

## SPATIAL SCALE OF AUTOCORRELATION OF ASSEMBLAGES OF BENTHIC INVERTEBRATES IN TWO UPLAND RIVERS IN SOUTH-EASTERN AUSTRALIA AND ITS IMPLICATIONS FOR BIOMONITORING AND IMPACT ASSESSMENT IN STREAMS

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(Received 15 February 2005; accepted 8 April 2005)

**Abstract.** Spatial autocorrelation in ecological systems is a critical issue for monitoring (and a general understanding of ecological dynamics) yet there are very few data available, especially for riverine systems. Here, we report here on assemblage-level autocorrelation in the benthic-invertebrate assemblages of riffles in two adjacent, relatively pristine rivers in south-eastern Victoria, Australia (40-km reaches of the Wellington [surveys in summers of 1996 and 1997] and Wonnangatta Rivers [survey in summer of 1996 only], with 16 sites in each river). We found that analyses were similar if the data were resolved to family or to species level. Spatial autocorrelation was assessed by using Mantel-tests for the data partitioned into different sets of spatial separations of survey sites (e.g. 0–6 km, 6–12 km, etc.). We found strong small-scale ( $\leq 6$  km) autocorrelation in the Wellington River, which is consistent with known dispersal abilities of many aquatic invertebrates. Surprisingly, there were strong negative correlations at longer distance classes for the Wellington River in one of the two summers (20–40 km) and the Wonnangatta River (12–20 km). That two largely unimpacted, adjacent rivers should have such different autocorrelation patterns suggests that impact assessment cannot assume dependence or independence of sites *a priori*. We discuss the implications of these results for use of “reference” sites to assess impacts at nominally affected sites.

**Keywords:** ausrivas, baci designs, dispersal, drift, mantel tests, oviposition, riffles, rivpacs

### 1. Introduction

Monitoring ecological condition has become an important responsibility for natural resource managers worldwide. In Australia, for example, much funding has been spent on an on-going program *The National Land and Water Resources Audit* (Commonwealth of Australia, 2001). Australia has invested significantly in both terrestrial (e.g. *Second Australian Bird Atlas*, Barrett *et al.*, 2003; vegetation condition, Parkes *et al.*, 2003) and aquatic (e.g. AUSRIVAS [Australian River Assessment System], Coysh *et al.*, 2000) monitoring protocols. The impetus underlying this work is to provide management with assessment tools usable for larger-scale assessments of ecological condition and especially to track change and potential responses to management actions.

Many monitoring protocols seek to determine impacts on the biota by comparing nominally affected sites with one or more ‘control’ locations. For example, many impact assessments are underlain by a ‘before-after-control-impact’ or ‘BACI’ construction (Underwood, 1992) in which nominally unaffected sites are used as references to assess ecological impacts at sites thought to have suffered an impact. At broader scales, freshwater ecologists have conceived of a scheme by which environmental and biotic measurements are linked such that the biota at a particular location are ‘predicted’ from physical and chemical measurements based on a collection of reference sites (e.g. Townsend *et al.*, 2003). This methodology underlies the British RIVPACS (River Invertebrate Prediction and Classification System, Wright *et al.*, 1984) and the Australian AUSRIVAS (Coysh *et al.*, 2000) protocols.

While these are laudable approaches to dealing with serious challenges, there is a problem with both the BACI and RIVPACS/AUSRIVAS logic, which relates to the potential impact on the statistical inference of spatial autocorrelation (Legendre *et al.*, 2002, 2004; Diniz-Filho *et al.*, 2003). Formally, autocorrelation is the degree to which assemblages are similar spatially and can be defined as: “when it is possible to predict the values . . . at some points of space (or time), from the known values at other sampling points, whose spatial (or temporal) positions are also known” (Legendre and Fortin, 1989). The problems are these. First, if one were use one or more locations as a ‘reference condition’ for the state of a particular site, then the sites should be ecologically autocorrelated in the absence of an impact (e.g. the constitution of the faunal assemblages should be related). If the nominal impact and reference sites were unrelated to one another if there were no impact, then of what use would the reference site be in attempting to assess whether the nominally impacted site was affected? Second, and somewhat conversely, if sites are within an autocorrelation range, then, as has been documented extensively (e.g. Cressie, 1993), the effective degrees of freedom associated with statistical tests is changed according to the level of autocorrelation,  $\rho$ . For large sample size  $N$ ,  $N_{\text{effective}} \sim N/[(1 + \rho)/(1 - \rho)]$  (Cressie, 1993). These effects can be dramatic. For example, for  $N = 10$  and  $\rho = 0.25$ ,  $N_{\text{effective}} \sim 6$ , and for  $N = 10$  and  $\rho = -0.25$ ,  $N_{\text{effective}} \sim 16.7$ .

These are the issues that stimulated our work here. While we do not attempt to provide a general analysis of methods of impact assessments, it is nonetheless true that there are very few data on spatial autocorrelation distances and levels for most ecosystems (Tobin, 2004), and especially for riverine ones with which we are concerned here. In this sense, our work is an initial foray into attempting to document the autocorrelation structure of assemblages of freshwater fauna in two rivers that are largely unimpacted.

### 1.1. ECOLOGICAL AUTOCORRELATION IN RIVERINE INVERTEBRATES

The spatial relationships between the biota at different points in a landscape tell us much about whether those assemblages are highly or only marginally

interactive in the sense that organisms move between the points (Cooper *et al.*, 1998; Lichstein *et al.*, 2002). The degree of “openness” of the local biota (*sensu* Wiens, 1984) has critical implications for the possibilities that the assemblages will be structured mainly by local processes or by processes beyond the site (Mac Nally, 1995). Statistically significant autocorrelation of assemblages implies that the systems are open and that there is movement by adults or propagules through space (Wiens, 1984; Koenig and Knops, 1998; Koenig, 1999; Perry *et al.*, 2002).

Rivers are special cases in an ecological-spatial sense because the two- or three-dimensionality of terrestrial (Legendre, 1993) or lacustrine (e.g. Kienel and Kumke, 2002) landscapes is largely compressed into one dominant direction (and one dimension), namely, downstream (Wiens, 2002). This means that one might expect that assemblages of aquatic organisms might be inter-linked because of the assisted movements through water flows (Hynes, 1970; Soininen *et al.*, 2004). Such linkages should be expressed as autocorrelation of assemblage composition.

There is an extensive literature on movement by benthic invertebrates (our focus) in rivers, especially in North American and European rivers. Movement typically is through drifting on the moving water, flight by adults, females selecting oviposition sites, and by active benthic crawling. Drifting distances are very variable, typically relatively short distances in any one action (e.g. <100 m, Townsend and Hildrew, 1976; Erman, 1986; Otto and Söderström, 1986; Jackson *et al.*, 1999). However, many organisms drift night-after-night, often leading to journeys of up to 10 km along rivers (Neves, 1979; Hemsworth and Brooker, 1979; Goedmakers and Pinkster, 1981). Distances flown by dispersing adults of aquatic insects typically are  $\leq 10$  km (Hershey *et al.*, 1993; Bagge, 1995; Delettre and Morvan, 2000), although very long flights have been recorded, possibly as adults are swept along by prevailing winds (Crosskey, 1990). Studies based on genetic analyses also suggest that several km may be the upper limit of exchanges of individuals between points within rivers (e.g. Jackson and Resh, 1992; Robinson *et al.*, 1992; Gornall *et al.*, 1998). These reports suggest that sites more than a few km apart may be effectively independent of one another, statistically and dynamically, and a few km might be the scale at which one would expect to find significant autocorrelation of invertebrate assemblages.

Autocorrelation patterns also might depend upon the degree of taxonomic resolution. Assemblages that are resolved to species may be found to be spatially autocorrelated at smaller scales than those identified to family because geographic ranges of most species are smaller than those of families. This zonation may lead to autocorrelation of more highly resolved taxonomic groups (genera or species) at scales smaller than those of larger taxonomic groups (families). In effect, the dispersal distances of families are equal to the summed dispersal abilities of the most mobile species or genera within each family, so that autocorrelation would be expected to occur at a larger scale for families.

In this paper, we focus on data from surveys of riffle-dwelling invertebrates conducted along 40-km reaches of the Wellington and Wonnangatta Rivers, two largely unimpacted rivers of south-eastern Victoria, Australia. We sought to establish whether there is strong spatial autocorrelation of assemblage composition along river lengths and if so, over what spatial scales are these relationships expressed. Do these two adjacent, largely pristine rivers have similar patterns of autocorrelation as one might expect given their generally similar taxonomic constitutions (see below)? And last, what are the implications of our findings for the application of methods such as BACI, RIVPACS and AUSRIVAS to monitoring in rivers over large spatial scales?

## 2. Materials and Methods

### 2.1. STUDY SITES

The work was conducted in the Alpine National Park, in south-eastern Victoria, Australia (Licola 37°38'S, 146°37'E). The climate is temperate with cool winters and warm, dry summers. The Wellington and Wonnangatta Rivers are south-flowing in the Victorian Alps Mountain Range. These rivers are in adjacent catchments. Both rivers are relatively unimpacted upstream of 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 is the larger river. Both rivers are fourth order at this point, but the Carey River has a higher discharge (I. C. Campbell, *unpublished data*) and the Wellington River is partially impeded because it drains from Lake Tali Karng through a natural barrier, which was caused by a rock-slide 1500 ybp (Salas, 1981). The Wonnangatta River is unimpeded. Both are spring rivers according to the classification of Haines *et al.* (1988) and, for Australian rivers, experience relatively low hydrologic variability (Hughes and James, 1989).

Discharge data from the Macalister River at Licola (downstream of the Wellington River) and Glencairn (upstream of the Wellington River) and the Wonnangatta River at Crooked River were provided by Theiss Environmental Services.

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. Notwithstanding these similarities, the rivers differ markedly in size. Where sampled, 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 rivers also occur in catchments with somewhat different geological and riparian vegetation characteristics (Table I).

TABLE I  
Characteristics of the Wellington and Wonnangatta Rivers

| Variable                                | Wellington River                                                                            | Wonnangatta River                                                                                                             |
|-----------------------------------------|---------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|
| Altitude                                | 480 m–240 m ASL*                                                                            | 340 m–260 m ASL*                                                                                                              |
| Stream order                            | 2–6*                                                                                        | 7                                                                                                                             |
| Stream width                            | 4–30 m*                                                                                     | 11–35 m*                                                                                                                      |
| Catchment area                          | 97 km <sup>2</sup> –324 km <sup>2</sup> *                                                   | 972 km <sup>2</sup> –1138 km <sup>2</sup> *                                                                                   |
| Mean daily discharge<br>(January 1996)# | 204 ML/d                                                                                    | 581 ML/d                                                                                                                      |
| Distance from source                    | 7–51 km*                                                                                    | 54–87 km*                                                                                                                     |
| Runoff/catchment area                   | 0.630 ML/d/ km <sup>2</sup>                                                                 | 0.5105 ML/d/km <sup>2</sup>                                                                                                   |
| Slope                                   | 0.68–0.79 m/100 m*                                                                          | 0.29–0.23 m/100 m                                                                                                             |
| 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                        | Quaternary alluvium and Silurian siltstone and mudstone                                     | Quaternary alluvium                                                                                                           |
| Catchment vegetation                    | Native open forest                                                                          | Native open forest                                                                                                            |
| Riparian vegetation                     | Native with limited <i>Rubus fruticosus</i> invasion                                        | Predominantly native with moderate <i>R. fruticosus</i> invasion, limited <i>Salix babylonica</i> and pasture grasses planted |

Discharge data from Theiss Environmental Services, \*Range is from uppermost site to lowermost site.

#at Licola downstream of the Wellington and Macalister confluence.

## 2.2. SAMPLING DESIGN AND PROCESSING

### 2.2.1. Spatial Sampling Protocol

A 40 km length was selected in both rivers and divided into eight contiguous 5 km sections. The 40 km lengths began at the uppermost accessible part of the river. The entire studied length of both rivers is accessible on foot, so randomly selected sites were sampled. In order to prevent overlap of sampling in two adjacent sections, 500 m at each end 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 found 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 that set of riffles. These methods therefore yielded 16 sites per river per season. While Legendre and Fortin (1989) recommended at least 30 sites for autocorrelation analysis, this is a heuristic and strong patterns, if they occur, may well emerge from sets with fewer than 30 sites (J. A. Diniz-Filho, pers. commun.).

### 2.2.2. Temporal Sampling Protocol

Sampling was conducted in the austral summers of 1995–1996 (January 26 to February 14, 1996) and 1996–1997 (February 4–12, 1997). After processing a fraction of the 1996 samples, we estimated that samples could not have been processed in a reasonable time-frame if both rivers were resampled in 1997. Therefore, we chose to survey only the Wellington River in the second year because we were interested in having some information about temporal repeatability of patterns.

The sampling order of sections within each river was partially randomized. We sampled two or three sections consecutively from each river in order to minimize travelling time between the two rivers and to keep the entire sampling period as short as possible. The sampling seasons were kept brief to decrease potentially confounding factors of major changes in weather, spates and insect emergence.

The distance between the two riffles sampled in a section was paced out. The map coordinates of the riffles were ascertained by reference to topographic features. Signal distortion by the steep valley walls precluded the use of a global positioning system to calculate position. Digital image analysis of the map with marked coordinates was used to measure river distance between sampling points (Logan, 2000).

### 2.2.3. Invertebrate Sampling

Invertebrate assemblages were sampled by using a Surber sampler (Surber, 1937). Justification for its use is given by Lloyd *et al.* (in review). The frame was placed against the substrate with the net attached to the rear. 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 2 min. All detached material was collected in the net. Animals attached to the rocks were removed by hand and included in the sample, which was washed thoroughly with water to separate organic and inorganic components. The organic component was retained and preserved in 2% formalin (in 1996) or 70% ethanol (in 1997).

Five Surber samples were taken at each riffle using a 22.5 cm × 22.5 cm Surber sampler with 300 μm mesh. Five samples were considered sufficient to characterize 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 (Lloyd, 2001: Figure 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 (see also Metzeling *et al.*, 1984).

#### 2.2.4. *Sample Processing in the Laboratory*

Samples were washed thoroughly on a 300  $\mu\text{m}$  sieve and sub-sampled. Sub-samples of 25% (Wrona *et al.*, 1982) were examined using a binocular dissector. Every invertebrate was identified to the lowest taxonomic level. This most often was to species level, but for some difficult taxa (e.g. Chironomidae), generic identification was used. Subsampling was used because samples contained large amounts of organic material and many invertebrates. Sufficient characterizations of samples have been obtained with 25% subsamples in previous Australian studies (Marchant *et al.*, 1989, Walsh, 1997). Subsamples produce results almost indistinguishable from full samples based on a pilot analysis (Lloyd *et al.*, in review).

### 2.3. STATISTICAL METHODS

We present results for two data sets for each of the three river-by year-combinations. These data are resolved to the family level and to the species level but exclude any taxa that were recorded at only one site in a given river-by-year combination. We refer to these data sets as non-unique, family-level or species-level sets.

#### 2.3.1. *Dissimilarities and Distances*

Sixteen sites yield  ${}^{16}\text{C}_2 = 120$  site-pair combinations. There were two matrices of site-pair distances relating to: (1) geographic distances between each pair of sites (in m along the rivers); and (2) invertebrate assemblage dissimilarities between each pair of sites. For (2), Bray-Curtis dissimilarity indices were calculated between all pairs of sites, employing the fourth-root transform of abundances as the basic information (see Clarke and Gorley, 2001). The Bray-Curtis dissimilarity index is a measure of the assemblage dissimilarity between sites (Clarke, 1993). This index has been found to be sensitive to community differences and is robust to noise (Hruba, 1987; Pontasch and Brusven, 1988; Faith *et al.*, 1991).

#### 2.3.2. *Autocorrelation analysis*

Autocorrelation-analysis was based on Mantel's test, which tests for linear relationships between two sets of distance-based data (Mantel, 1967). The normalized Mantel-test statistic is that given in Legendre and Legendre (1998). This statistic was tested for statistical significance by comparing it to a distribution obtained by randomly permuting the data and recalculating the test statistic many times ( $N = 1999$  in our tests) for those permutations using the R-package software (Casgrain and Legendre, 2001). If the null hypothesis of no correlation between the two sets of distance values is correct, then the value of the test statistic for the observed data,  $R_{\text{obs}}$ , would not be in the upper tail (5%) of the distribution of values for  $R$  calculated from the randomly permuted data (Sokal, 1986). Although the Mantel-test makes no assumptions about the distribution of the variables tested, the test assumes a linear relationship between the two variables. Scatterplots were used to check whether the relationship appeared linear.

We emphasize that because the analyses map faunal dissimilarity onto spatial separations, a positive autocorrelation indicates that the fauna become more dissimilar (i.e. less similar) the further sites are apart. Conversely, negative autocorrelation suggests that the fauna are less dissimilar (more similar) the further apart they are.

### 2.3.3. *Influence of Spatial Scale on Relationships*

Autocorrelation may be detectable statistically only at certain scales, and in this section we describe our methods for undertaking scale-dependent analyses, which are similar to previously published studies (e.g. Pinckney and Sandulli, 1990, Wildi, 1990; Koenig, 1999). We first grouped site-pairs into distance classes and only the values of geographic distance and invertebrate dissimilarity within a particular distance class were used to calculate the Mantel  $R$ . Subsets of the data were created and linear Mantel correlations were tested within these specified intervals.

Site-pairs for each of the three rivers-by-years sampling programs 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 because they contained approximately equal numbers of site pairs for all scales for all sampling seasons, so that all tests had similar statistical power (Legendre and Fortin, 1989).

The multiple-scale tests involve re-use of the data up to four times, so we employed adjustments for Type-I error rates (Legendre and Fortin, 1989) using Holme's modified-Bonferroni protocol (Holme, 1979).

## 3. Results

### 3.1. INVERTEBRATE FAUNA OF THE WELLINGTON AND WONNANGATTA RIVERS

Taxa were predominantly insects from the orders of Ephemeroptera, Plecoptera and Trichoptera (collectively referred to as EPT), Coleoptera, Diptera, Odonata and Megaloptera. Other important components were the orders Hydracarina and Oligochaeta. Ephemeropterans, trichopterans and dipterans were the most abundant taxa, while the trichopterans and dipterans were the most species-rich groups. Thus, the proportion of EPT taxa was high for both abundance and taxonomic richness. Few individuals of the Platyhelminthes and Nematoda were collected. The Wellington River 1996 samples yielded 209 morphospecies from 50 families. There were 180 morphospecies from 49 families in the Wellington River data in the 1997 sampling season. The Wonnangatta samples yielded 150 morphospecies from 43 families (lists available from second author).

Many taxa (128 morphospecies) were found in every sampling event. However, six taxa were unique to the Wonnangatta 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 (list available from second author).

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

### 3.2. FAMILY-LEVEL RESOLUTION

Spatial autocorrelation of the benthic invertebrate fauna was deemed statistically significant for the smallest scale (0–6 km) of geographic separations for the Wellington River in both 1996 and 1997 (Table II) for the four-interval analysis. There was little evidence for relationships between geographic distance and invertebrate dissimilarity in either year for intermediate scales (6–12 km, 12–20 km). The invertebrate assemblages separated by the largest geographic distances (20–40 km) were negatively autocorrelated in 1996 but not in 1997, notwithstanding larger sample sizes in the latter (Table II). The invertebrate assemblages of the Wonnangatta River were autocorrelated only at the 12–20 km distance class; again this was a strong negative correlation (Table II).

### 3.3. SPECIES-LEVEL RESOLUTION

The results of all Mantel-tests performed at species-level were virtually the same as the results from the tests at family-level resolution (Table II).

TABLE II

Mantel tests for species and family-level invertebrate data-sets for the four-partition scale analyses, with numbers of site-pairs per distance range in parentheses

| Geographic distance range | Wellington River |             |            |            | Wonnangatta River |             |
|---------------------------|------------------|-------------|------------|------------|-------------------|-------------|
|                           | 1996             |             | 1997       |            | 1996              |             |
|                           | Species          | Family      | Species    | Family     | Species           | 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)   |

\*Deemed statistically significant. Type-I error rate,  $\alpha$ , was corrected for multiple tests by using the sequential Bonferroni method of Holme (1979).

## 4. Discussion

### 4.1. SPATIAL SCALES OF AUTOCORRELATION

The patterns of invertebrate autocorrelation in the two rivers were to us unexpected. The consistent (both summers) small-scale ( $\leq 6$  km) positive spatial autocorrelation in the Wellington River assemblages is potentially explicable by the known scales of dispersal documented for benthic invertebrates (Section 1). Therefore, drift, flight by adults and benthic movements are consistent with, and may account for, the pattern of spatial autocorrelation seen in these invertebrate assemblages. This was a not unexpected result. However, the absence of small-scale positive autocorrelation in the Wonnangatta River was not anticipated and seems hard to explain given the faunal similarities between the rivers (Section 3.1).

Even more unexpected was the appearance of *negative* spatial autocorrelation at scales exceeding 20 km in the Wellington River in 1996 (but not 1997) and between 12–20 km in the Wonnangatta River in 1996. Negative spatial correlation indicates, over the spatial ranges involved, that the faunal assemblages become more similar (or equivalently, less dissimilar) the further they are apart. Unfortunately, with only a single summer's data for the Wonnangatta River it is difficult to assess whether that pattern would be a consistent one, but the negative correlation was the greatest absolute value ( $-0.53$ ) recorded in any of the twelve comparisons for each of the taxonomic resolutions. This may indicate that the results are likely to be consistent from year to year. Our univariate analyses of autocorrelation of environmental features cannot account for these negative autocorrelations because only *positive* significant autocorrelations were found (i.e., width of riparian zone, retentivity, substrate composition, sediment; see Table V of Lloyd *et al.*, in press).

Our results suggest that the two rivers have different autocorrelation structures, with evidence for pronounced positive autocorrelation at small scales for the Wellington River but not the Wonnangatta Rivers, and larger-scale negative autocorrelation for both rivers, at least in some years. Given the overall faunal similarities, it seems possible that the differences relate to the different physical structures of the rivers. The sampling of the Wellington River spanned five river orders, while the Wonnangatta, where sampled, was of one single order (seven) (Table I). Another major difference is that there are 17 tributaries flowing into the surveyed section of the Wonnangatta River, but only twelve into the Wellington River (Table I).

Tributaries may influence the availability of drifting invertebrates and change physical, chemical and hydraulic factors and stream communities in the main channel downstream of the junction (Rice *et al.*, 2001; Poole, 2002), potentially diminishing the potential for autocorrelation to occur. The possible role of tributaries in producing discontinuities (Poole, 2002) may be more pronounced in the Wonnangatta River than the Wellington River due to the section of each river sampled. The Wonnangatta River was sampled along a flatter portion (elevation range of 80 m)

of its longitudinal profile than was the Wellington River (elevation range of 240 m) (Table I). This may mean that spatial patterns of near-bed hydraulic variables, which are influenced by the average slope of a river section (Statzner and Higler, 1986) and have been very important in influencing invertebrate fauna in other studies (e.g., Statzner and Borchardt, 1994; Doisy and Rabeni, 2001), were more affected by the incoming tributaries of the Wonnangatta River than the Wellington River.

Whether these physical factors can account for the unexpected negative correlation at larger spatial scales requires further analysis, possibly linked to the spatial separations and configurations of confluences and the degrees to which physical, chemical and faunal impacts of the confluences are manifested downstream (Poole, 2002).

Our results indicate that there most likely will be idiosyncratic patterns of spatial autocorrelation in different rivers, even those for which human impacts are slight (like ours). This suggests that one cannot assume *ab initio* the nature of spatial autocorrelation in a given target river and, even more unfortunately, that heavily degraded rivers for which prior information is unavailable will be difficult to treat correctly in a monitoring program.

#### 4.2. CORRELATION “LENGTHS”

Notwithstanding its importance to characterizing the “openness” of ecological assemblages (Wiens, 1984), spatial autocorrelation at the assemblage level has not been as widely studied as one might have hoped (Storch *et al.*, 2002), and there are few reports on correlation lengths in different ecosystem types and taxa. We are not aware of any compilation of correlation lengths of ecological assemblages. Our results indicate a positive correlation distance of about 6 km in one of our rivers (Wellington) for stream invertebrates, which was consistent for family and species-level taxonomic resolutions. It is difficult to make much sense of the larger scale negative correlations apart from the potential impact river physiognomy.

We know of few comparable estimates in autocorrelation lengths streams, although there is a smattering of values from other ecosystems. Kienel and Kumke (2002) reported significant spatial autocorrelation in diatom assemblages in a Siberian lake at scales of up to 55 km. Lekve *et al.* (2002) stated that coastal fish assemblages in the Baltic Sea had correlation lengths of ca tens of km, although these assemblages also were influenced by regional-scale hydrodynamic processes. Franklin and Mills (2003) described very small scale correlation lengths in analyses of DNA similarities of soil microbial assemblages, typically <6 m. There are likely to be many sources of data from which to estimate spatial correlation lengths, especially for large data compendia such as the Christmas Bird Counts in North America and the Birds Australia Atlas scheme (Barrett *et al.*, 2003). Relating correlation lengths of assemblages to geographic, climatic and edaphic variation and to taxonomic characteristics (body size, mobility, lifetime) would seem to be a field that is underdeveloped and may provide much more information than analyses of

either species-specific or species-richness biogeographic analyses (Lichstein *et al.*, 2002; Tobin, 2004).

#### 4.3. SPECIES VS FAMILY LEVEL RESOLUTION

The consistency between family- and species-level analyses of scale may be the result of species within families having similar dispersal distances and habitat requirements, contrary to expectations (i.e. characteristics of families should be supersets of any individual species within its family). Few data are available for Australian taxa, but most species appear to have limited dispersal ability compared with the families to which they belong (e.g. Crosskey, 1990). 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 disperse and colonize 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 among constituent species of a given family. For example, beetles of the subfamily Elminae were an important component of the fauna found in the Wellington River. These animals do not fly as adults (Glaister, 1999). 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, have a high propensity to drift (Hynes, 1970; Brittain and Eikeland, 1988) and some species have been recorded drifting 50–60 m overnight (Waters, 1965). Baetid adults from the northern hemisphere fly 1.9 km (Hershey *et al.*, 1993) to 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.

Relatively coarse taxonomic resolutions (family-level) provided similar inferences to resolutions to the finest available levels (species or morphospecies). Our results showed that one cannot assume that rivers even in nominally good condition and subject to relatively little anthropogenic disturbances will have similar longitudinal patterns of faunal distributions. Many other rivers need to be analyzed in comparable ways to the methods we have used so that we can assess whether the disparate spatial structures of autocorrelation of the two rivers upon which we report is typical. If even similar rivers have such dissimilar patterns, then the potential for generalization seems slight.

## 5. Conclusions

How do our results relate to the use of benthic stream invertebrates for monitoring using a BACI (Underwood, 1992), RIVPACS (Wright *et al.*, 1984) or AUSRIVAS (Coysh *et al.*, 2000) protocol? If there were no intermediate to longer scale negative autocorrelation, then our interpretations would be easy to express. Given the consistent small-scale ( $\leq 6$  km) patterns in the Wellington River, only sites in the Wellington River  $>6$  km apart are likely to be effectively independent of each other with respect to the composition of invertebrate assemblages. Therefore, such sites could be used in studies where the results are tested using classical inference (e.g. BACI designs). On the other hand, if one wishes to use the fauna present at one or more sites to “predict” the fauna that should occur at a test site (e.g. as “reference” sites for the AUSRIVAS or RIVPACS protocols), the sites should be situated  $\leq 6$  km. Conversely, sites at any separation are statistically independent in the Wonnangatta Rivers and so, could be used for classical inference but clearly not for the AUSRIVAS or RIVPACS protocols.

The presence, though inconsistent, of larger-scale *negative* autocorrelation in the Wellington River, and also in the Wonnangatta River in the only sampled summer, renders such a simple conclusion potentially invalid. Such autocorrelation structures have been rarely considered before and the implications are that one needs very detailed ecological and physical knowledge of a given river before making statistical assessments. For example in the Wonnangatta River, the invertebrate assemblages are more similar at 20 km separations than at 12 km distances, which implies that a better reference site for a given point is one 20 km away than one much nearer (12 km). If this were consistent through time, then one could be confident that the distant sites are good models and nearer ones less useful. We need more rivers sampled more frequently to make clearer judgments on such counter-intuitive outcomes.

## Acknowledgments

We acknowledge the financial support of the Cooperative Research Centre for Freshwater Ecology and the School of Biological Sciences, Monash University. The following provided important guidance on our thinking or provoked us to consider alternatives: Pierre Legendre, Marie-Josée Fortin, and Phillippe Casgrain, Richard Norris, and Tony Underwood. The following persons made invaluable contributions to this project: Ian Campbell, Murray Logan, Leon Barnuta, Edward Tsyrlin, Simon Treadwell, Michael Shirley, Miryl Parker, Elizabeth Lloyd, Adam Shirley, Alena Glaister, Daryl Nielsen, Mark Harvey, Rhonda Butcher, Kylie Lewin, Peter Cranston, Tanya Rankin, Barbara Dworakowski, Shane Brooks, and John Shirley. This is publication number 77 from the *Australian Centre for Biodiversity: Analysis, Policy and Management* at Monash University.

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