24

Aquatic Conservation Planning: Using Landscape Maps to Predict Ecological Reference Conditions for Specific Waters

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24.1 Introduction

Regional planning for conservation and management of aquatic ecosystems is an extremely challenging task, involving integration of information across the breadth of disciplines involved in water resources management. Consideration must be given to hydrologic, sediment, and water-quality regimes; local geomorphic processes and habitat structures; network connectivity of water bodies; and maintenance of source populations of both characteristic and rare biota.

In this chapter, we highlight a promising new approach to estimating specific expected or reference conditions for various ecological parameters that is based on ideas from the field of landscape ecology. In Section 24.2, "Concepts, Principles, and Emerging Ideas," we provide some definition, historical background, and description of this emerging approach. In Section 24.3, we review "Recent Applications" of this approach across a variety of aquatic ecosystem types and in several areas of the world. In Section 24.4, we provide "Principles for Applying Landscape Ecology" derived from reviewing recent applications. In Section 24.5, we identify primary theoretical and empirical "Knowledge Gaps" that hinder further development. Finally, in Section 24.6, "Research Approaches," we lay out a series of steps to provide guidance for development of new applications.

24.2 Concepts, Principles, and Emerging Ideas

24.2.1 Information Required for Aquatic Conservation Planning

Resource inventory and assessment are commonly the first steps in regional conservation planning. *Inventory* involves enumerating the distribution and status of waters, and it is a prerequisite to strategic prioritization of management opportunities

within a region. *Assessment* involves normalizing observed ecological conditions for a water body through the use of some potential or reference condition (Gallant et al. 1989; Claessen et al. 1994). The *reference condition* is typically estimated from characteristics of a regional set of least-disturbed (reference) waters. The *assessed status* of a water body can be expressed either as a deviation from the reference condition (e.g., IBI-type scores; Karr et al. 1986) or as a ratio of observed and reference conditions (Hakanson 1996).

24.2.2 Historical Approaches to Modeling Reference Conditions Across a Large Region

To simplify their task, aquatic resource managers responsible for large geographic areas have often turned to classifying water bodies (Davis and Henderson 1978; Zonneveld 1994). Classifications allow extrapolation of attributes from sampled to unsampled water bodies, to create comprehensive regional coverage. Traditional aquatic classifications have generally followed either a site-based or a regionalization approach (these are sometimes termed bottom-up and top-down approaches, respectively; Figure 24.1; Zonneveld 1994).

Scale of measure of input variables

	Landscape context-based	Site-based

Form of response variable

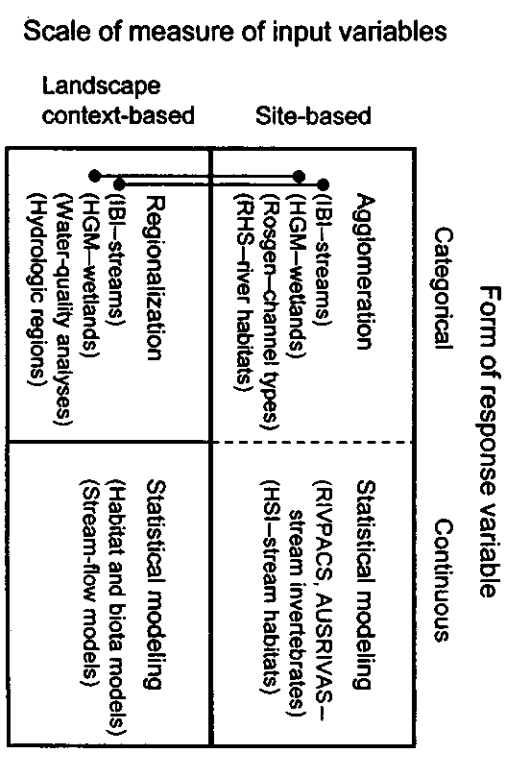|	Categorical	Continuous
Agglomeration	(IBI–streams) (HGM–wetlands) (Rosgen–channel types) (RHS–river habitats)	Statistical modeling (RIVPACS, AUSRIVAS– stream invertebrates) (HSI–stream habitats)
Regionalization	(IBI–streams) (HGM–wetlands) (Water-quality analyses) (Hydrologic regions)	Statistical modeling (Habitat and biota models) (Stream-flow models)

FIGURE 24.1. Classification of common approaches (shown in parentheses) to developing reference characteristics for aquatic systems. The lines connecting dots indicate a weaker differentiation between classes. The dashed line indicates that some approaches bridge multiple classes. Abbreviations are IBI—Index of Biotic Integrity; HGM—Hydro-Geomorphic Approach; RHS—River Habitat Survey; RIVPACS and AUSRIVAS refer to stream invertebrate assessment protocols used in Great Britain and Australia, respectively; HSI—Habitat Suitability Indices.

Site-Based Approaches (Agglomeration and Statistical Modeling)

Classification by agglomeration groups sampled, similar water bodies and asks, "What are water bodies in this group like?" The primary goal is simplification, achieved by categorizing many individual water bodies into groups that share similar attributes. Both diagnostic (easily measured indices) and response (e.g., biota) attributes are first measured for a subset of water bodies (learning set). Attributes are measured on-site with a fair degree of accuracy and precision. Water bodies with similar diagnostics are then clustered into groups whose attributes are summarized (e.g., mean and range). Group membership for additional waters is based on shared diagnostics. The reference condition for a water body is modeled from the summarized response attributes of a "least-impacted" subset within each group. Regional assessment is only achieved when an adequate sample of all system types is collected.

The strength of agglomeration lies in the accuracy and precision of local diagnostic measures. Confidence in these initial data is especially valued when managers are responsible for estimating difficult-to-measure attributes or complex processes, or when response attribute predictions are controversial (such as in regulatory programs). Examples of agglomeration-based assessment programs include the U.S. Hydrogeomorphic (HGM) Wetland Classification program (Hauer and Smith 1998); many lake and stream classifications used for prediction of water quality, habitat quality, or fishery potential (Schupp 1992; Rosgen 1996; Thorn and Anderson 1999; Emmons et al. In press); and the European River Habitat Survey (RHS) program (Raven et al. 1997).

A continuous-data modeling variation on the site-based approach also is used to predict aquatic reference conditions. Examples include: the U.S. Habitat Suitability Index (HSI) models (Terrell et al. 1982) that are widely used to predict potential distributions of fishes in streams; and the closely related River InVertebrate Prediction And Classification System (RIVPACS; Wright et al. 1997) and AUStralian RIVers Assessment Scheme (AUSRIVAS; Simpson and Norris In press) models that are being used in Great Britain and Australia (respectively) to predict potential occurrence of stream invertebrates.

Despite wide use, site-based approaches have several weaknesses. First, it is prohibitively expensive to measure on-site attributes everywhere within a region (Meixler and Bain 1998). Although fairly comprehensive data on selected attributes will eventually accumulate (e.g., Raven et al. 1997; Wright et al. 1997), this will not always be a viable regional approach. Second, much of the site-specific accuracy inherent in this process is actually lost in the classification process, because each water body assumes the "average" attributes of the group. Third, this process generally includes no information on the positional context of a water body in the landscape, so one cannot draw inferences about the landscape-scale processes that largely shape the character of each aquatic ecosystem (Zonneveld 1994). This emphasis on accuracy of local measures rather than on landscape context sets up the risk of sometimes knowing "what" but not "why" (sensu Holling 1998; Davies 1999) and can provide a false sense of confidence in the final estimates.

Regionalization (Landscape Context-Based Classification)

An alternative classification approach is regionalization, in which we group water bodies that lie together within a relatively similar geographic subregion and ask the question, "What are waters like that share the coarse-scale, ecological processes characteristic of this region?" Goals include simplification for planning and communication, and comprehensive regional coverage through use of landscape maps. Regionalization begins with the study of a series of overlay maps showing spatial concurrence of selected landscape characteristics thought to be diagnostic of ecosystem processes (e.g., climate, geology, soils, and topography). The larger landscape is divided into relatively similar subregions (i.e., ecoregions), each containing a number of water bodies (Davis and Henderson 1978; Gallant et al. 1989). These subregions are typically large; for example, a midwestern U.S. state may contain three to five ecoregions. Attributes of these regions are typically measured for a subset of waters (learning set), and then summarized (as means and ranges). Group membership is based on a shared location within the subregion such that all waters within the subregion would have the same predicted potential condition (Gallant et al. 1989). The model for predicting potential condition of any given water body is the summarized condition for the learning set (a selected reference set).

Regionalization's strength is comprehensive geographic coverage. Its generalized descriptions of both landscape-scale attributes and processes, and selected ecological potentials for water quality and aquatic biota (Gallant et al. 1989; Klijn 1994; Davis and Simon 1995; Davis et al. 1996). However, this top-down approach also has limitations because ecoregions are quite heterogeneous at the scale pertinent to aquatic ecosystems (Bryce and Clarke 1996). Thus, regional generalizations often do not provide accurate estimates for specific unsampled water bodies, and it becomes impossible to differentiate between a deviation from the reference condition caused by human impacts and one caused by geographic variation. Furthermore, because river catchments often are not nested cleanly within subregions, analyses across multiple contiguous regions may be required.

Two common variations on basic regionalization help to overcome these weaknesses. Regionalization can be combined with agglomeration by developing detailed classifications of measured water body characteristics within specific subregions. This brings some generalized landscape setting to the agglomeration process but still demands heavy investment in on-site measures. In the HGM wetlands classification (Hauer and Smith 1998) and various biological (Davis et al. 1996; Yoder and Smith 1998) and water quality monitoring programs (Gallant et al. 1989), agglomeration classes have been developed within subregions. This effectively stratifies subregions by water body type (determined from site-level diagnostics), and produces fairly useful predictive models. Alternatively, subregions can be further divided into smaller, more homogeneous units such as

land-type associations (Comer et al. 1997) or ecotopes (Claessen et al. 1994). Relating aquatic systems to a mosaic of these smaller land units represents movement toward the modeling approach described in Section 24.2.3.

24.2.3 Statistical Modeling From a Landscape Context

Many of the weaknesses of traditional classification and site-based modeling approaches are addressed by the integrative discipline known as landscape ecology. Through landscape ecology, we explore the patterns, dynamics, and ecological consequences of spatial heterogeneity in the environment (Risser et al. 1984; Turner 1998). We emphasize the importance of a site's unique placement in the larger landscape in explaining local ecological characteristics (Turner 1998). Landscape ecology encourages study of hierarchical relationships between coarse-scale variables descriptive of landscape character and local ecological attributes, and the identification of system-level patterns and processes that only emerge when viewed at coarse scales (Levin 1992; Wessman 1990). It explicitly recognizes the importance of human effects in the landscape.

Evaluating a water body's position in the landscape enables us to incorporate information on landscape-scale processes that shape the character of rivers (Lotspeich 1980; Schlosser 1991), lakes (Hakanson 1996; Kratz et al. 1997; Soranno et al. 1999), and wetlands (Hauer and Smith 1998). We can consider potential movements of water, sediments, and nutrients across landscape units and into the water body (Turner 1998). We can characterize movements and storage of these materials within water networks (connected bodies of lakes, streams, and wetlands), and we can consider movements of organisms among critical habitats within the system (Schlosser 1991; Kratz et al. 1997). We can consider the influence of landscape geomorphology on water body morphology. To assist planners, who examine mostly managed landscapes, we also can incorporate human effects on riverine processes (Risser et al. 1984; Wessman 1990).

A landscape-ecology approach suggests that coarse-scale information can be useful for characterizing and understanding potential characteristics of individual water bodies (Klijn 1994; Rabeni and Sowa 1996; Higgins et al. 1998; Davies 1999). Hierarchical systems theory suggests that higher-level, coarse-scale variables constrain and shape variables at lower levels and finer scales (O'Neill et al. 1986; Bourgeron and Jensen 1994). In addition, because coarse-scale variables are typically mapped for entire regions, it is possible to describe the unique geographical position of each water body within a region. This idea challenges the traditional view that site-scale measures are useful only for planning regional policy, whereas coarse-scale measures are needed to address site-management issues.

This ability of the landscape perspective to characterize hierarchical relationships provides both a conceptual and an empirical basis for development of statistical models that relate patterns in coarse-scale, contextual variables to site-scale, ecological response variables (Risser et al. 1984). Only modeling allows for exploration of relationships across large ranges in scale (Levin 1992; Holling 1998). Coarse-scale descriptions of the climatic, physiographic, and land-cover

settings of a water body, and its position and connectivity within the hydrologic network, are readily derived from available maps. By matching location-specific, coarse-scale contextual data with site-level ecological data, statistical models can be developed that use maps to predict the likelihood of occurrence of a habitat or species within specific waters. Ultimately, the potential distribution of an ecological characteristic can be predicted for waters across an entire region (Meffe and Carroll 1997; Higgins et al. 1998; Turner 1998).

We argue that ecological classification and statistical modeling are similar in intent and form. Perhaps less clear is the relationship between empirical modeling from landscape data and what is often called ecosystem process modeling. Process models attempt to infer structure from function (i.e., by integrating state variable derivatives) and typically focus on temporal intrasite variation via dynamic mathematical models. Process models can be driven by landscape-scale input variables, as in lumped-parameter water-quality models (e.g., Cosby et al. 1985). However, an unfortunate (and we believe false) dichotomy is often made between linear regression-based landscape models and process models (e.g., Thomann 1987; Thiefelder 1998), suggesting that process models are mechanistic and empirically parameterized regression models are not. In both cases, the modeling approaches are actually mechanism-neutral. In fact, both methods can be used to parameterize models based on explicit mechanistic hypotheses. Building regression models from explicit causal hypotheses (causal modeling sensu Retherford and Choe 1993) has a long and productive history in ecology (Asher 1983; Wooton 1994).

Classification, statistical, and dynamic-process models can all be used (singly or in combination) to infer site characteristics from landscape context (Wessman 1990; Haber 1994). Statistical models may be particularly appropriate for problems of intermediate complexity in which intersite variance is important and predictable, and when time-averaged characteristics are useful (Haber 1994). Conservation planning and regional management typically involve assessing potential value at an array of sites and making strategic decisions about the investment of limited management dollars. Detailed temporal behaviors are less important in this context than are long-term average conditions. On the other hand, detailed restoration strategies for particular sites may require additional detailed, time-dependent process modeling.

24.2.4 Application of Landscape-Context Statistical Modeling to Aquatic Ecosystems

The emerging practice of landscape-context statistical modeling has a key role to play in the assessment of the reference condition and status of aquatic ecosystems. Such modeling is very similar to traditional methods of ecological classification (agglomeration or regionalization) in both philosophy and intent. All are modeling exercises in the sense that they abstract complex realities into simpler representations of essential features (Kerr 1976). Ecological classification, for example, generates inferences about a particular site based on decision rules for

class membership generated from analyses of data from a subsample of sites. Statistical models likewise generate inferences about individual sites based on parameterization of models from large subsamples of site-referenced data. Both statistical modeling and classification focus on the intersite variation in ecological properties and use methods to partition and explain the observed variance.

Landscape-context modeling builds on the strengths of agglomeration and regionalization. We can identify any specific water body and ask, "What are the expected properties of this water body, given its unique position in the landscape?" The goal is to provide maximum descriptive information about potential properties of a water body.

Landscape-context models are developed using learning sets of map-scale and local diagnostic data compiled for subsets of waters (Figure 24.2). Statistical models are developed that predict potential water body properties from position-specific landscape data. For example, the composition and proximity of upstream landscape units might be used to predict the discharge regime of a particular stream (Wiley and Seelbach In press). Quantitative models are typically applied using position-specific geographic information system (GIS) measurements as inputs (Hakanson 1996), but interpretive models also have been applied by expe-
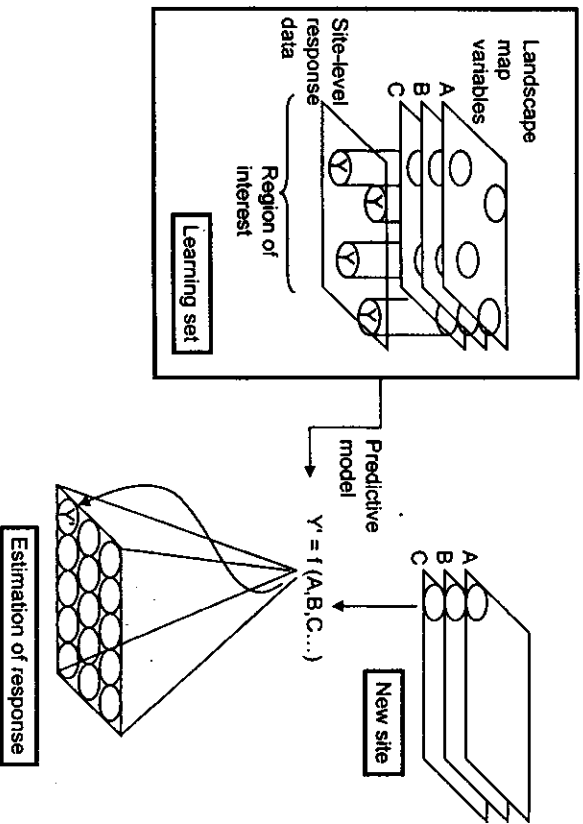

FIGURE 24.2. Generalized diagram of process for building landscape-based statistical models and applying them to estimate response characteristics of sites not in the learning set (indicated by Y').

rienced ecologists to draw qualitative inferences. For example, Seelbach et al. (1997) and Higgins et al. (1998) developed estimates of "first-cut" attribute types for all river valley segments across a region based on interpretation of landscape map overlays.

The landscape-based modeling approach has a number of strengths. Like regionalization, it provides comprehensive regional coverage, so any and all water bodies within the modeled region can be addressed. Like agglomeration, it often provides accurate characterization of individual water bodies. It provides an explicit description of the specific landscape context of each water body, so a sense of the hierarchical processes driving and constraining each system is obtained (Bourgeron and Jensen 1994). In addition, the use of continuous data often provides more accuracy than does the use of categorical or class data (Latour et al. 1994; Zonneveld 1994), and statistical modeling can provide error bounds for predicted conditions (Hakanson 1996). Finally, such models enable planners to explore costs and benefits of alternative management scenarios (Claessen et al. 1994; Hakanson 1996).

An often-overlooked value of a modeling approach is that it provides not only specific outputs, but also opportunities to study and learn about the structure and function of ecological systems. The initial steps of describing and mapping data characteristics and patterns are invaluable (Seelbach et al. 1997; Emmons et al. In press). Hypotheses and assumptions about how system components interact can be stated, tested, and revised. This heuristic value of modeling is important in shaping the thinking and judgments of resource managers and planners, and in providing a common conceptual base to a diverse set of users. Even as our information systems grow, human interpretation and judgment will remain a critical part of the management process.

The primary weakness of this approach is similar to that of regionalization: predictions do not necessarily provide accurate estimates of the local attributes of a specific unsampled water body. This uncertainty should, however, be less than that associated with regionalization because of the added positional and landscape information included for each unsampled water body. In addition, prediction uncertainty can be quantified as a confidence range on the estimate of a response variable. Integration of map-based modeling with agglomeration or regionalization can greatly reduce this prediction uncertainty. Predictive power can be strengthened by adding some site-level diagnostic measures to models, or by developing a hierarchical two-step approach (e.g., Claessen et al. 1994; Higgins et al. 1999).

24.3 Recent Applications

We did an extensive search of the recent literature, and we personally contacted key experts, to build a rough inventory of the extent to which landscape-context statistical modeling is actually being applied in aquatic assessment efforts. Our

TABLE 24.1. Recent applications of map-based modeling to aquatic ecosystems. Examples covered in the text are highlighted in bold type.

Applications	Dependent variable(s)	Locations	References
Comprehensive regional planning			
Streams and rivers	**Macrohabitat and faunal classes**	**USA, Great Lakes Basin, Illinois River Basin**	**Higgins et al. 1998; S. Miller et al., unpublished report[a]**
	Macrohabitat and faunal classes	USA, Missouri	Sowa et al. 1999
	Macrohabitat and fish distribution	USA, Michigan	Seelbach et al. 1997
	Fish distribution	France	T. Oberdorff et al., unpublished report[b]
	Stream flow	USA, Michigan	Wiley and Seelbach, In press
Lakes	**Water quality and yields of biota**	**Sweden**	**Hakanson and Peters 1995; Hakanson 1996; Thierfelder 1998**
	Sensitivity to acidification	USA, Northeast	Young and Stoddard 1996
Wetlands	**Floral community distribution**	**The Netherlands**	**Claessen et al. 1994; Latour et al. 1994; R. van Ek, personal communication.**
	Riparian habitat and floral community classification	USA, Michigan	M. Baker, unpublished manuscript[c]
Subregional model development			
Streams and rivers	Fish community structure	USA, New York	Meixler and Bain 1998
	Macrohabitat and faunal classes	USA, Colorado	A. Reed et al., unpublished report[d]
	Habitat and fish rehabilitation targets	**USA, Michigan**	**Wiley et al. 1998**
	Fish distribution	USA, Rocky Mountains	Nelson et al. 1992; Rahel and Nibbelink 1999
	Invertebrate indices of ecological integrity	Australia	Davies 1999
Lakes	**Water chemistry and biota**	**USA, Northern Wisconsin**	**Riera et al. In press**
	Water chemistry	USA and Canada, scattered	Soranno et al. 1999
	Fish distribution	USA, Minnesota	Cross and McInerny 1995
Wetlands	**Habitat and floral distribution**	**USA, Michigan**	**D. Merkey, unpublished manuscript[e]**

[a] S. Miller, J. Higgins, and J. Perot. 1998. The Classification of Aquatic Communities in the Illinois River Watershed and Their Use in Conservation Planning. Peoria: The Nature Conservancy of Illinois.

[b] T. Oberdorff, D.Chessel, B. Hugueny, D. Pont, P. Boet, and J. P. Porcher. A Statistical Model Characterizing Riverine Fish Assemblages of French Rivers: A Framework for the Adaptation of a Fish-Based Index. Contact D. Pont, Laboratory Ecologie des Hydrosystemes Fluviaux, Universite Lyon 1, France.

[c] M. Baker. 1998. Doctoral Dissertation Proposal. School of Natural Resources and Environment. Ann Arbor: University of Michigan.

[d] A. Reed, J. Higgins, and R. Wiginton. 1998. Aquatic Community Classification Pilot for the San Miguel Watershed. Boulder, Colorado: The Nature Conservancy.

[e] D. Merkey. 1999. Doctoral Dissertation Proposal. School of Natural Resources and Environment. Ann Arbor: University of Michigan.

search naturally focused on North America, but we did locate parallel activities, in several cases quite intensive, around the globe. It appeared that recent development and use of such models to assess and manage aquatic ecosystems is fairly widespread, apparently following on the heels of rapid growth in the availability of GIS technology (Table 24.1). Variations on the common approach diagrammed in Figure 24.2 are being applied across riverine, lake, and wetland ecosystems, and at two different planning scales (Tables 24.2–24.7). Although water body

TABLE 24.2. Ecological classification of river valley segments for U.S. regional and national conservation planning.

Water body:	River valley segment
Management region:	U.S. ecoregions
Management goal:	Prioritizing aquatic sites for biodiversity conservation
Developing agency:	The Nature Conservancy, Freshwater Initiative (Higgins et al. 1998; Higgins et al. 1999)
Map input variables:	Climate, landform
	Catchment size, network position, surficial geology, bedrock geology, topography
	Channel, valley, and lake morphology
	Connectivity to other aquatic ecosystems
Model form:	Developed by U.S. Ecoregions (regionalization)
	Delineation of river valley segment and lake units
	Assignment of attribute types
	Assignment to potential hydrologic regime type using visual interpretation of GIS map overlays and decision rules (Figure 24.3)
	Assignment to potential macrohabitat types using cluster analysis
	Macrohabitats, combined with zoogeographic patterns, used as a surrogate for potential biodiversity
Ecological ouputs:	GIS database with river segment and lake attribute classes, including size, network position, valley slope, connectivity, and estimated hydrologic regime
	Potential macrohabitat type membership
Implementation status:	Initial draft completed for entire U.S. Great Lakes Basin, Idaho batholith and prairie forest border ecoregions, Illinois River Basin; evaluation and revision underway
	Work ongoing in lower New England and superior mixed forest ecoregions
	Validated assumption that macrohabitats are predictive of biological communities in Michigan (Higgins et al. 1998; M. Wiley et al., unpublished report[a]) and Illinois River Basin (S. Miller et al., unpublished report[b])
	Used with terrestrial classifications in ecoregional conservation prioritization process (Higgins et al. 1999)

[a] M. Wiley, M. Baker, and P. Seelbach. 1998. Summer Field Sampling and Preliminary Analysis of Michigan Stream Assemblages. Chicago: The Nature Conservancy, Great Lakes Program Office.
[b] S. Miller, J. Higgins, and J. Perot. 1998. The Classification of Aquatic Communities in the Illinois River Watershed and Their Use in Conservation Planning. Peoria: The Nature Conservancy of Illinois.
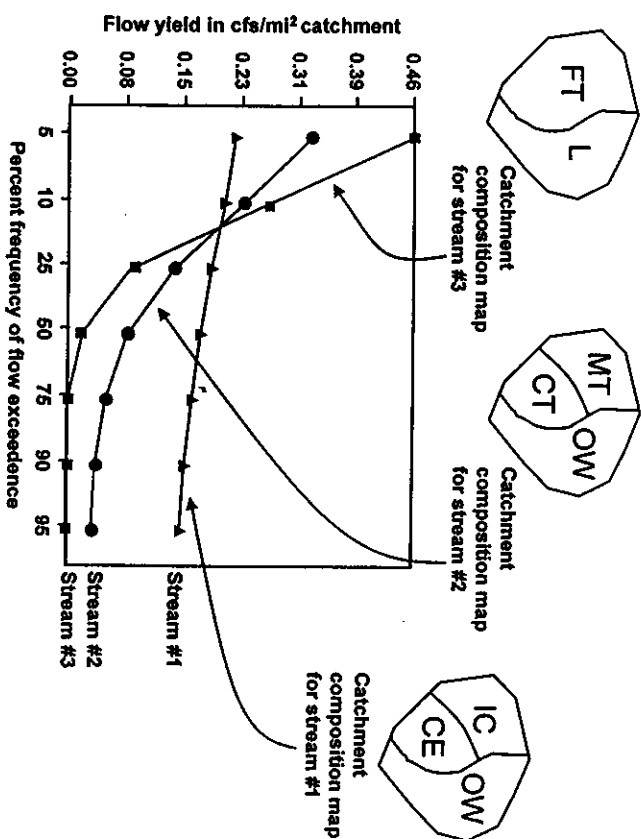
FIGURE 24.3. Examples of typical flow duration curves for streams in Michigan's Lower Peninsula. Assignment rules using catchment surficial geology data are: Stream #1—groundwater dominated; catchment composed of coarse outwash (OW) plain in stream valley, downslope of sizable coarse-textured ice-contact (IC) or end moraine (CE) ridges. Stream #2—runoff dominated with some groundwater; catchment with gentle topography composed of diverse mixture of coarse- (CT) and medium-textured (MT) till plains, and coarse outwash. Stream #3—runoff dominated; catchment with flat topography composed of fine-textured tills (FT) and lacustrine silts, clays, and sands (L). Stream flow yield at a specific exceedence frequency represents the stream flow generated per unit area of the upstream catchment that is exceeded for that specified percentage of each year. Stream flow yield is represented in cubic feet per second (cfs) per square mile (1 cubic foot = 0.0283 cubic meters, and 1 square mile = 2.59 square kilometers).

types and management regions and goals are unique in each example, common steps included: using map-based catchment and local landscape attributes as input variables; developing empirical models relating such variables to site-scale ecological response attributes; predicting reference conditions for additional waters across a large region based on unique landscape position data for each; and in some cases, integrating either an agglomeration or a regionalization approach.

Work on rivers appeared to be most popular, perhaps reflecting a gradient in the relative importance of landscape position versus local geomorphic and biological factors in determining ecological character. Rivers, as predominantly

TABLE 24.3. Modeling potential water quality for lakes across Sweden.

Water body:	Small glacial lakes
Management region:	Swedish subregions; potentially all of Sweden (81,000 lakes!)
Management goal:	Assessment of ecological status of lakes
Developing agency:	Uppsala University, Institute of Earth Sciences (Hakanson 1996)
Map input variables:	Catchment size and relief, land covers and till depth
	Lake morphometry
Model form:	Multiple linear regression
	Correction factors accounting for widespread temporal changes
Ecological outputs:	Attributes, including potential lake pH, total phosphorus, water color
	Indices of potential abundance of fishes, phytoplankton, benthic invertebrates; contaminants in fishes
	Actual condition/potential condition = index of status
	Combined indices into overall index of lake ecosystem status
Implementation status:	Summarized for lakes within selected subregions; illustrated use of indices to track lake attributes and overall status through time
	Estimated response of water quality and biological communities to chemical management actions, and developed a cost/benefit analysis to compare alternative actions
	Evaluated and supported use of spatially distributed catchment characteristics as input variables (Theirfelder 1998)
	Apparently not widely used to date

rapid flow-through systems, are strongly driven by catchment deliveries of water and sediment. In contrast, basin morphology is a known key in structuring physical habitat in lakes, and scientists are only recently beginning to examine the relative importance of catchment inputs (Eilers et al. 1983; Rochelle et al. 1989; Webster et al. In press). Wetlands range from systems clearly driven by position in the hydrologic landscape (e.g., northern white cedar [*Thuja occidentalis*] swamps or river floodplains), to those depressions where specific basin morphologies help define their hydrologic character, to bogs that (through time) become largely divorced from landscape influence. The form of models linking landscape characteristics to aquatic ecosystems also varies. Multiple linear regression models (Hakanson 1996), statistical summaries (Wiley et al. 1998; Riera et al. In press), empirically based decision rules (Seelbach et al. 1997; Higgins et al. 1998), and literature-based decision rules (Meixler and Bain 1998; Sowa et al. 1999) have all been used successfully.

24.4 Principles for Applying Landscape Ecology

Our literature review indicated that landscape-based statistical modeling is emerging as a viable tool for planners to determine ecological potential of aquatic ecosystems. Model-based information systems allow not only among-site comparison and prioritization of management actions, but also comparisons of costs

TABLE 24.4. Raster-based modeling of potential wetland values across The Netherlands.

Water body:	Wetlands
Management region:	The Netherlands
Management goal:	To estimate responses of wetland ecosystems to alternative regional and local water management scenarios
Developing agency:	Institute for Inland Water Management, Ministry of Transport, Public Works and Water Management (Claessen et al. 1994)
Map input variables:	1-km raster map of ecoseries and ecotope landscape units; these denote changes in water table elevation and soil types
Model form:	Develop by ecoseries units (regionalization)
	DEMNAT has empirically derived dose-response functions that translate changes in water table elevation into changes in soil moisture, nutrient levels, and acidity
	Additional functions that translate physical and chemical changes into changes in vegetative association
	Calculation of nationally normed, potential nature value through summing indices of vegetative community structure (rarity, completeness, and percent coverage for specific associations)
Ecological outputs:	Potential vegetation associations
	Potential nature value, useful for examining regional resource patterns under alternative water management scenarios, and as a reference condition for status assessment
Implementation status:	Recent improvements in the model include sensitivity analyses, added range coverage for dose-response models, links to site-scale hydrology and conservation value models, improved ecoseries classifications (founded on improved national vegetative survey database), and an improved computer interface (R. van Ek, personal communication)
	DEMNAT 2.1 has been operational since 1996
	Has been fundamental to a nation-wide study of future desiccation problems and management scenarios, climate change, and land subsidence—the "Dutch Aquatic Outlook"
	Has been used to develop ecologically based water management policy for subregions

and benefits of alternative management strategies at each site (Hakanson 1996; Wiley et al. 1998). Based on research conducted to date, we identified several principles that planners can apply to the conservation and management of aquatic ecosystems.

Successful model response variables usually have high among-system variability. Hakanson (1996) suggested that variables with high within-system variance may not be modeled easily; however, such high-frequency variation can be summarized (e.g., stream discharge exceedence frequencies; Wiley and Seelbach In press) to portray significant variation in pattern among water bodies. Landscape-context modeling also implicitly requires large sample sizes of waters in the learning set. Thus, subregions need to be extensive and heterogeneous enough to provide both a large sample of waters and some variation among them.

Conservation planning is often considered a "crisis discipline" (Meffe and Carroll 1997), meaning that management decisions and actions often cannot afford to wait for development of fully accurate scientific understanding and information. Thus, decision-support tools must be developed and iteratively updated using the best available science. In our review, applications seeking broad regional coverage often employed some form of analytical shortcuts: regionalization (Claesson et al. 1994; Latour et al. 1994), raster-classified landscape units (Claesson et al. 1994), interpretive estimation of landscape position and characteristics (Seelbach et al. 1997; Higgins et al. 1998), literature-based decision rules (Meixler and Bain 1998; Sowa et al. 1999), or estimation of current status from land-use maps (Higgins et

TABLE 24.5. Modeling ecological targets for rehabilitation of the Rouge River, Michigan.

Water body:	River valley segment
Management region:	Rouge River, Michigan
Management goal:	To develop a suite of ecological targets to guide stormwater rehabilitation efforts on this severely degraded urban river; specific focus on fish community targets to serve as integrated signal of future system recovery
Developing agencies:	University of Michigan, School of Natural Resources and Environment; and Institute for Fisheries Research, Michigan Department of Natural Resources (Wiley et al. 1998), for the Wayne County, Rouge Project Office
Map input variables:	For stream discharge: catchment area, precipitation, slope, surficial geology, soils, land covers For fishes: catchment area, estimated baseflow yield
Model form:	Regression models of stream discharge following standard hydraulic geometry relations (Wiley and Seelbach In press) Statistical summary of fish abundance—coarse-scale habitat affinities for Michigan streams (Zorn et al. 1997); standard deviations from the mean were used to gauge likelihood of occurrence given a particular attribute value For selected rehabilitation target fishes: the large regional, relational database was queried in reverse and typical summer thermal and stormflow regimes calculated (agglomeration of sites by fishes)
Ecological outputs:	Potential fish community structure Acceptable summer thermal regime to support selected fishes Acceptable summer and stormflow regimes to support selected fishes (Figure 24.4)
Implementation status	Enabled feasibility assessment of alternative stormwater mitigation measures for specific segments by Rouge Project Office; allows determination of where rehabilitation is not feasible Illustrated overall ecological structure of the river system, and highlighted priority problems and opportunities Provided realistic fishery rehabilitation goals for specific segments; for example, it became clear that some tributaries should not be expected to support sport fisheries. Alternatively, new attention has been drawn to recreational potentials in other segments

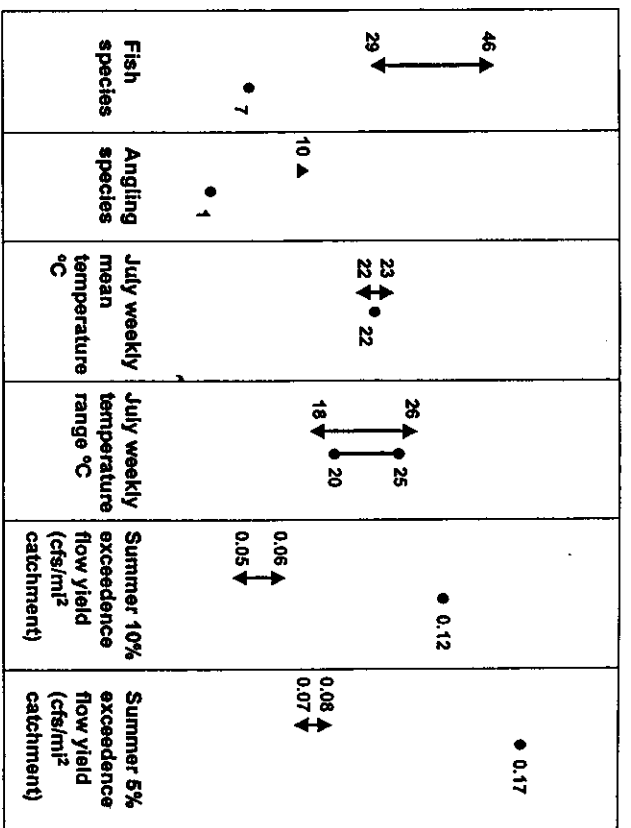| Fish species	Angling species	July weekly mean temperature °C	July weekly temperature range °C	Summer 10% exceedence flow yield (cfs/mi² catchment)	Summer 5% exceedence flow yield (cfs/mi² catchment)
46 29 • 7	10 ▲ • 1	23 22 ▲ • 22	26 25 18 20	0.06 0.05 • 0.12 • 0.17	0.08 0.07

FIGURE 24.4. Predicted reference conditions (triangle, or lines bounded by triangles) and observed conditions (circle, or lines bounded by circles) for a suite of ecological parameters on the Rouge River, Michigan. July temperatures fell within expected ranges; however, measures of fish community structure and summer stormflows were clearly different from predicted conditions.

TABLE 24.6. Examining importance of landscape context to characteristics of Wisconsin lakes.

Water body:	Lakes
Management region:	Northern Wisconsin
Management goal:	Explanation of landscape-driven heterogeneity in lake ecological attributes
Developing agency:	University of Wisconsin, Center for Limnology (Riera et al. In press)
Map input variables:	Lake order (position in surface and subsurface flow networks)
Model form:	One-way ANOVA to test for differences among lakes in different lake-order classes
Ecological outputs:	Potential lake and catchment size Major ions, nutrients, fish species richness, chlorophyll Distribution and abundance of aquatic biota and humans
Implementation status:	Has not yet been applied to management; in early stages of exploring relationships and building models

TABLE 24.7. Initial modeling of hydrologic context for depressional wetlands in southern Michigan.

Water body:	Depressional wetlands
Management region:	Subregions in southern Michigan
Management goal:	To estimate potential wetland types and associated functions across subregions in Michigan for use as the reference condition in assessment and planning
Developing agency:	University of Michigan, School of Natural Resources and Environment; and Institute for Fisheries Research, Michigan Department of Natural Resources (D. Merkey, unpublished manuscript*)
Map input variables:	Wetland size
	Catchment summaries of climate, topography, surficial geology, and soils
	Potential groundwater deliveries derived from theoretical interactions between local topography and surficial geology textures (Wiley and Seelbach In press)
	Position in the surficial flow network
Model form:	Develop by subregions (regionalization)
	Multiple linear regression to predict hydrologic, chemical, and vegetative attributes
	Ecological classification based on statistical analysis and literature
	Ecological functions assigned according to literature guidelines (Hauer and Smith 1998)
Ecological outputs:	Potential hydrologic source and hydroperiod
	Potential water chemistry
	Potential vegetative associations
	Potential wetland hydrogeomorphic type (Hauer and Smith 1998)
	Additional ecological context related to a wetland's landscape position, including relationships with interconnected water bodies and nearby uplands
Implementation status:	Has not yet been applied to management; new study

* D. Merkey. 1999. Doctoral Dissertation Proposal. School of Natural Resources and Environment. Ann Arbor: University of Michigan.

al. 1999). Despite their generalities, these applications have been immediately and eagerly employed in management planning processes (R. van Ek, personal communication; Higgins et al. 1999).

Many examples also emphasize that creative use of several approaches will be needed to simplify and describe complex ecosystems effectively. Most studies incorporated some form of agglomeration or regionalization with landscape-context modeling to control for coarse-scale climatic and geologic variables. For example, Higgins et al. (1999) used a two-step procedure, with a regionalization accounting for coarse-scale patterns in climate and historical zoogeography, and landscape-context interpretive modeling used to estimate site-specific ecological potentials.

It is clear that landscape-context modeling cannot account for all variables important to aquatic ecosystems (Claessen et al. 1994). In fact, models ideally should contain only a small number of independent landscape variables to

highlight the fundamental system processes (Thierfelder 1998). Thus, there will be variance (noise) associated with predictions, and this should be explicitly communicated as model output. Some of this noise is due to the following factors: the inability to account for important local, modifying processes; noise in the landscape input variables (maps); the limits of modeling from finite, subsample databases; and current limits in our conceptual understanding of ecosystem processes (e.g., processes driving the distribution of biota are especially complex).

24.5 Knowledge Gaps

Landscape-context modeling is a nascent discipline, and many challenges lie ahead. Three general areas need development: conceptual models of hierarchical processes that drive aquatic systems, assembly of standardized regional data sets, and integration of site-scale data into landscape-based models.

Models will improve as our conceptual understanding and empirical bases improve. Currently, significant gaps in our conceptual understanding of landscape-driven, hierarchical aquatic ecosystems limit development of formal models (hypotheses) of landscape-driven, hierarchical aquatic processes. Such models have only recently begun to be developed and tested. The examples reviewed above are among the first to explore such processes quantitatively. These initial hypothetical models will highlight cross-scale relationships and expose conceptual holes, leading to new rounds of hypotheses, data collection, and improved model development.

Landscape-context modeling requires extensive map and site-level data. Extensive digital map coverages exist, but these can suffer from coarse scales of resolution or classification schemes inappropriate for analyses of local aquatic ecosystems. In addition, modeling requires that numerous catchment or local summaries be developed for waters of interest (and for waters to be extrapolated to). Large sets of site-scale assessment data exist for many areas, typically for certain water quantity, water quality, and biological variables. However, these data vary greatly in their variable selection, representative site coverage, and sampling methodologies. We feel that such shortcomings will be overcome, in time, through the iterative, adaptive management process. Only by assembling existing data sets, and analysis of the performance and sensitivities of formal models, will we be able to design more appropriate sampling schemes.

With their conscious focus on hierarchy, efficiency, and simplicity, initial landscape-based models have stressed map-scale physical input variables. It is likely that the addition of certain easily measured site-scale habitat variables could greatly improve predictive power of the models. For example, the current AUSRIVAS models of stream invertebrate communities (Simpson and Norris In press) are based on site-level habitat variables that provide useful predictions.

The addition of key landscape-scale drivers would provide such models with landscape context, map efficiencies, and potentially greater statistical power, ideas that are beginning to be explored (Davies 1999). The idea of requiring some limited site data for models would not make the assessment process less efficient, as some on-site measurement of observed condition is needed for complete assessment anyway. In some systems), especially lakes and wetlands (perhaps less controlled by abiotic variables), the addition of key biological variables may be critical. For example, in lakes, food-web structure accounts for roughly half of the variance observed in pelagic primary production (Carpenter et al. 1991). Thus, food-web structure would appear to be a desirable variable in water-quality models. We do not yet understand whether landscape forces act directly on primary production or indirectly through influences on food-web structure.

Initial models have generally targeted response variables that characterize the average condition over several years. Such low-frequency information is appropriate for coarse-scale modeling and often useful for providing ecosystem reference conditions; however, many management questions will undoubtedly require estimation of responses over shorter time periods. These questions will require employing a different class of models that operate on shorter time steps and that perhaps have more detailed input variables and mechanistic analyses—referred to earlier as ecosystem process models. We see these process models as complementary to, not opposing, landscape-context models. Map-based models could provide an initial rough cut, or stratification for a site, leading to the appropriate application of various site- or type-specific process models. We need to identify the respective strengths and limitations of the different modeling scales, and use all scales and approaches to full advantage.

24.6 Research Approaches

Implementation of a landscape-context modeling approach to aquatic conservation planning requires commitment to a long-term, iterative development program, a form of adaptive management (Meixler and Bain 1998). The overall goal is to link regional landscape (map) data and detailed site databases already in existence (or to be collected in the future) through ecologically realistic models.

Step 1 is to use process-level theory and the local experience of managers to develop initial conceptual hypotheses and models regarding relationships between landscape-level data and aquatic ecosystems of interest.

Step 2 is to compile map and site data from existing assessment programs into a GIS; this information system must be designed to handle a variety of queries about a suite of response variables, and to provide opportunities for building and testing the models. Often, existing assessment programs house plenty of site and map data, but these are not being used in the proper context or in combination with each other. Both map and local site data have their

weaknesses and associated errors related to data resolution, prior goals, and criteria for classification and sampling. These errors must be acknowledged and incorporated into error assessments throughout the process. However, we argue strongly that model development should proceed using available data, at available resolutions and data quality. We can learn much from incomplete or semiquantitative data, and the iterative process will produce continuous improvements.

Step 3 is to develop and test analytical models that predict ecological response from landscape context. Modeling approaches may include graphing, statistical summary, multiple linear regression, logistic regression, or path analysis. Analytical techniques such as path analysis (Retherford and Choe 1993) were specifically designed to explore hierarchical relationships (e.g., Hinz and Wiley 1999; Wehrly 1999). Model calibration and validation are used to identify the utility and limits of current models, and additional sampling needs (Haber 1994; Walters 1997). Understanding limitations and weaknesses of the models is critical. In particular, sensitivity analyses are used to highlight the variables and scales (Hakanson 1996; Rabeni and Sowa 1996) that are most influential and that should therefore be focused on in future sampling designs.

Step 4a is to use the current models in management planning, with explicit recognition of prediction error (perhaps as confidence limits). These would be the best available, regionally comprehensive estimates of ecological potential for each water body.

Step 4b occurs simultaneously with Step 4a and involves a return back to Step 1: development of new conceptual models of how the hierarchical system works, thus beginning a second cycle of modeling in which strategic data are gathered and an improved set of models is constructed.

Modeling in The Netherlands (Claessen et al. 1994; R. van Ek, personal communication) of wetland responses to water table fluctuations provides an excellent example of the suggested iterative approach. They initially used existing science to formulate conceptual models of how water table levels should influence soil moisture and chemistry and, therefore, vegetation communities. They compiled existing data on water table, landscape, and vegetation characteristics and then built and tested initial predictive models of potential vegetation. These models were used to estimate wetland responses to proposed alternative water management scenarios throughout The Netherlands. At the same time, the investigators initiated a second cycle of model testing and development. They incorporated improved and expanded landscape and vegetation data sets; performed sensitivity analyses; determined probabilities of occurrence of site-level features (e.g., clay lenses) within landscape types; established links to site-level hydrology and conservation-value models for increased management resolution; made the models more user-friendly; and were able to use model predictions to assist in national water management planning. Ongoing work (R. van Ek, personal communication) identified weaknesses in the second-version model, setting the stage for continued development.

References

Asher, H. 1983. *Causal Modeling*. Newbury Park, New Jersey: Sage Publications.

Bourgeron, P.S., and Jensen, M.E. 1994. An overview of ecological principles for ecosystem management. In *Volume II: Ecosystem Management: Principles and Applications*, eds. M. Jensen and P. Bourgeron, pp. 45–57. General Technical Report PNW-GTR-318. Portland, Oregon: USDA Forest Service, Pacific Northwest Research Station.

Bryce, S.A., and Clark, S.E. 1996. Landscape-level ecological regions: linking state-level ecoregion frameworks with stream habitat classifications. *Environ. Manage.* 20:297–311.

Carpenter, S.R., Frost, T.M., Kitchell, J.F., Kratz, T.K., Schindler, D.W., Shearer, J., Sprules, W.G., Vanni, M.J., and Zimmerman, A.P. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems. In *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*, eds. J. Cole, G. Lovett, and S. Findlay, pp. 67–96. New York: Springer-Verlag.

Claessen, F.A.M., Klijn, F., Witte, J.P.M., and Nienhuis, J.G. 1994. Ecosystem classification and hydro-ecological modelling for national water management. In *Ecosystem Classification for Environmental Management*, ed. F. Klijn, pp. 199–222. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Comer, R.A., Albert, D.A., and Delain, C.J. 1997. *Landtype Associations of the Leelanau and Grand Traverse Peninsulas: Subsection VII.5*. Technical Report and Map. Lansing: Michigan Natural Features Inventory.

Cosby, B.J., Hornberger, G.M., Galloway, J.N., and Wright, R.F. 1985. Modeling the effects of acid deposition: assessment of a lumped-parameter model of soil water and streamwater chemistry. *Water Resour. Res.* 21:51–63.

Cross, T.K., and McInerny, M.C. 1995. *Influences of Watershed Parameters on Fish Populations in Selected Minnesota Lakes of the Central Hardwood Forest Ecoregion*. Fisheries Investigational Report 441. St. Paul: Minnesota Department of Natural Resources.

Davies, N. 1999. *Prediction and Assessment of Local Stream Habitat Features Using Large-Scale Catchment Characteristics*. Honours Thesis in Applied Science. Belconnen, Australia: University of Canberra.

Davis, L.S., and Henderson, J.A. 1978. Many uses and many users: some desirable characteristics of a common land and water classification system. In *Classification, Inventory, and Analysis of Fish and Wildlife Habitat*, general chairman A. Marmelstein, pp. 13–34. Report FWS/OBS-78/76. Washington, DC: U.S. Fish and Wildlife Service.

Davis, W.S., and Simon, T.P. 1995. *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making*. Boca Raton, Florida: Lewis Press.

Davis, W.S., Snyder, B.D., Stribling, J.B., and Stoughton, C. 1996. *Summary of State Biological Assessment Programs for Streams and Wadable Rivers*. Report EPA-230-R-96-007. Washington DC: U.S. Environmental Protection Agency.

Eilers, J.M., Glass, G.E., Webster, K.E., and Rogalla, J.A. 1983. Hydrologic control of lake susceptibility to acidification. *Can. J. Fish. Aquat. Sci.* 40:1896–1904.

Emmons, E.E., Jennings, M.J., and Edwards, C. In press. An alternative classification method for northern Wisconsin lakes. *Can. J. Fish. Aquat. Sci.*

Gallant, A.L., Whittier, T.R., Larsen, D.P., Omernik, J.M., and Hughes, R.M. 1989. *Regionalization as a Tool for Managing Environmental Resources*. Report EPA/600/3-89/060. Corvallis, Oregon: U.S. Environmental Protection Agency.

Haber, W. 1994. Systems ecological concepts for environmental planning. In *Ecosystem Classification for Environmental Management*, ed. F. Klijn, pp. 49–68. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Hakanson, L. 1996. Predicting important lake habitat variables from maps using modern modelling tools. *Can. J. Fish. Aquat. Sci.* 53(Suppl. 1):364–382.

Hakanson, L., and Peters, R.H. 1995. *Predictive Limnology—Methods for Predictive Modelling*. Amsterdam, The Netherlands: SPB Academic Publishing.

Hauer, F.R., and Smith, R.D. 1998. The hydrogeomorphic approach to functional assessment of riparian wetlands: evaluating impacts and mitigation on river floodplains in the U.S.A. *Freshwater Biol.* 40:517–530.

Higgins, J., Lammert, M., and Bryer, M. 1999. *Including Aquatic Targets in Ecoregional Portfolios: Guidance for Ecoregional Planning Teams*. Designing a Geography of Hope Update Number 6. Arlington, Virginia: The Nature Conservancy.

Higgins, J., Lammert, M., Bryer, M., DePhilip, M., and Grossman, D. 1998. *Freshwater Conservation in the Great Lakes Basin: Development and Application of an Aquatic Community Framework*. Final Project Report. Chicago: The Nature Conservancy, Great Lakes Program Office.

Hinz, L.C., and Wiley, M.J. 1998. *Growth and Production of Juvenile Trout in Michigan Streams: Influence of Potential Ration and Temperature*. Fisheries Research Report 2042. Ann Arbor: Michigan Department of Natural Resources.

Holling, C.S. 1998. Two cultures of ecology. *Conserv. Ecol.* [online] 2:4. Available from the Internet: www.consecol.org/vol2/iss2/art4.

Karr, J.R., Fausch, K.D., Angermeier, P.L., Yant, P.R., and Schlosser, I.J. 1986. *Assessing Biological Integrity in Running Waters: A Method and Its Rationale*. Special Publication 5. Champaign: Illinois Natural History Survey.

Kerr, S.R. 1976. Ecological analysis and the Fry paradigm. *J. Fish. Res. Board Can.* 33:329–332.

Klijn, F. 1994. Spatially nested ecosystems: guidelines for classification from a hierarchical perspective. In *Ecosystem Classification for Environmental Management*, ed. F. Klijn, pp. 85–116. Dordrecht, The Netherlands: Kluwer Academic Publishers.

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

Latour, J.B., Reiling, R., and Wiertz, J. 1994. A flexible multiple stress model: who needs a priori classification? In *Ecosystem Classification for Environmental Management*, ed. F. Klijn, pp. 183–198. Dordrecht, The Netherlands: Kluwer Academic Publishers.

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

Lotspeich, F.B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. *Water Resour. Bull.* 16:581–586.

Meffe, G.K., and Carroll, C.R., eds. 1997. *Principles of Conservation Biology*. Second Edition. Sunderland, Massachusetts: Sinauer Associates.

Meixler, M.S., and Bain, M.B. 1998. *Aquatic Gap Analysis: Demonstration of a Geographic Approach to Aquatic Biodiversity Conservation.* Final Project Report. Reston, Virginia: U.S. Geological Survey, Biological Resources Division.

Nelson, R.L., Platts, W.S., Larsen, D.P., and Jensen, S.E. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. *Trans. Am. Fish. Soc.* 121:405-426.

O'Neill, R.B., DeAngelis, D.L., Waide, J.B., and Allen, T.F.H. 1986. *A Hierarchical Concept of Ecosystems.* Princeton: Princeton University Press.

Rabeni, C.F. and Sowa, S.P. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. *Can. J. Fish. Aquat. Sci.* 53(Suppl. 1): 252-259.

Rahel, F.J. and Nibbelink, N.P. 1999. Spatial patterns in relations among brown trout (*Salmo trutta*) distribution, summer air temperature, and stream size in Rocky Mountain streams. *Can. J. Fish. Aquat. Sci.* 56(Suppl. 1):43-51.

Raven, P.J., Fox, P., Everard, M., Holmes, N.T.H., and Dawson, F.H. 1997. River Habitat Survey: a new system for classifying rivers according to their habitat quality. In *Freshwater Quality: Defining the Indefinable?*, eds. P.J. Boon and D.L. Howell, pp. 215-234. Edinburgh: Scottish Natural Heritage Press.

Retherford, R.D., and Choe, M.K. 1993. *Statistical Models for Causal Analysis.* New York: John Wiley and Sons.

Riera, J.L., Magnuson, J.J., Kratz, T.K., and Webster, K.E. In press. A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, U.S.A. *Freshwater Biol.*

Risser, P.G., Karr, J.R., and Forman, R.T.T. 1984. *Landscape Ecology—Directions and Approaches.* Special Publication 2. Champaign: Illinois Natural History Survey.

Rochelle, B.P., Liff, C.I., Campbell, W.G., Cassell, D.L., Church, M.R., and Nusz, R.A. 1989. Regional relationships between geomorphic/hydrologic parameters and surface water chemistry relative to acidic deposition. *J. Hydrol.* 112:103-120.

Rosgen, D.L. 1996. *Applied River Morphology.* Pagosa Springs, Colorado: Wildland Hydrology.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.

Schupp, D.H. 1992. *An Ecological Classification of Minnesota Lakes with Associated Fish Communities.* Section of Fisheries Special Publication 417. St. Paul: Minnesota Department of Natural Resources.

Seelbach, P.W., Wiley, M.J., Kotanchik, J.C., and Baker, M.E. 1997. *A Landscape-based Ecological Classification System for River Valley Segments in Lower Michigan.* Fisheries Research Report 2036. Ann Arbor: Michigan Department of Natural Resources.

Simpson, J., and Norris, R.H. In press. Biological assessment of water quality: development of AUSRIVAS models and outputs. In *RIVPACS and Similar Techniques for Assessing the Biological Quality of Freshwaters*, eds. J.F. Wright, D.W. Sutcliffe, and M.T. Furse. Ambleside, United Kingdom: Freshwater Biological Association and Environmental Agency.

Soranno, P.A., Webster, K.E., Riera, J.L., Kratz, T.K., Baron, J.S., Bukaveckas, P.A., Kling, G.W., White, D.S., Caine, N., Lathrop, R.C., and Leavitt, P.R. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. *Ecosystems* 2:395-410.

Sowa, S.P., Morey, M.E., Sorensen, G.R., and Annis, G. 1999. Predicting the biological potential of each valley segment. In *Implementing the Aquatic Component of Gap*

Analysis in Riverine Environments: A Training Workbook, ed. S.P. Sowa, Section 5. Columbia: Missouri Resource Assessment Partnership.

Terrell, J.W., McMahon, T.E., Inskip, P.D., Raleigh, R.F., and Williamson, K.L. 1982. *Habitat Suitability Index Models: Appendix A. Guidelines for Riverine and Lacustrine Applications of Fish HSI Models with the Habitat Evaluation Procedures.* Report FWS/OBS-82/10.A. Washington, DC: U.S. Fish and Wildlife Service.

Thierfelder, T.K.E. 1998. *An Inductive Approach to the Modeling of Lake Water Quality in Dimictic, Glacial/Boreal Lakes.* Comprehensive summaries of Uppsala Dissertations from the Faculty of Science and Technology 399. Uppsala, Sweden: Uppsala University.

Thomann, R.V. 1987. *Principles of Surface Water Quality Modeling and Control.* New York: Harper and Row.

Thorn, W.C., and Anderson, C.S. 1999. *A Provisional Classification of Minnesota Rivers with Associated Fish Communities.* Special Publication 153. St. Paul: Minnesota Department of Natural Resources.

Turner, M.G. 1998. Landscape ecology. In *Ecology*, ed. S.I. Dodson, pp. 77-122. New York: Oxford University Press.

Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. *Conserv. Ecol.* [online] 1:1. Available from the Internet: www.consecol.org/vol1/iss2/art1.

Webster, K.E., Soranno, P.A., Baines, S.B., Kratz, T.K., Bowser, C.J., Dillon, P.J., Campbell, P., Fee, E.J., and Hecky, R.E. In press. Structuring features of lake districts: geomorphic and landscape controls on lake chemical responses to drought. *Freshwater Biol.*

Wehrly, K.E. 1999. *The Influence of Thermal Regime on the Distribution and Abundance of Stream Fishes in Michigan.* Ph.D. dissertation. Ann Arbor: University of Michigan.

Wessman, C.A. 1990. Landscape ecology: analytical approaches to pattern and process. In *An Ecosystem Approach to the Integrity of the Great Lakes in Turbulent Times*, eds. C.J. Edwards and H.A. Regier, pp. 285-299. Special Publication 90-4. Ann Arbor, Michigan: Great Lakes Fishery Commission.

Wiley, M.J., and Seelbach, P.W. In press. *Hydrology of Rivers in Michigan's Lower Peninsula.* Fisheries Research Report 2039. Ann Arbor: Michigan Department of Natural Resources.

Wiley, M.J., Seelbach, P.W., and Bowler, S.P. 1998. *Ecological Targets for Rehabilitation of the Rouge River.* Final Report RPO-PI-SR21.00. Detroit, Michigan: Wayne County Rouge Project Office.

Wooton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Ann. Rev. Ecol. Syst.* 25:443-466.

Wright, J.F., Moss, D., Clarke, R.T., and Furse, M.T. 1997. Biological assessment of river quality using the new version of RIVPACS (RIVPACS III). In *Freshwater Quality: Defining the Indefinable?*, eds. P.J. Boon and D.L. Howell, pp. 102-107. Edinburgh: Scottish Natural Heritage Press.

Yoder, C.O., and Smith, M.A. 1998. Using fish assemblages in a state biological assessment and criteria program: essential concepts and considerations. In *Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities*, ed. T.P. Simon, pp. 17-56. Boca Raton, Florida: CRC Press.

Young, T.C. and Stoddard, J.L. 1996. The TIME project design: I. Classification of Northeast lakes using a combination of geographic, hydrogeochemical, and multivariate techniques. *Water Resour. Res.* 32:2517-2528.

Zonneveld, I.S. 1994. Basic principles of classification. In *Ecosystem Classification for Environmental Management*, ed. F. Klijn, pp. 23–47. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Zorn, T.G., Seelbach, P.W., and Wiley, M.J. 1997. *Patterns in the Distributions of Stream Fishes in Michigan's Lower Peninsula*. Fisheries Research Report 2035. Ann Arbor: Michigan Department of Natural Resources.

Section V
Synthesis and Conclusions