Freshwater Biology (1997) **37,** 107–111

SPECIAL APPLIED ISSUES SECTION

Catchment-scale analysis of aquatic ecosystems

J. DAVID ALLAN AND LUCINDA B. JOHNSON
School of Natural Resources & Environment, The University of Michigan, Ann Arbor, MI 48109–1115 U.S.A.
Centre for Water and the Environment, Natural Resources Research Institute, University of Minnesota, 5013 Miller Trunk Highway, Duluth, MN 55811 U.S.A.

Introduction

Aquatic ecologists have a rich history of including a landscape perspective in theories about lakes and rivers. Position in the landscape and underlying geology provided critical insights into differences among lake types that led to the formation of lake trophic classification (Wetzel, 1983). Comparative studies of multiple lakes within a single lake district lent much impetus to the development of limnology since the early twentieth century (Pearsall, 1930; Macan, 1970), and continues to be a useful approach to this day (Schindler *et al*., 1990). Early studies of riverine systems emphasized physical and biological changes that occurred along a river's course (Huet, 1949; Illies & Botosaneanu, 1963), leading to the formulation of the River Continuum Concept (Vannote *et al*., 1980), the template of which is longitudinal position. Some 20 years ago, Hynes (1975) synthesized then current knowledge of landscape–stream interactions to argue with lasting effect that, 'in every respect, the valley rules the stream'. Investigations of the land–water ecotone continue to progress on these firm foundations. The field gains new impetus from the growing realization that large-scale, human alteration of landscapes has widespread implications (generally negative) for the well-being of aquatic ecosystems (Naiman *et al*., 1995). On a positive note, however, technical and conceptual advances continue to improve our ability to study and understand the linkages between landscapes and freshwater ecosystems. The following series of papers addresses such issues and points to future directions for this important area of inquiry.

A focus on the influence of the landscape on riverine and lake ecosystems leads quickly to questions regarding the appropriate scale of investigation (Levin, 1992), and ultimately, of management as well. The riparian or streamside corridor obviously is important; the land–water interface, or ecotone (Naiman & Décamps, 1990), directly influences critical processes such as organic matter inputs, shade and nutrients (Sweeney, 1992; Osborne & Kovacec, 1993). But the entire catchment also influences the rivers and lakes within its boundaries, via larger-scale controls on chemistry, hydrology and sediment delivery. The landscape influences its water bodies through multiple pathways and mechanisms, operating at different spatial scales, and at present there is only a limited understanding of how these inter-relate. A spatial conceptualization of aquatic ecosystems suggests a hierarchical organization of physical units, perhaps most clearly captured for rivers in the hierarchy: habitat–reach–segment–subcatchment–basin (Frissell *et al*., 1986; Hawkins *et al*., 1992), and in the nested classification of stream order (Strahler, 1964). Allan, Erickson & Fay (1997) and Johnson & Covich (1997) point out that particular mechanisms of landscape–freshwater interactions operate at different scales. For example, inputs of coarse particulate organic matter depend upon local, streamside vegetation, whereas hydrologic regime (which affects sediment delivery and channel conditions) is the product of regional climate, geology and vegetation. Whether and how these processes might be hierarchically structured requires much more investigation across multiple spatial scales.

Tools and approaches

Spatial analysis takes place as an almost subconscious activity whenever we gaze across a landscape from some vantage point. However, geographical information systems (GIS) and image processing (IP) together provide powerful new tools for development and analysis of spatial data (Johnson & Gage, 1997), enabling researchers to address multiscale issues much more effectively. Aerial photography (since early in this century) and satellite imagery (since about 1970) now produce geographically referenced images of increasingly fine spatial resolution and information content from the use of multiple wavelengths. Indeed, the present availability of spatial data, incremented at time intervals often as short as days to weeks, seriously challenges our ability to manage, let alone analyse, this rich source of landscape information. Fortunately, powerful tools are available to aid in the development and analysis of spatial data (Johnson & Gage, 1997). The ability to integrate GIS with a variety of mathematical models further expands the utility of GIS for describing, understanding and predicting spatial phenomena. Landscape data also present an array of challenges for statistical analysis. Spatial statistics, multivariate statistics, structural equation modelling and fuzzy logic are just some of the tools reviewed by Johnson & Gage that hold promise for understanding landscape influences upon aquatic ecosystems.

Wiley *et al.* (1997) have combined spatial analysis of landscapes with traditional tools for site-specific analysis of aquatic ecosystems to argue that viewing the same ecological system from both a site- and landscape-scale perspective can lead to contradictory interpretations concerning factors shaping communities. At the largest spatial scales, species assemblages appear predictable, and governed by large-scale patterns in hydrology and geology. In contrast, site-based studies tend to reveal high variability, and emphasize the importance of local physical and biological factors. Wiley and colleagues suggest that only by having both spatially (landscape-scale) and temporally (repeated site-based sampling) intensive data sets can one quantify the relative importance of these two perspectives. Using factorial analysis of variance to decompose variance for two fish and three insect data sets from a series of streams in Michigan into time, space, and time–space interactions, they show that each taxon had a unique variance structure, and also that the observed variance structure was strongly influenced by sampling effort. In the absence of temporal sampling, all variance is accounted for as spatial variance, and vice versa. Their analyses of coldwater streams in Michigan suggest that extensive temporal sampling (at least 15–20 years for fish, and 5–7 years for insects) is necessary to stabilize estimates of variance structure (Wiley *et al*., 1997).

Landscape–river interactions: findings

Johnson & Covich (1997) undertook a spatially hierarchical analysis of the influence of riparian vegetation upon organic matter abundance in a prairie river in Oklahoma, U.S.A. The river continuum concept (Vannote *et al*., 1980) provides a useful overview of expected changes in the supply of coarse (CPOM) and fine (FPOM) particulate organic matter along a river's length. However, prairie rivers may differ from rivers of the deciduous biome in having less forest within their headwaters (Wiley, Osborne & Larrimore, 1990). Equally important, human activities have fragmented and restricted the extent of riparian vegetation over much of the landscape. Using hand-held sighting tubes to estimate canopy cover over 50 m reaches and SPOT satellite imagery to quantify vegetation within a 150 m wide corridor extending 500–2000 m upstream of a site, Johnson & Covich show that these estimates are largely independent. Suspended leaf litter was best estimated from vegetation 500–1000 m upstream of a sampling site, leaf fragments were best predicted by longitudinal position (an even larger spatial scale), and site vegetation proved to be an ineffective estimator of either. These authors conclude that control of coarse organic matter abundance needs to be placed in a hierarchical context where distance downstream is the large-scale control, riparian forest cover the meso-scale control, and retention is the fine-scale mechanism regulating detritus distribution. Owing to the paucity of woody debris, this particular river exhibited low retentiveness, hence processes operating at larger spatial scales were most critical to organic matter dynamics.

Glacial geology and extent of agricultural land use were demonstrated to be effective predictors of some water chemistry variables within multiple subcatchments of the Saginaw River basin in central Michigan (Johnson *et al*., 1997). However, specific relationships depended upon the variable and changed seasonally, indicative of differences in driving mechanisms. For example, nitrogen concentrations, alkalinity and TDS were more sensitive to agricultural land use during the summer and to underlying geology during the autumn, presumably reflecting seasonal changes in controlling mechanisms. In this catchment, land use within the riparian region and throughout the catchment were equally effective predictors of total nitrogen, nitrate, orthophosphate and alkalinity. However, some variables (total phosphorus and total suspended solids) were better explained by land use within the riparian region than by catchment-wide variables, indicating the dominance of local controlling mechanisms; whereas others (ammonium and total dissolved solids) exhibited the opposite pattern, indicating regional control.

Kratz *et al.* (1997) provide an intriguing demonstration of how a landscape attribute—hydrologic position within the regional flow regime—can affect many physical, chemical and biological properties of lakes. In a groundwater-dominated lake district of northern Wisconsin, lakes high in the landscape receive more of their input waters from precipitation, whereas lakes lower in the landscape are more influenced by groundwater. Concentrations of base cations (calcium and magnesium) and silica are demonstrably influenced by lake position, and are differentially affected by extended periods of drought. The biological implications are diverse, ranging from the vertical extent of primary production, to the distribution of crustaceans, to the robustness of spicules that can affect the vulnerability of freshwater sponges to grazing snails. Groundwater inputs, determined by topography and geology, likewise were important to the ecology of Michigan streams studied by Wiley *et al.* (1997). By strongly influencing the range of discharge and temperature conditions, landscape measures derived from geology predicted the location of cold-water stream fish assemblages with a high degree of accuracy.

Studies of aquatic insects and fish, using various metrics derived from taxonomic collections, provide further evidence that measurements of both landscape and local variables are useful predictors of biotic variables. Physical features of local habitat have long been considered the 'template' for local biotic diversity (Southwood, 1977), and this increasingly has been formalized by stream ecologists into habitat assessment protocols for environmental monitoring (Platts *et al*., 1983; Meador *et al*., 1993). There is an implicit assumption of local control, which undoubtedly exists; however, inclusion of landscape variables along with reach variables provides the opportunity to elucidate further controlling mechanisms.

Macroinvertebrate traits in a mixed land use basin in Michigan showed significant concordance with both reach and landscape features (Richards *et al*., 1997). Reach-scale variables including bankfull cross-sectional area, extent of shallows and amount of fine substrate, were the most important local variables, and surficial geology rather than land use was the most effective regional variable influencing macroinvertebrate traits. It is interesting that, within the same river basin, water chemistry variables were fairly evenly split between local and regional control (Johnson *et al*., 1997), whereas invertebrates appeared more strongly under the influence of local reach habitat (Richards *et al*., 1997).

Allan, Erickson & Fay (1997; see also Roth, Allan & Erickson, 1996) assess the same question, of the relative importance of local vs. landscape control of biological assemblages, but with a different approach. Focusing on fish and instream habitat using standard assessment protocols, they found that land use throughout a subcatchment upstream of a site generally was a better predictor of habitat quality and biotic integrity than either riparian corridor or reach surveys, although local streamside vegetation was marginally effective as a predictor. In a theme that echoes through a number of studies in this symposium, differences in study design have a substantial effect on interpretation. Intensity of sampling effort within *v* between subcatchments influences findings regarding the scale at which variation is explained. Although it may seem an obvious point, it should be noted that studies which separately quantify land use and surficial geology (e.g. Richards *et al*., 1996, 1997) provide some separation of natural landscape influences *v* those due to human modifications, whereas studies that only quantify land use (e.g. Allan *et al*., 1997; Townsend *et al*., 1997) may attribute causation to land use that in fact is caused by underlying geology.

Townsend and colleagues (1997) also investigated the relationship of both chemistry and macroinvertebrates to landscape and reach-scale measures for eight subcatchments of the Taieri River, New Zealand. Using three sampling scales (eight subcatchments representing four major land uses, with two to four tributaries per catchment and two to three sites per tributary), the strongest relationships of variables to land use occurred at the scale of sites within tributaries, largely because of greater replication at that level of investigation. Townsend *et al.* point out that the hierarchical nature of their study design results in greatest statistical power at the lowest spatial scale, yet multiple sites within a tributary increases power without necessarily increasing the biological significance of the result as adjacent sites within a tributary are not entirely independent. A related problem is the low number of replicates at the subcatchment level, due in part to the effort involved in including additional subcatchments and partly to the difficulty of identifying suitable replicates of land-use categories.

Management implications

Taken together, these studies of freshwater ecosystems within a landscape framework have important management implications. Rivers and lakes are strongly influenced by the geology, valley contours and vegetation of their catchments, and by human activities that alter land cover, hydrologic pathways, and ultimately affect many important land–water couplings. Processes operating at spatial scales ranging from the local to the regional are affected, and a deeper understanding of these scale-dependent processes is fundamental to sound management of freshwater ecosystems.

In the case of rivers, altered hydrology is a particularly important and far-reaching indicator of human interference with natural ecosystem function, whether directly via impoundments and diversions or indirectly through changes to the pathways whereby water reaches river channels. With the provocative question, 'How much water does a river need?', Richter *et al.* (1997) argue that discharge is characterized by multiple hydrologic parameters, which collectively describe the range of natural variability that should be the target in management strategies such as dam operation or river restoration. Conservation of ecosystem function and native aquatic biodiversity will probably require such a comprehensive approach, in place of the minimum flow requirements currently in wide use.

Finally, in discussing the growing interest in catchment-based management and decision-making, Allan *et al.* (1997) point out some challenges in reconciling catchment boundaries with political boundaries. Their 2800 km^2 basin in south-eastern Michigan is 'managed' by multiple agencies at the national, state and local level. Land-use decisions are made mainly at the local level of counties, townships, cities and villages. Often, a concern for the river basin exists, but the influence of these governing bodies does not extend appreciably upstream or down, and co-ordination among multiple units and levels of government requires great effort. Increasingly, studies of the physical, chemical and biological properties of aquatic ecosystems show these to be related to the catchment basin in complex and scale-dependent ways. Improving this understanding, and making the linkages to management, are important challenges for all aquatic ecologists.

Prospectus

This collection of papers documents that aquatic ecologists are making significant progress toward understanding how landscape variables influence the physical, chemical and biological properties of freshwater systems. CPOM dynamics, water chemistry, invertebrates and fish each are shown to be affected by both local measures (reach habitat and riparian vegetation) and regional characteristics (land use, geology, topography). Which type and scale of data are shown to have the strongest influence depends on the variable measured, and on study design as well. As aquatic scientists build on existing experience with spatially scaled studies, increasing attention should be paid to temporal *v* spatial distribution of effort and the hierarchical structure of spatial data. An improved understanding of the spatial and hierarchical relationships among linkages across the land–water ecotone would do much to guide future study designs.

Acknowledgments

The editors of this special issue would like to thank the members of Program Committee of the 1995 North American Benthological Society conference, particularly Alan Covich and Cathy Tate, for their support and encouragement in organizing the Plenary Session and Special Symposium, upon which these papers are based. We would also like to thank the Environmental Protection Agency for donating funds in support of the Plenary Session and the compilation/editing of these manuscripts. Reviewers who generously donated their time and efforts contributed to a vastly improved final product; we appreciate their efforts and those of the contributing authors, as well.

References

Allan J.D., Erickson D.L. & Fay J. (1997) The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology*, **37**, 149–162.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. (1986) A hierarchical framework for stream habitat classification:

viewing streams in a watershed context. *Environmental Management*, **10**, 199–214.

Hawkins C.J., Kerschner J.L., Bisson P.A., Bryant M.D., Decker L.M., Gregory S.V., McCoullough D.A., Overton C.K., Reeves G.H., Steedman R.J. & Young M.K. (1993) A hierarchical approach to classifying stream habitat features. *Fisheries*, **18**, 3–11.

Huet M. (1949) Aperçu des relations entre la pente et les populations piscicoles deseaux courantes. *Schweiz. Z. Hydrol*., **11**, 333–351.

Hynes H.B.N. (1975) The stream and its valley. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 1–15.

Illies J. & Botosaneanu L. (1963) Problemes et methodes de la classification et de la zonation ecologique de eaux corantes, considerees surtout du point de vue faunistique. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **12**, 1–57.

Johnson L.B. & Gage S.H. (1997) A landscape approach to analysing aquatic ecosystems. *Freshwater Biology*, **37**, 113–132.

Johnson L.B., Richards C., Host G.E. & Arthur J.W. (1997) Landscape influences on water chemistry in midwestern stream ecosystems. *Freshwater Biology*, **37**, 193–208.

Johnson S.L. & Covich A.P. (1997) Scales of observation of riparian forests and distributions of suspended detritus in a prairie river. *Freshwater Biology*, **37**, 163–176.

Kratz T.K., Webster K.E., Bowser C.J, Magnuson J.J. & Benson B.J. (1997) The influence of landscape position on lakes in northern Wisconsin. *Freshwater Biology*, **37**, 209–217.

Levin S. (1992) The problem of pattern and scale in ecology. *Ecology* **73**, 1943–1967.

Macan T.T. (1970) *Biological Studies of the English Lakes*. Longman Group Limited, The Camelot Press, London, United Kingdom.

Meador M.R., Hupp C.R., Cuffney T.F. & Gurtz M.E. (1993) *Methods for characterizing stream habitat as part of the national water-quality assessment program*. U.S. Geological Survey Open-File Report 93–408. 48 pp.

Naiman R.J. & H. Décamps, eds. (1990) *The ecology and management of aquatic- terrestrial ecotones*. Man and the Biosphere Series number 4. Paris: UNESCO; Carnforth, England: Parthenon.

Naiman R.J., Magnuson J.J., McKnight D.M. & Stanford J.A. (1995) *The Freshwater Imperative*. Island Press, Washington, D.C.

Osborne L.L. & Kovacic D.A. (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*, **29**, 243–258.

Pearsall W.H. (1920) The aquatic vegetation of the English Lakes. *Journal of Ecology*, **8**, 163–201.

Platts W.S., Megahan W.F & Minshall G.W. (1983) *Methods for evaluating stream, riparian, and biotic conditions.* U.S. Forest Service, General Technical Report No. INT-138, Ogden, Utah. 70 pp.

Richards C., Johnson L.B. & Host G.E. (1996) Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences* **53** (Suppl. 1), 295–311.

Richards C., Haro R.J., Johnson L.B. & Host G.E. (1997) Catchment and reach- scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology*, **37**, 219–230.

Richter B.D., Baumgartner J.V., Wigington R & Braun D.P. (1997) How much water does a river need? *Freshwater Biology*, **37**, 231–249.

Roth N.E., Allan J.D. & Erickson D.E. (1996) Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology*, **11**, 141–156.

Schindler D.W., Beaty K.G., Fee E.J., Cruikshank D.R., DeBruyn E.R., Findlay D.L., Linsey G.A., Shearer J.A., Stainton M.P. & Turner M.A. (1990) Effects of climatic warming on lakes in the central boreal forest. *Science*, **250**, 967–970.

Southwood T.R.E. (1977) Habitat, the template for ecological strategies. *Journal of Animal Ecology*, **46**, 377–365.

Strahler A.N. (1964) Quantitative geomorphology of drainage basins and channel networks (ed. Ven te Chow), *Handbook of Applied Hydrology* section 4–2, McGraw-Hill, New York.

Sweeney B.W. (1992) Streamside forests and the physical, chemical, and trophic characteristics of piedmont streams in Eastern North America. *Water Science* and *Technology*, **26**, 2653–2673.

Townsend C.R., Crowl T.A., Arbuckle C.J. & Scarsbrook M.R. (1997) The relationship between land use and physicochemistry, food resources and macro-invertebrate communities in tributaries of the Taieri River, New Zealand: a hierarchically scaled approach. *Freshwater Biology*, **37**, 177–192.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Wetzel R.G. (1983) *Limnology*, 2nd edn. Saunders.

Wiley M.J., Kohler S.L. & Seelbach P.W. (1997) Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. *Freshwater Biology*, **37**, 133–148.

Wiley M.J., Osborne L.L. & Larrimore R.W. (1990) Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 373–384.

(*Manuscript accepted 30 June 1996*).