tested using a randomisation test in the same method as correlograms (Table 6.2). The difference between these and standard correlograms is that each site is included only once in the analysis for modified correlograms, whereas in standard correlograms every site-pair combination is included. This analysis provides a test of autocorrelation in the different distance classes that is absolute, rather than relative to the other distance classes, as in correlograms and Mantel correlograms (Koenig & Knops, 1998). That is, correlograms and Mantel correlograms have the same number of negative and positive R values, whereas a modified correlogram may not. Therefore, the advantage presented by modified correlograms is that comparisons may be made between similar studies that have been conducted at different spatial or temporal scales.

Semivariograms (often called variograms) are plots of the lag between data points (i.e geographic, temporal or some unit measure) versus the semivariance (Rossi *et al.*, 1992)(Table 6.2). The semivariance is a measure of the "average squared difference between samples aligned in a particular direction and separated by some common lag" (Rossi *et al.*, 1992, p. 291). Semivariograms can either be computed over all directions in the one analysis, or particular directions can be examined separately. Two-dimensional analysis refers to the maps that can be produced if different directions

are analysed separately (Legendre & Fortin, 1989). Underwood & Chapman (1996) used semivariograms in their study of the variation of abundance of intertidal molluscs on rocky shores. They documented large small-scale variability, with autocorrelation predominantly only significant at very small scales, i.e. 1-2 m.

$$\gamma(h) = 1/2N(h) \sum_{i=1}^{N(h)} (2(x_i) - 2(x_i+h))^2$$

where h is the distance between site pairs and $N(h)$ is the number of site pairs separated by h

A disadvantage of the semivariogram is the requirement for 'stationarity', or constancy of mean and variances throughout the sampling space. This requirement is rarely met in ecological data (Rossi *et al.*, 1992). For this reason correlograms are often favoured by ecologists.

Serial autocorrelation is a variation of spatial analysis in which the autocorrelation coefficient is calculated for each lag (Table 6.2). This requires a specific sampling design, a regular grid or transects so that each lag is well represented. The significance of each coefficient is tested using permutations. Underwood & Chapman (1996) used univariate serial autocorrelation to examine the spatial patterns of intertidal invertebrates of rocky shores. The advantage of this approach is that it provides a precise scale of independence, although it requires a large number of samples in a regular transect or grid design in order to provide sufficient data for each lag.

The fractal dimension, D, has been used to quantify complex geometric patterns at a number of scales when the scale of measurement (the grain) influences the resulting measurement; e.g. the measurement of coastline length, or tree circumference (Sugihara & May, 1990) (Table 6.2). D is a measurement of self-similarity at different scales, or the relationship between scale of measurement and resulting measurement. Truly fractal patterns have a linear relationship i.e. D is constant. D can be valuable for documenting boundaries of hierarchical processes and, therefore, provide insight into extrapolating from one scale of measurement to another. For example, Bradbury *et al.* (1984) measured the self-similarity of coral-reef boundaries at a number of scales to determine whether there were natural scale hierarchies. They found that D was effectively constant within three scales of measurement and changed abruptly between these scales. The implication of this finding is that different ecological processes produced the self-similar patterns (Bradbury *et al.*, 1984). Burrough (1981) calculated that the relationship between the slope of the double logarithmic plot of a semivariogram m and D is given by:

$D = (4-m)/2.$

This relationship signifies that D can summarise the spatial dependence of data (at a given scale) in addition to summarising self-similarity. D is generally between 1 and 2, values of D near 1 indicate strong spatial autocorrelation, whereas values of D near 2 indicate weak spatial dependence. Palmer (1988) used values of D obtained from contiguous quadrats along transects in different plant communities to determine appropriate sampling quadrat sizes. Moreover, the use of D has been extended into measurements of populations over time and can be used to detect temporal autocorrelation (Sugihara & May, 1990). Suggestions for calculations and ecological applications of D are given by Sugihara & May (1990) and Fielding (1992).

6.7.2 Ameliorating autocorrelation problems with data

Hurlbert (1984) suggests that the primary problem with autocorrelated data is the analysis and interpretation. If data are known or suspected to be autocorrelated several techniques for analysis have been suggested. The use of permutation tests, which are distribution free, sidesteps the assumptions of normality of the classical inferential tests (Anderson. 2000). In addition, permutation tests are "valid even without random samples" (Manly, 1997, p. 1). Indeed, the Mantel-test, used extensively in this thesis, is an example of such a test. Permutation tests, including the Mantel-test, are thoroughly discussed by Manly (1997). The disadvantage of such tests is that they do not cover the full spectrum of test styles available to inferential methods, although a non-parametric multivariate analysis of variance has been developed by Anderson (2000). In addition, because they are not inferential tests, they do not necessarily provide conclusions that are applicable to a population of interest. If data are non-random, permutation tests merely suggest whether "a certain pattern of data is or is not likely to have arisen by chance" (Manly, 1997, p. 2).

An alternative technique is to alter the error term and/or degrees of freedom used in inferential tests. Effective degrees of freedom are overestimated by autocorrelated replicates, and error terms may be incorrect (see section 6.6). However, if the degrees of freedom are reduced and the error terms increased to account for autocorrelation of the data, an inferential test will become more conservative. Cliff & Ord (1973) proposed modified standard error terms to use in simple linear regression. This idea has been extended to include linear correlation, multiple regression and ANOVA (Legendre, 1993). Cressie (1991, p. 15) provided the formula for calculating the effective degrees of freedom under autocorrelated conditions.

$$n_{eff} = n/C, \text{where}$$
$$C = [1+2\{\rho/(1-\rho)\}\{1-1/n\}-2\{\rho/(1-\rho)\}^2(1-\rho^{n-1})/n]$$

where ρ is the autocorrelation coeficient and n is the number of samples

The use of alternative null models has also been advocated to overcome the problem of non-independent data (Watkins & Wilson, 1992; Palmer & van der Maarel, 1995; Roxburgh & Chesson, 1998). The standard null model is that of independently assigned data, sampled randomly from an independently distributed population. Three alternative null models, the 'patch model', the 'random shifts' model, and the 'random patterns' model have been proposed, although their usefulness has been debated (Roughgarden, 1983; Simberloff, 1983; Fox & Brown, 1995; Wilson, 1995). Roxburgh & Matsuki (1999) tested each of these null models under different levels of spatial autocorrelation by applying them to the detection of pairwise species associations. The null models were assessed by measuring the distribution of P-values when the test was applied to randomly generated data. Therefore, the probability of making a type I error under different regimes of autocorrelated data was calculated. Roxburgh & Matsuki (1999) found that spatial autocorrelation sometimes invalidated the statistical tests based on the null models, but that the influence of autocorrelation was different for the different models. For example, the patch model became more conservative with increasing spatial autocorrelation, whereas the random shifts model became less conservative. The conclusions from this work were that autocorrelation should be checked before statistical analysis, and the choice of null model should take into consideration the spatial distribution of the data. Therefore, the use of an alternative model is not necessarily valid in the presence of unquantified autocorrelation.

Although the use of non-parametric statistics and alternative analyses is increasing, and these techniques complement the inferential statistics traditionally used by ecologists, it is not ideal to sidestep the factor of space (or time) that is the root of the autocorrelation. Because spatial and temporal autocorrelation will usually have a biological basis, it seems far more sensible to incorporate potential autocorrelation in the design of sampling or experimental programs. Some suggestions for incorporating space within designs are given below.

6.7.3 Explicitly incorporating space within analyses

Space (or time) may be one of a number of possible descriptors of the distribution of a variable. It is possible to use Mantel-tests to compare matrices derived from models as well as those comprising collected spatial or temporal data (Legendre, 1993). Spatial factors, such as stream connectivity, or temporal relationships can be modelled and tested in this way. Douglas & Endler (1982) examined four competing evolutionary models for the geographic pattern of colour polymorphism in Trinidadian guppies (*Poecilia reticulata*). Each of the models was expressed as a matrix of distances and was correlated with the matrix of differences in colour polymorphisms. In this way the authors were able to demonstrate that predator density (itself related to altitude) was the likely cause of the colour polymorphisms, and to rule out historical factors and isolation by distance.

Cross-correlations examine the spatial or temporal relationship between two co-occurring variables. Rossi *et al.* (1992, p. 299) gives the formulae for calculating the cross-correlation coefficient. Following calculation of the cross-correlation coefficient, cross-variograms or cross-correlograms can be produced. As with standard variograms, cross-variograms or cross-correlograms can be all-directional or only examine one direction. Liebhold *et al.* (1995) used cross-correlograms to examine the spatial distribution of gypsy moth (*Lymantria dispar*) egg masses and tree defoliation. This analysis improved the prediction of regional defoliation by adult moths from local sampling and, therefore, led to improved pest control. Ranta *et al.* (1997a) used the cross-correlation coefficient for time series given by Chatfield (1989) to examine the synchrony of lynx (*Lynx canadensis*) population cycles over 68 years in Canada. They found that pairs of populations drifted in and out of synchrony over several generations in accordance with patterns of delayed density dependence. Koenig & Knops (1998) used modified cross-correlograms to examine cross-correlation between acorn production and tree-ring increase over a number of spatial scales and several years. In years with large acorn crops, trees had small tree-ring growth.

Extensions of the Mantel-test, also known as partial Mantel-tests, can be used to test the relationship between three variables in an analogous method to multiple regression (Smouse *et al.*, 1986) (section 2.4.1.2). Residual matrices are produced from regressions of the original matrices. The two residual matrices are tested using the standard Mantel-test. This technique explores the relationship between two matrices in the absence of an effect of the covariate matrix. In this thesis, both habitat dissimilarity and geographic distances were treated as the covariate in separate analyses to examine whether either or both were important in the absence of the other. The covariate need not be independent of either of the main factors. Similar methods have been developed by Dow & Cheverud

(1985) and Hubert (1985). Moreover, Mac Nally *et al.* (*in press*) used Mantel-tests to compare multiple matrices at once, rather than just two. In their study of the utility of ecological vegetation classes in characterising different faunal groups, they related dissimilarity matrices of bird, reptile, terrestrial invertebrate, nocturnal flying invertebrate, mammal faunas with geographic separations and habitat structure (Mac Nally *et al.*, *in press*).

Spectral analysis is a time-series analysis technique in which "the variance of the series of numbers about their mean is partitioned into contributions at frequencies that are harmonics of the length of the data set" (Platt & Denman, 1975, p. 191). This approach can also be used to examine the spatial distributions of variables. However, this technique requires sample sizes in excess of 80 (Platt & Denman, 1975). Logerwell *et al.* (1998) used spectral analysis to investigate the relationship between a seabird (*Uria lomvia*) and its prey over a number of spatial and temporal scales. Moloney *et al.* (1991) used simple models to investigate the patterns produced by patch forming processes. They showed the utility of spectral analysis in characterising the scale of ecological process under certain conditions. In addition to using correlograms, variograms, cross-correlations, partial Mantel-tests and spectral analysis to examine the spatial or temporal distribution with respect to other ecological factors, it is possible to produce predictive models on the basis of autocorrelation patterns.

6.7.4 Using autocorrelation to produce predictive models

Kriging is a form of mapping using the known spatial structure of the variable to interpolate nearby areas. The known values for local points are given weights according to their distance from the point to be estimated and a theoretical variogram that has been adjusted using the values from the variogram calculated from the region. In addition to providing estimates, this technique produces standard deviations of the estimates. Robertson (1987) provides an excellent introduction to kriging techniques. Kriging requires large numbers of samples and would be restricted to data that are easily collected, such as satellite-photograph data and automatic data logging. Kriging was used to produce a model of hydrodynamic water-quality for predicting eutrophication in Moreton Bay, Queensland (Gabric *et al.*, 1998; McEwan *et al.*, 1998). Sampling of water chemistry and current flow was conducted over 174 locations within the bay (Gabric *et al.*, 1998).

6.7.5 Specific recommendations for future research in lotic community ecology

Perhaps the most interesting question to arise from this work is whether one of the two rivers studied in this project (the Wonnangatta River) was anomalous or whether a high proportion of rivers have benthic macroinvertebrate fauna that shows no spatial dependence. Further research at the scale of rivers is needed to investigate general patterns of autocorrelation in rivers. This would provide answers about how common autocorrelation is, and perhaps in which types of rivers we might expect to find autocorrelated benthic fauna.

Another issue requiring further examination is the causes of autocorrelation in benthic invertebrates. Small scale studies (e.g. up to 5km of separation between sites) with a more comprehensive analysis of environmental variables, particularly hydraulic variables and physico-chemical variables, would be suitable to investigate environmental causes of spatial patterns. In addition, small scale studies could compare a few taxa with differing dispersal abilities to specifically investigate the role of dispersal in causing spatially autocorrelated patterns. Such studies would be limited in the choice of taxa to study because documentation of dispersal abilities exists for only a few Australian taxa.

The above suggestions for research could economise on study sites within one river by omitting the larger site separations used in this work. Results from this study indicate that sample processing time could be reduced by identification to family level only without significantly affecting the ability of the Mantel-test to detect spatial autocorrelation. This may mean that data collected for routine assessment in Australia-wide programs such as AUSRIVAS may be analysed for autocorrelation if sufficient sites along one river are sampled.

The most useful analysis techniques to pursue in freshwater research include Mantel-tests, correlograms, serial autocorrelation, partial Mantel tests and cross-correlation. The Mantel-tests' flexibility, modest requirements for sample size and analytical simplicity make it very practical to use in a number of experimental and sampling applications. Furthermore, the ability to use model matrices in addition to real data in the Mantel-test provides even greater flexibility.

Patch size is very ecologically informative and two methods are suitable for determining patch size in ecological data. Correlograms and Mantel-correlograms will provide approximate patch size without the need for excessive site numbers (30 sites are required) or grid or transect sampling design. If precise estimates of patch size are required then the best option is serial autocorrelation, which does require a grid or transect

sampling design but is, like correlograms, analytically simple.

Partial Mantel-tests and cross-correlation are the two most applicable methods for relating two non-idependent ecological variables within a spatial or temporal context. Therefore, they are particularly useful to investigate causes of autocorrelation. Partial Mantel-tests are a simple way to relate three matrices in a non-parametric analogue to multiple regression. Cross-correlation is a more involved analysis technique. Nevertheless, it has great potential to explore ecological questions that have been difficult to investigate with inferential methods. For example, Walker (1990) was able to relate the degree of closure of the Murray River mouth with changes in flow of the river, and to calculate the temporal lag between flow changes and mouth alterations.

6.8 Conclusion

Autocorrelation analysis is very useful to test spatial pattern and investigate the underlying ecological processes. Although autocorrelation is generally assumed to be ubiquitous, this is the first study to demonstrate that two neighbouring/adjacent and apparently similar systems show very different spatial patterns, in which autocorrelation (at least at scales $<$8 km) was significant in one river and absent from another river. This finding highlights the importance of quantifying spatial patterns, both for statistical considerations in study design for research in lotic habitats and ecology generally and as an important ecological phenomenon with a biological basis.

Table 6.1: Community models.

Community Model	Control	System	Role of dispersing propagules	Major factor(s) controlling community composition	Role of stochastic forces	Cause(s) of community spatial autocorrelation
Deterministic: -niche concept -keystone predator hypothesis	local	open	provision of recruits to replace aging individuals	intraspecific and interspecific competition for simple, major resources, e.g. light	none	strong autocorrelation would result from strongly autocorrelated resources
Deterministic: -habitat template models (including RCC RIVPACS, AUSRIVAS biotic integrity models)	local	open	provision of recruits to replace aging individuals	suite of environmental variables - species exist in a location if tolerant to environmental conditions (eg. physio-chemical, geomophological, substratal, hydraulic etc)	none	autocorrelation of important environmental variables will result in community autocorrelation

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Community Model	Control	System	Role of dispersing propagules	Major factor(s) controlling community composition	Role of stochastic forces	Cause(s) of community spatial autocorrelation
Non-equilibrium: -intermediate disturbance hypothesis -patch dynamics concept -disturbance-productivity-diversity model	local	open	provision of recruits to recolonise denuded patches	interspecific interactions and environmental variables determine community composition between disturbance events	important - hydrologic disturbance denudes patches stochastically (in space and time)	highly variable community structure results from frequent/patchy disturbances - autocorrelation not expected. Between disturbances autocorrelation could result from autocorrelation pattern of environmental variables

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Community Model	Control	System	Role of dispersing propagules	Major factor(s) controlling community composition	Role of stochastic forces	Cause(s) of community spatial autocorrelation
Stochastic models -competitive lottery model -equal-chance hypothesis	local	open	influence colonisation of patches stochastically	habitat provides a number of possible templates, resulting community dependent upon stochastic recruitment	important - recruitment of individuals is stochastic	weak autocorrelation may result from attenuated dispersal and/or strongly autocorrelated environmental variables. However, variability of patch composition is high because recruitment is stochastic and therefore only weakly related to supply of recruits

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Community Model	Control	System	Role of dispersing propagules	Major factor(s) controlling community composition	Role of stochastic forces	Cause(s) of community spatial autocorrelation
Dispersal models	regional	open	both emigrating and immigrating individuals strongly influence community composition of established patches in addition to denuded patches	ongoing stochastic immigration and emigration of individuals due to biotic interactions and environmental conditions	important- recruitment is stochastic and ongoing. stochastic disturbance also	attenuated dispersal provides for weak autocorrelation. Because recruitment is stochastic highly variable communities result

Table 6.2: Autocorrelation analysis techniques.

Analysis technique	Univariate or multivariate	Sites required	Aspect of autocorrelation measured	Analysis output
Mantel test	either	5	significance of linear relationship between two matrices Adv:samples need not be independant. Very widely applicable	significance test
Correlograms Mantel correlograms	univariate either	>30	compares relative strength of autocorrelation between distance categories† within study Adv:indicates approx. patch size, characeteristic shapes related to spatial distributions	graph with significance test for each point (distance category)
Modified correlograms	as above	as above	plot of autocorrelation coefficient for each distance category Adv:can be compared across studies	as above

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† category including several lags

∗ spatial or temporal distance between two sampling points

Table 6.2: (continued from previous page)

Analysis technique	Univariate or multivariate	Sites required	Aspect of autocorrelation measured	Analysis output
Semivariograms	univariate	large	average of replicate differences between values of variable for each lag∗ Adv:gives precise patch size Disadv: stationary of data required. Ecological data rarely conforms	graph of lag vs semivariance i.e. each lag distance is represented on graph
Serial autocorrelation	either- depends upon autocorrelation coefficient used	large	plot of autocorrelation coefficient for each lag (rather than distance category) Adv:provides precise patch size Disadv: study design must be transect or grid (or uniform temporal samples) to provide sufficient data points for each lag	significance test for each lag, can be graphed

continued on next page

† category including several lags

∗ spatial or temporal distance between two sampling points

Table 6.2: (continued from previous page)

Analysis technique	Univariate or multivariate	Sites required	Aspect of autocorrelation measured	Analysis output
Fractal dimension D	either	large	D is a measurement of self-similarity at different scales of measurement. Due to its linear relationship with the double log of a semivariogram it indicates the strength of autocorrelation	single value summary of strength of autocorrelation

† category including several lags
* spatial or temporal distance between two sampling points

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