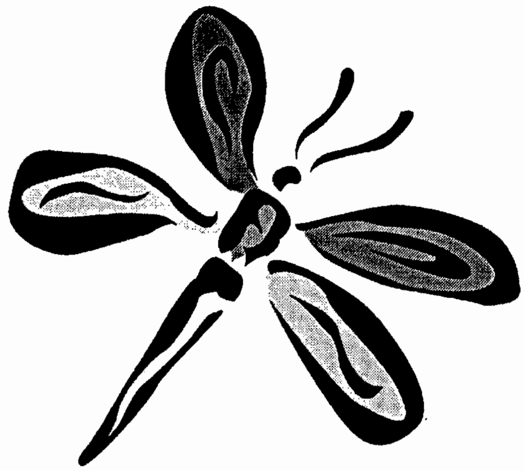

SCALES OF MACROINVERTEBRATE DISTRIBUTION IN RELATION TO THE HIERARCHICAL ORGANISATION OF RIVER SYSTEMS

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PhD Thesis

Cooperative Research Centre for Freshwater Ecology

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May 2001

ABSTRACT

The distribution of macroinvertebrate communities is influenced by a myriad of abiotic environmental factors. However, many of these environmental factors do not occur randomly within a river system. Rather, they occur as a result of geomorphological processes that operate hierarchically to constrain the expression of environmental factors at successively nested levels. As a result of the hierarchical expression of geomorphological processes, environmental factors occur at characteristic scales within a river system and can be used to define spatial scales of river system organisation. Previous studies have examined multiscale patterns of benthic macroinvertebrate community distribution using scales of measurement such as ecoregions, catchments, rivers, reaches and functional habitats. However, none of these studies used scales derived from a geomorphological hierarchy to examine patterns of macroinvertebrate distribution. Given that macroinvertebrates are often deterministically influenced by environmental factors, and these environmental factors occur at characteristic scales within a geomorphological hierarchy, it is possible that the multiscale distribution of macroinvertebrate communities may correspond to the hierarchical arrangement of a river system. This study used scales of measurement derived from a geomorphological hierarchy to examine whether there was any congruence between the distribution of macroinvertebrate communities and the organisation of a river system at the catchment, zone, reach and riffle scales.

The Upper Murrumbidgee River Catchment study area (13 005km^2) was divided into catchments, zones within catchments, reaches within zones and riffles within reaches. Macroinvertebrate collection was stratified across these scales according to a balanced nested hierarchical design, and environmental data were also collected at the catchment, zone, reach and riffle scales. Simultaneous multiscale treatment of biological and environmental data allowed identification of multiscale patterns of macroinvertebrate distribution in relation to the hierarchical organisation of a river system, as well as identification of hierarchical interactions between macroinvertebrate communities and environmental factors. Multivariate (ANOSIM, classification, ordination) and univariate (Nested ANOVA) statistical techniques were employed, and each analysis was performed at the species and family levels of taxonomy.

Macroinvertebrate communities were highly similar within a reach, because this is the point in the geomorphological hierarchy where environmental conditions become more homogeneous, relative to larger scales. Conversely, communities were dissimilar at the larger zone and catchment scales because environmental conditions become more heterogeneous, relative to smaller scales. However, the reach within zone scale also represents the point where sampling reaches become distinct across the landscape, and the similarity of macroinvertebrate communities within a reach may also be related to the spatial proximity of samples. Hence, macroinvertebrate community distribution is only congruent with the smaller scales of river system organisation.

Despite the lack of congruence between macroinvertebrate community distribution and the larger catchment and zone scales of river system organisation, there was a strong regional pattern of distribution in the Upper Murrumbidgee River Catchment. This regional-scale pattern self-emerges from biological information, and is larger than the geomorphologically derived catchment scale. Partitioning of macroinvertebrate data into regional groups subsequently revealed some congruence between macroinvertebrate distribution and the catchment and zone scales of river system organisation. An alternative hierarchy consisting of biological regions, biological clusters, geomorphological reaches and geomorphological riffles was marginally better able to capture patterns of macroinvertebrate distribution than the original catchment, zone, reach and riffle scales. Thus, consideration of the hierarchical organisation of stream systems from a purely physical perspective may fail to encompass scales that are relevant to biota, and biological information should be included as a primary hierarchical component of landscape-scale studies of macroinvertebrate distribution.

The pattern of region and reach-scale macroinvertebrate distribution was matched by a general pattern of large catchment and local reach-scale environmental influence. This occurred despite testing of catchment, zone, reach and riffle-scale environmental variables against both the scaled and non-scale pattern of macroinvertebrate distribution. Macroinvertebrate communities were influenced by local reach-scale characteristics such as riparian vegetation character and channel morphology, but riffle-scale hydrological variables were also associated with some headwater communities. However, macroinvertebrate communities also sit within a broader landscape context and are influenced by large catchment-scale factors such as landuse, or by factors indicating the geographical position of the sample or the size of the stream. The large and local-scale environmental variables that influence macroinvertebrates are related within a geomorphological hierarchy, and macroinvertebrates may respond deterministically to the same type of environmental factor expressed at different scales. These responses should not be treated as statistical correlates, but rather, they should be viewed in the context of a hierarchy of river system organisation.

There was little difference in the overall scale-related findings between species and family level. Family-level macroinvertebrate communities were similar within a reach and dissimilar among reaches, zones and catchments and there was a large regional-scale pattern of family-level community distribution. Local reach-scale and large catchment-scale environmental factors were most strongly associated with family-level macroinvertebrate distribution. Replication of these scale-related findings at both levels of taxonomy indicates that aggregation from species to family level does not result in loss of ecological information pertaining to primary hierarchical patterns. However, the difference between species and family level was pronounced when tracing the hierarchical occurrence of individual taxa, in the context of theories such as the landscape filters hypothesis and habitat based model. In particular, there was a shift in the scale at which families began to be removed from the hierarchy from the region to the smaller cluster scale. This shift was related to the lowered distinctiveness of family-level regional macroinvertebrate groups, but also suggests that environmental filters may act differently on species and families. The use of family-level data is not recommended for the testing of theories of hierarchical taxon occurrence, because these theories rely on the accurate detection of precise macroinvertebrate-environment relationships.

The use of scales of measurement derived from a geomorphological hierarchy provides a process-based foundation for marrying the biological and physical domains, and for examining the hierarchical interactions that may occur between these domains. However, the results of this study indicate that overlaying the biological and physical domains is not a straightforward task, because the biological domain may be influenced by factors other than the deterministic relationship between macroinvertebrates and environmental conditions. Regardless, this study has taken some basic principles of fluvial geomorphology and incorporated them into the design of a standard stream ecology study. Given the relatively advanced state of knowledge that exists individually in the disciplines of fluvial geomorphology and stream ecology, integration and application of concepts across disciplines represents an exciting future opportunity in aquatic science.

ACKNOWLEDGMENTS

A PhD is an epic journey, along a road littered with emotional landmines, academic debris and physical barricades. It is the role of the supervisor to help navigate the student around these obstacles and lead them safely towards the final destination. My supervisors, Richard Norris and Martin Thoms, have been wonderful guides and have generously and openly provided expert knowledge, support, friendship and advice on all legs of the journey. Along the way I have learnt many lessons from you, not all of which were about science, but all of which I will treasure. In particular, I thank you for your patience and understanding during my episodes of road rage, when I wanted nothing more than to ram this PhD off the road and over a cliff. Thanks also to the CRC for Freshwater Ecology, and to Peter Cullen, for providing many tangible and intangible opportunities and resources. Financial support for this study was provided by a CRC for Freshwater Ecology Postgraduate Scholarship and an Australian Postgraduate Award.

For assistance with fieldwork, a huge thank you must go to Melanie Stutsel, Cathy Francis, Kylie Peterson, Matt Hensalite, Chris Williams, Louisa Oswald, Lorne Doig, Ken Thomas and Elizabeth Kimberly. This project would not have been possible without your help to weigh tonnes of sediment, collect duplicate kicknet samples, measure riffle gradients and laugh with me (and at me!) when things went wrong. Thanks also to the many land-holders and management authorities who allowed access to various rivers. In particular, thank you to Wayne West for a memorable stay on the banks of the beautiful Goodradigbee River.

Many other people helped with aspects of the project including the pilot study, mapping work, administration, taxonomy, data collection and computing. For your contribution to these tasks, thank you to Nerida Davies, Bob Parsons, Robyn Bevitt, Oscar Mamalai, Heather McGinness, Sean Grimes, Mat Allanson, Kate Roberts, Vic Hughes, Cindy Hazell, Phil Sloane, Craig Johnston, Nicole Norris, Jo Berryman, Karen Markwort, Sue Nichols, Dan Mawer, Julie Coysh, Meredith Walton, Dianne Flett, Claire Townsend, Melanie Saxinger, Paul Blackman, Simon Hogan, Kristine Phan, Craig Miller, Gill Eades, Gypsy Bhalla, Leah Moore, Ian Lawrence, Mike Palmer-Allen and Paul Sheehan.

Statistical advice was patiently and cheerfully provided by Wayne Robinson, Arthur Georges, Richard Marchant and Ken Thomas. Discussions with Lisa Evans, Patrick Driver, Justen Simpson, Daryl Nielsen, Chris Wilson and Iwona Ciesielka also led to an increased level of statistical clarity, ecological understanding and personal harmony. When statistics became too much to bear, Victoria, Emma, Geri, Mel B. and Mel C. provided diversionary fun and J. Springer put some perspective back into life during those laborious and emotionally charged writing days.

On a personal note there are several people who also helped to create a clear road along which to travel. Most significantly, thank you to Michelle for your wisdom and insight, and for helping me to know the wider implications of what I was doing. Thank you to Freyja for your selfless and unconditional gifts. Thank you to Jacqui, Craig, Sue, Bronwyn, Nicky and Pam for your unending encouragement, support, understanding and patience. Thank you to my family for teaching me that I could do anything, and be anything I wanted. Finally, thank you to Melissa for your perseverance, belief and determination to find some light in the darkness that is a PhD, and for being willing to learn how easy it is for a sparkling soul to die when it endures something that it does not love.

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