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Recent developments in landscape approaches for the study of aquatic ecosystems

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Abstract. We summarized landscape approaches used in the study of freshwater ecosystems, updated recent literature reviews on interactions between terrestrial and lotic ecosystems, and discussed the influence of *J-NABS* on developments in the field. We focused primarily on studies of freshwater ecosystems done at or above the catchment scale. Special issues of *J-NABS* and other journals have advanced our understanding of the effects of spatially distributed characteristics and phenomena on aquatic ecosystems. Topics that have been well covered in *J-NABS* include use of classification to predict biotic assemblages and impacts of human disturbance (especially urbanization) on stream structure and function. Early work focused on correlative relationships between landscape variables and various biotic components of stream systems, whereas later studies addressed causal linkages between landscape and biota, including landscape effects on hydrology, habitat at various spatial scales, and ecosystem processes. At large spatial scales (i.e., catchments or regions), landscape context and heterogeneity are important predictors of compositional, structural, and functional attributes of streams and lakes. The size of the study region and catchments and the level of disturbance across the region can interfere with our ability to generalize results across studies. Geographical information systems and remote sensing technologies are important tools for understanding and quantifying these relationships, and new sophisticated tools are available for measuring landscape pattern and context. Lotic ecosystems are challenging to study because of the directional flow of water across (and beneath) the landscape. However, new spatial analysis tools can incorporate hydrologic connectivity. Limited data on surface and groundwater connections and lack of available watershed delineations make finding similar connections between lakes and wetlands and their surrounding landscapes challenging.

Key words: landscape, scale, review, watershed, catchment, aquatic ecosystem, *J-NABS*, hierarchy, region, connectivity.

The *landscape* is a relatively new study unit in the environmental sciences that has been embraced with enthusiasm by river, wetland, and lake ecologists in both management and conceptual frameworks. The landscape approach in aquatic ecology evolved from attempts to describe spatial patterns in biological communities through numerous classification systems identifying distinct zones within a river channel (Huet 1954, Illies and Botosaneanu 1963, Hawkes 1975). These individuals perceived rivers as linear features, with distinct habitat characteristics that served as a template for structuring biotic communities (e.g., Southwood 1977). Thus, landscape ecology principles were incorporated into their thinking even before the concepts of patches (Pickett and White 1985; Fig. 1), ecotones (Naiman and Décamps 1990; Fig. 1), and hierarchies of scale (Allen and Starr 1982; Fig. 1) had been defined in the modern field of landscape ecology. The landscape approach in aquatic ecology considers attributes, such as the spatial distribution, size, pattern, heterogeneity, connectivity, and boundary dynamics of discrete patches, and the effects of these factors on chemical, physical, or biological characteristics of an aquatic ecosystem. In our paper, we use the term *landscape* as a set of patches (areas with similar structure or composition) whose spatial extent is defined by the organism or process of interest (sensu Wiens 1989; Fig. 1). Landscapes can vary in size from a collection of localized habitats within a single ecosystem to complexes of large interlinked ecosystems (e.g., South America's Orinoco catchment, the Florida Everglades).

Our objectives for this paper were to: 1) summarize landscape approaches used in the study of aquatic (primarily freshwater) ecosystems, 2) update recent literature reviews on interactions between terrestrial

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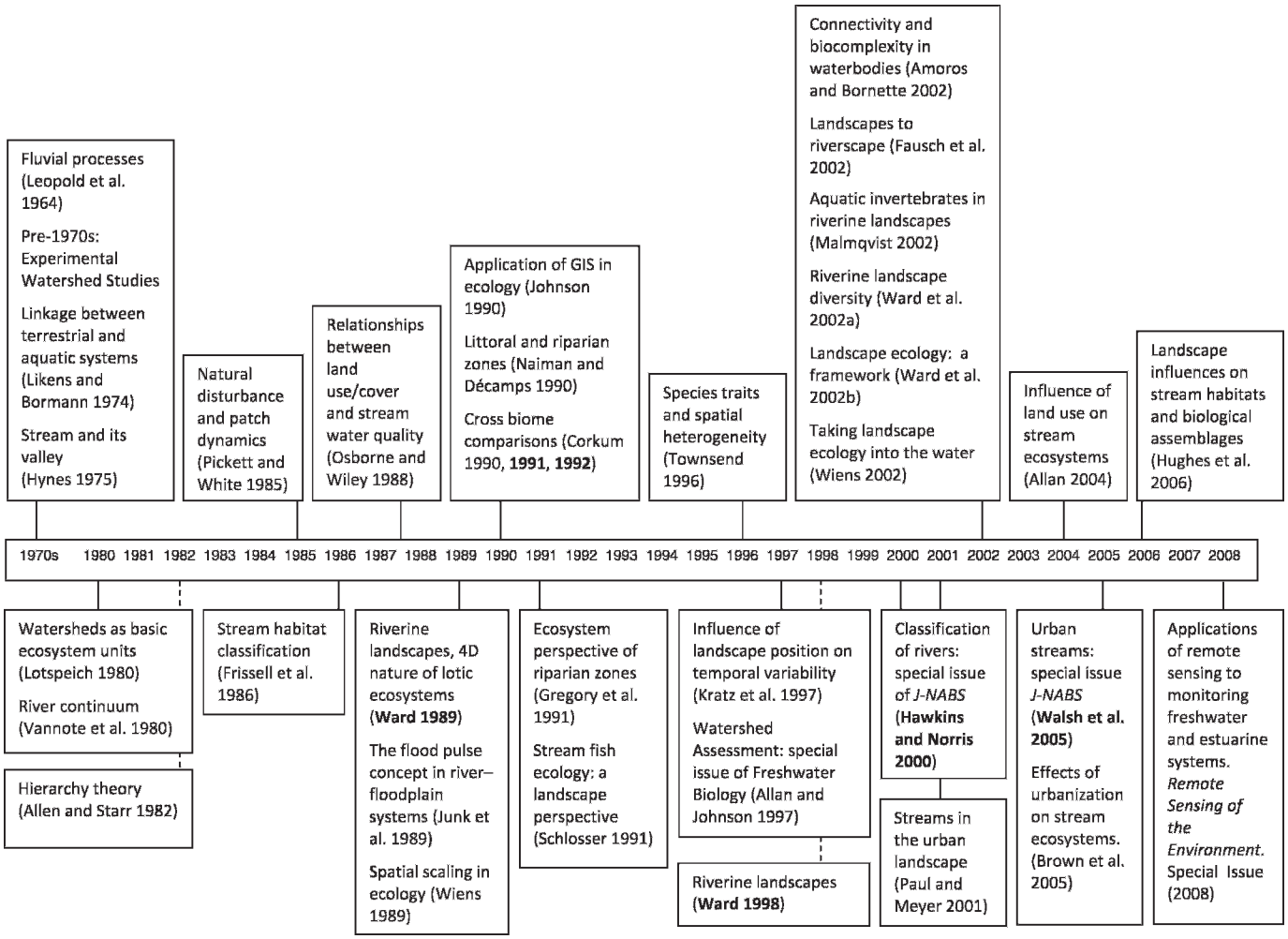

FIG. 1. A timeline of significant contributions to aquatic studies based on a landscape approach, with emphasis on those at the scale of catchments or coarser. GIS = Geographical Information system, 4D = 4-dimensional. Dashed lines are used for clarity when a connecting line passes behind a box. Boldface indicates papers published in *J-NABS*.

and aquatic ecosystems, and 3) discuss developments in the field of ecology as influenced by *J-NABS*. We focused primarily on phenomena occurring at spatial scales at or above the scale of catchments, whereas Winemiller et al. (**2010**[1]) addressed the application of landscape ecology principles at the scale of patches, including processes that either interact with or structure communities and habitats. Stream hydrogeomorphology is addressed by Poole (**2010**). Additional topics that touch on landscape ecology are addressed elsewhere in this issue and include: linkages among aquatic ecosystems (**Lamberti et al. 2010**), disturbance (**Stanley et al. 2010**), environmental assessment (**Dolédec and Statzner 2010**), reference conditions (**Hawkins et al. 2010**), and conservation (**Strayer and Dudgeon 2010**). Our review covered lotic ecosystems and emphasized the last 5 y because several significant reviews (Johnson 1990 [Fig. 1], Johnson and Gage 1997, Paul and Meyer 2001 [Fig. 1], Gergel et al. 2002, Allan 2004 [Fig. 1], Gregory 2004, Steinman and Denning 2005, Wang et al. 2006a) have covered earlier periods. Landscape approaches in lentic ecosystems have been poorly covered in the past reviews. Therefore, we extended our review to that earlier literature where appropriate. We focused our assessment of the role of *J-NABS* on the period from 1986 to 2008.

We reviewed aquatic ecological literature (primarily for freshwater ecosystems) during the period from 1986 through 2008, focusing on papers that incorporated landscape ecology concepts and tools. We reviewed titles and abstracts to screen for articles related to aquatic ecology. Book chapters are not covered well by many search engines, so they were included only when the authors had personal

[1] Boldface indicates paper was published in *J-NABS*

knowledge of the compilations. Our reference database consisted of >865 publications distributed across >120 journals and books.

We analyzed counts of several key words directly related to landscape ecology including: landscape, landuse, scale, patch, ecoregions, and landscape change. During the period from 1986 through 1995, relatively low, but consistent, numbers of papers referenced these terms (hereafter, landscape papers). The number of landscape papers increased sharply from 1995 to 1997, and then doubled between 1997 and 2008 (Table 1). Articles in *J-NABS*, *Freshwater Biology*, *Environmental Management*, *Hydrobiologia*, the *Canadian Journal of Fisheries and Aquatic Sciences*, and book chapters accounted for >½ of the publications (Table 1). *J-NABS* was not the first ecological journal to become 'literate' in landscape issues, but the contribution of *J-NABS* to the landscape/aquatic ecology literature has been substantial, especially when compared to other aquatic journals (Table 1). Fewer landscape papers were published in *J-NABS* than in *Freshwater Biology* (101 vs 147) between 1986 and 2008, but the other aquatic journals together published <140 landscape papers. In 1997, *Freshwater Biology* published a special issue on watershed studies (Allan and Johnson 1997; Fig. 1). Articles in this special issue originated from a plenary session and special symposium on landscape ecology at the 1995 annual conference of the North American Benthological Society (NABS). After this special issue was published, aquatic ecology papers addressing issues of *scale* and *landuse* increased. Articles referring to *ecological classifications* and *landscape patches* increased in 2000, in part because of a *J-NABS* special issue, "Landscape Classifications: Aquatic Biota and Bioassessments" (volume 19, issue 3), which originated from the classification symposium at the annual NABS conference in 1998 (**Hawkins and Norris 2000**; Fig. 1). Manuscripts incorporating concepts of *landscape change* became prevalent in 2005, possibly in response to the release of the 2001 National Land Cover Dataset (NLCD), which provided a complementary dataset to the 1992 NLCD. Last, beginning in 2005, *urbanization* became the focus of numerous papers, an increase that coincided with the *J-NABS* special issue, "Urbanization and Stream Ecology" (volume 24, issue 3) (**Walsh et al. 2005**; Fig. 1) and the American Fisheries Society proceedings on "Effects on Urbanization in Stream Ecosystems" (Brown et al. 2005; Fig. 1).

Early History and Development of Landscape Studies

Early studies of land–water interactions were conducted in experimental catchments (reviewed by Ice and Stednick 2004). Catchment–scale experiments initially focused on quantifying the role of forests in regulating stream flow. Researchers, including G. E. Likens, F. H. Bormann (Hubbard Brook Experimental Forest), D. W. Chapman (Alsea Experimental Forest), F. J. Swanson, and J. R. Sedell (H. J. Andrews Experimental Forest), were among the earliest to identify the effects of land management activities on stream ecosystem properties. Their work had far-reaching implications for policies and regulations influencing land management (e.g., Forest Practices Act of 1971), in addition to focusing attention on the land–water interface (e.g., Likens and Bormann 1974; Fig. 1).

From the late 1960s through the 1980s, lotic ecosystem studies that incorporated a landscape perspective aimed to: 1) identify fundamental processes regulating aquatic ecosystem structure and function at local scales; 2) quantify responses to localized disturbances, including impacts of human activities (e.g., agricultural or urban runoff, forest harvest) on ecosystem properties, such as biota, habitats, and physicochemical properties; 3) quantify implications of broad-scale phenomena (e.g., climate, landform) on ecosystem properties; and 4) quantify linkages between upland (especially riparian zones and floodplains) and riverine ecosystems (Table 2). Study of the direct and indirect impacts of human activities on channel morphology began about the same time (reviewed by Gregory 2004 and discussed by **Poole 2010**).

Ecologists studying lentic systems recognized the importance of the landscape context (especially with respect to geology, climate, topography, soils, and vegetation) in controlling physical, chemical, and biological processes and communities. These relationships were incorporated into the development of various classification systems (e.g., Cowardin et al. 1979) to group similar wetlands based on inherent biophysical or physicochemical characteristics, including the surrounding landform, types and saturation of soils, and vegetation cover types (reviewed by Mitsch and Gosselink 2000). In contrast, lake classification was based mainly on trophic conditions, either directly from nutrient measurements or by algal community metrics (Rawson 1956, Carlson 1977, Canfield and Bachmann 1981). Unlike lotic ecosystems, the primary focus of attention for lentic systems was on internal processes, and effects of atmospheric factors, such as acid rain, with relatively little attention devoted to interactions within catchments until the mid 1990s (see **Lamberti et al. 2010** for further discussion of such linkages).

Modern landscape approaches for studying lotic ecosystems can be traced variously to Leopold et al.

TABLE 1. Distribution of publications addressing the use of the landscape approach among mainly aquatic journals (*FWB* = *Freshwater Biology*, *Environ Manage* = *Environmental Management*, *CJFAS* = *Canadian Journal of Fisheries and Aquatic Sciences*), other ecological journals, and book chapters from 1986 to 2008. Citations for similar studies from the journal *Landscape Ecology* are included for reference. Blanks denote lack of publications meeting our criteria.

Year	*FWB*	*J-NABS*	*Environ Manage*	*Hydrobiologia*	*CJFAS*	Other journals	Book chapters	*Landscape Ecology*	Total
1986	1		1			2	1		5
1987		1				3		1	5
1988		7			2	8	2		19
1989	1	3			1	9	1	1	16
1990	4		1	1	4	15		2	27
1991	1	4		1	3	9	2	1	21
1992	3	1		2		9	2	1	18
1993	2	3	1	2		6	2	2	18
1994	2	1	1	1		6	3		14
1995	3	2		2	2	5	1		15
1996	4	4			1	12		4	25
1997	10	11	1	1		19	2	1	45
1998	7		2			14			23
1999	10	2	2	2	2	22	1	1	42
2000	14	16		1	2	14	4	3	54
2001	4	4	5	1		21		3	38
2002	20	4	2	1	2	27	8	3	67
2003	9	6	3	1	1	18	2	3	43
2004	6	6	4	1	1	16	2	3	39
2005	7	10	6	2	3	18	20	4	70
2006	5	8	2	9		18	31	2	75
2007	14	6	5	5	3	30		7	70
2008	20	2	9	29	5	26	1	6	98
Total	147	101	45	62	32	327	85	48	847

(1964; Fig. 1), who apparently first coined the term 'river landscape' and Hynes (1975; Fig. 1), who eloquently discussed the connection between a stream and its valley (see review of this topic by Gregory 2004 and **Poole 2010**). However, Vannote et al. (1980; Fig. 1) codified a conceptual framework linking upland and aquatic ecosystems in the river continuum concept (RCC). The RCC led to an enormous body of work and multiple refinements, including the discontinuum (Perry and Schaeffer 1987, **Townsend 1989**, Montgomery 1999, Poole 2002), serial discontinuity (Ward and Stanford 1983), flood pulse (Junk et al. 1989; Fig. 1), and catchment hierarchy (Townsend 1996; Fig. 1), among others. In the 1980s, aquatic ecologists began to acknowledge more fully the complexity and heterogeneity of running water systems, links to the physical processes that form them, and the biological interactions associated with particular habitats. By classifying catchments as areas of land controlled by climate and geology at one level and soil and vegetation at another, Lotspeich (1980; Fig. 1) was instrumental in defining a spatial unit that would become a fundamental focus of effort for resource management agencies. (Hereafter, we will use the term, *catchment*, to refer to the topographically defined area of land bounded by a watershed, although we recognize that the term, *watershed*, is the preferred term in some regions.) The need for a conceptual model that addressed physical complexities led Frissell et al. (1986; Fig. 1) to incorporate the hierarchical structure and geomorphic context of river basins into a classification system that sequentially identified features from the habitat scale to the whole catchment. Ward (**1989**; Fig. 1) articulated the importance of longitudinal and lateral connections and expanded upon the notion of a 2-dimensional riverine system by including the vertical exchange between the channel and ground water as a 3rd dimension and the temporal dynamics that encompass the range of patterns and processes observed in riverine ecosystems as a 4th. Ward was especially interested in how these factors affected biodiversity (Ward 1998, 2002b; Fig. 1).

Species–area relationships, habitat heterogeneity, and disturbance regimes have been acknowledged as some of the primary factors influencing biodiversity and richness patterns within a region (e.g., MacArthur 1957, Stanford and Ward 1983, **Statzner et al. 1988**, Junk et al. 1989), and numerous reviews have addressed the application of these concepts in lotic ecosystems (see **Resh et al. 1988**, Vinson and Hawkins

TABLE 2. Representative studies from the late 1960s to the early 1990s that addressed landscape phenomena in aquatic ecosystems.

Phenomenon	Reference
Structuring influences for biota, habitat, physical environment	
Assemblage composition	**Corkum and Ciborowski 1988**, Whittier et al. 1988, Corkum 1990 [Fig. 1], **1991**
Habitat	Southwood 1977, Barton et al. 1985, Statzner and Higler 1985, **Statzner et al. 1988,** Poff and Ward 1989
Disturbance	Dance and Hynes 1980, **Resh et al. 1988,** Weatherley et al. 1989
Factors structuring aquatic ecosystems	Minshall et al. 1983, Triska 1984, Naiman et al. 1988, **Townsend 1989**
Response to localized phenomena	
Urban land use: water quality	Wolman 1967 (as cited in Gregory 2004), Dillon and Kirchner 1975, Turner et al. 1975, Burton et al. 1977a, b, Faust and Goff 1977, Karr and Schlosser 1978, Hill 1980
Agricultural land use: water quality	Omernik 1976, Asmussen et al. 1979, Caporali et al. 1981, Omernik and Abernathy 1981, Osborne and Wiley 1988, Sharpley et al. 1988
Forest harvest impacts on habitat, biota, processes	Neary 1976, Gurtz et al. 1980, Newbold et al. 1980, Webster and Waide 1982, **Golladay and Webster 1987**, Beschta and Taylor 1988, Bilby 1988, Gregory et al. 1991
Large-scale phenomena	Minshall et al. 1983, Kansanen et al. 1984, Bott et al. 1985, Frissell et al. 1986, Hughes and Larsen 1986, Naiman et al. 1987, **Minshall 1988**, Kratz and Medland 1989
Land–water interactions	
Watershed and floodplain interactions with aquatic ecosystems	Likens and Bormann 1974, **Chauvet and Décamps 1989**, Collier and Jackson 1989
Influence of riparian vegetation on biota, nutrient and sediment inputs	Karr and Schlosser 1978, Schlosser and Karr 1981, Lowrance et al. 1985a, b, Peterjohn and Correll 1986, Hearne and Howard-Williams 1988, Osborne and Wiley 1988

1998, Ward 1998, Bunn and Arthington 2002). The RCC addressed longitudinal patterns of variation, whereas other workers (e.g., Welcomme 1979, Junk et al. 1989, Gregory et al. 1991 [Fig. 1], Ward 1998) emphasized the role of lateral interactions with the floodplain as drivers of species richness. Last, vertical patterns connecting rivers and floodplains with aquifers provided an additional dimension for enhanced biotic richness (**Ward 1989**, 1998). The temporal dynamics and corresponding spatial patterns characterizing natural riverine systems and their floodplains were recognized as major determinants of biodiversity patterns, with intermediate levels of disturbance thought to result in highest levels of richness (Hildrew and Townsend 1987).

Tools, Metrics, and Models for Landscape Analyses

Inherent to the landscape approach in aquatic ecology is a set of tools that has evolved over the past 2 to 3 decades, coincident with the development of low-cost computers, multivariate statistical tools, photogrammetry/remote sensing, and geographical information systems (GIS). Johnson (1990), Johnson and Gage (1997), and Gergel et al. (2002) reviewed the use of GIS, image processing, and spatial statistics for studies of spatial and temporal phenomena in aquatic ecosystems. Our early experiences and impressions suggested that many of the early investigations that used GIS and other spatial analysis tools were published in technical (as opposed to ecological) journals (e.g., *Photogrammetric Engineering*, and *Remote Sensing*, *Landscape Ecology*). We and others who attempted to publish in the ecological journals decades ago commonly complained of poor reviews because of a lack of understanding by reviewers and editors. This problem probably was a consequence of the nature of landscape analyses, including lack of true replication, reliance on space-for-time substitutions rather than experimental manipulation, and use of multivariate statistical techniques that required a unique skill set for both editors and reviewers.

GIS was a nascent technology in 1986. Nonetheless, in the late 1980s, GIS began to be used to generate data and test hypotheses on linkages between landscapes and aquatic ecosystems. A technical workshop and symposium entitled "Application of GIS and Remote Sensing in Aquatic Research Applications" at the 1992 NABS conference provided an introduction to these technologies. That symposium was followed by a plenary session and an accompanying symposium "Landscape Influences on Watersheds" in 1995, the year that marked a sharp increase in the number of papers in all of the major ecological journals that focused on GIS topics, including scale, land use, habitat, and biota (Table 1). Rapid developments in computers, statistical software, and improvements in GIS software led to 2 additional

technical workshops at NABS annual meetings, ''GIS Applications in Aquatic Environmental Impact Assessments'' in 1998 and ''GIS Workshop for Aquatic Professional'' in 1999.

Over the past decade, US federal and state agencies have developed massive repositories of available data, many of which have proven extremely valuable to landscape-scale analyses of aquatic ecosystems. Parallel efforts in Canada, the European Union, and elsewhere offer a range of aquatic and natural resource data. Remote sensing via satellite and airborne sensors has provided a means to acquire high-resolution, high-frequency images over large geographic regions. The 30-m resolution Landsat Thematic Mapper™ imagery has received wide use in landscape composition and pattern analyses for both terrestrial and aquatic ecology, and it provides the basis for the several land-cover classifications. More recent satellites, such as QuickBird and IKONOS, have increased spatial resolution (2.4 and 4 m, respectively), which enables mapping of features, such as submerged aquatic vegetation (Wolter et al. 2005). Spectral resolutions have also increased, and hyperspectral sensors allow spatial mapping of chlorophyll *a* distribution (Melack and Gastil 2001, Brezonik et al. 2005) and stream depth (Legleiter and Roberts 2005). More recently, airborne laser-induced direction and ranging (LiDAR) data are receiving increased attention for providing high-resolution elevation surfaces, with significant applications to watershed and bathymetric delineations (Lefsky et al. 2002, Jones et al. 2008, McKean et al. 2008a). A special issue of *Remote Sensing of the Environment* (2008, volume 112, issue 11; Fig. 1) contains 15 articles addressing remote sensing applications for monitoring freshwater ecosystems. Many of these articles describe methods that combine sensors with other tools (e.g., orthoimagery, models). Broad availability of high-resolution imagery has been accompanied by improvements in image analysis tools, such as texture-mapping or object-oriented approaches, that use the texture and patterns in groups of pixels to aid in image classification (Definiens eCognition™ Server; http://www.definiens.com/definiens-ecognition-server_6_7_8.html). Off-the-shelf (albeit expensive) technologies (e.g., Experimental Advanced Airborne Research; bathymetric LiDAR) now exist to map stream channels with sufficiently high accuracy to detect fish habitat (e.g., McKean et al. 2008b). Remote sensing of thermal characteristics of streams and lakes has provided particular insights into factors affecting distribution of fish habitat and populations. Technologies, such as aerial surveys to collect forward-looking infrared (FLIR) images, allow researchers to map temperatures quickly and continuously over many kilometers of stream (Torgersen et al. 2001, Beschta et al. 2003). FLIR analyses have been used to quantify relationships among continuous stream temperature, aquatic habitat, and fish species composition in mountainous catchments (Torgersen et al. 2006, 2007).

Quantifying the impact of human activities on freshwater ecosystems is one of the primary applications of a landscape approach. A staggering number of indices have been developed to quantify aspects of landscape structure and pattern. Gergel et al. (2002) reviewed many relevant metrics and approaches used for the purpose of assessing impacts on rivers. In most such studies, land use or impervious surface cover generally was summarized as a proportion of catchment area. Recent efforts by King et al. (2005), Gergel (2005), Baker et al. (2007), and Van Sickle and Johnson (2008) have implemented more refined techniques to quantify the distance dependencies of landuse effects within a catchment. Grid-based algorithms are used to quantify the potential influence of a particular landuse type given the relative distance of source pixels distributed throughout the catchment (King et al. 2005, Baker et al. 2006a, b, Van Sickle and Johnson 2008). Van Sickle and Johnson (2008) developed a distance–decay function to estimate the input, transport, and decay of solutes through the hydrologic network. Their method was tested using fish Index of Biotic Integrity (IBI) data in Oregon, USA. Flow distance weighting functions have been used with variable success in other regions (e.g., southeastern [King et al. 2005] and central [Wang et al. 2006a] US) and appear to be most effective in small catchments.

Simulation models incorporating spatial position refined our understanding of how riparian vegetation captures nutrients. Gergel (2005) modeled the spatial location of nutrient-source pixels and predicted that spatial arrangement would be most important in catchments with intermediate relative abundance of source or sink pixels. Small source or sink areas would not influence input or retention, regardless of location, and large sink or source areas would overwhelm the response. Spatial heterogeneity among the source and sink areas was important under different landscape configuration scenarios. These types of methods quantify an effective catchment area, a concept that has been applied to geomorphic studies to examine sediment transport processes (Fryirs et al. 2007), the buffering capacity of riparian zones (Osborne and Wiley 1988 [Fig. 1], McGlynn and Siebert 2007), and stress–response relationships within a catchment (Brazner et al. 2007b).

Several new metrics have been developed to assess the effect of riparian buffers on nutrient input as an alternative to the fixed-width buffer commonly used in GIS analyses. Baker et al. (2006b) tested mean

buffer width, gap frequency, and 2 measures of variation in buffer widths that were unconstrained by topography or topographic flow paths. Flowpath metrics improved model predictions compared to traditional fixed-distance measures.

Map resolution also is critical factor when assessing riparian processes, especially when catchment and riparian land use is weighted by flowpath distance (Baker et al. 2007). In some regions, streams can appear largely unbuffered on high-resolution maps relative to on coarse-resolution maps of the same region, and some flowpath distances become distorted. Hollenhorst et al. (2005) found that resolution of the land-cover maps can radically affect the width of interpreted riparian buffer strips. The size of these features can be greatly underestimated relative to data derived from aerial photographs, especially in agricultural regions where riparian buffer strips are narrow relative to the size of Landsat pixels (~30 m × 30 m).

None of the papers addressing methods for landscape analyses of aquatic ecosystems were published in *J-NABS* or other aquatic journals. An informal search of the table of contents of the journal, *Landscape Ecology*, from 1987 to the present suggests that early papers of an aquatic nature covered both the development of new techniques and their application. However, beginning in the mid 1990s, the prevalence of papers addressing application of landscape approaches has been balanced across the landscape and aquatic journals. (A keyword search similar to that done for the aquatic journals was not possible for this journal because the search terms did not disqualify nonaquatic topics.)

Recent Landscape-Scale Studies in Aquatic Ecosystems

Implementation of landscape perspectives in aquatic ecosystems

Work in aquatic ecosystems began to focus on interactions between aquatic systems and the surrounding landscape at multiple spatial scales as concepts from the field of landscape ecology, such as the influence of spatial scale (Wiens 1989, Levin 1992), spatial and temporal heterogeneity (Pickett and White 1985), boundary dynamics (Naiman and Décamps 1990), and the pattern of landscape elements (Forman and Godron 1986) became more widely accepted beyond terrestrial ecology. The foci of these studies included: 1) the river channel; 2) the river, floodplain, and riparian zone; and 3) the surrounding landscape that interacts with the river through surface and subsurface flow paths (Wang et al. 2006a). Recognition also was growing that the river included the wetted channel, side channel habitats, alluvial wetlands, springs, backwaters, floodplains, and floodplain lakes, and groundwater (Ward et al. 2002a; Fig. 1) and that river habitats were embedded in a shifting mosaic controlled by geology, hydrology, and climate (Arscott et al. 2002). This perspective was further developed by Townsend (1996), Fausch et al. (2002; Fig. 1), Ward et al. (2002a, b), and Wiens (2002; Fig. 1), who each emphasized the interactions between physical processes and spatial patterns and effects on the fluxes of biota, energy, and materials across patches and boundaries through time. Fausch et al. (2002) highlighted the work of Schlosser and colleagues, who pioneered new approaches based on this landscape paradigm. Schlosser and colleagues examined fish behavior in the context of their use of and movement across multiple habitat patches throughout their life cycle and translated their results in the context of disturbance ecology and conservation (Schlosser 1991 [Fig. 1], 1995, Schlosser and Angermeier 1995). This work was especially significant because it linked biotic processes with structural and functional aspects of streams and riparian zones at appropriate scales relevant to stream conservation and management planning (Fausch et al. 2002). We now accept that such approaches explicitly or implicitly incorporate theory and concepts from the disciplines of conservation biology (Ward 1998, Fausch et al. 2002, **Strayer and Dudgeon 2010**), geomorphology and hydrology (Statzner and Higler 1985, Townsend 1996, Poff et al. 1997, Poole 2002, **2010**, Thorp et al. 2006, Dollar et al. 2007), community ecology (Vinson and Hawkins 1998, Ward and Tockner 2001, Malmqvist 2002 [Fig. 1], Clarke et al. 2008, **Winemiller et al. 2010**), and population biology (**Newton et al. 2008**).

The NABS conference plenary session in 1995 (and the resulting special issue of *Freshwater Biology*) was one of the first compilations to focus on the influence of landscape and reach-scale variables on fish, invertebrates, water chemistry, coarse particulate organic matter (CPOM), and other attributes of lotic ecosystems (Allan and Johnson 1997). In a review of the influence of land use on stream ecosystems, Allan (2004) lamented that we have been only moderately successful in quantifying the underlying mechanisms accounting for the observed responses because: 1) covariation between the natural and anthropogenic factors on the landscape is considerable, 2) influences of these natural and anthropogenic factors are multifactorial and span several spatial scales, 3) landuse legacy effects are difficult to separate from present-day influences, and 4) many responses are nonlinear. Many of these topics are addressed below and in a 31-chapter volume on "Landscape Influences

on Stream Habitats and Biological Assemblages" (Hughes et al. 2006; Fig. 1).

Classification of aquatic ecosystems

The nomenclature of Frissell et al. (1986) was useful but did not fully account for the diversity and patchiness of hydrological characteristics (flow regime, flow history, and hydraulics) that occur within and across subcatchments and valley segments and that control many properties and processes within the ecosystem (Montgomery 1999, Poole 2002, **2010**, **Parsons et al. 2003**, Benda et al. 2004, Thorp et al. 2006). A classification system based on arrays of patches (hydrogeomorphic patches) formed by discontinuities in geomorphic and hydrologic conditions has been proposed (Thorp et al. 2006). The new field of ecohydrology incorporates tenets of ecology, geomorphology, and hydrology in water resource management (Zalewski et al. 1997, **Poole 2010**) and accounts for these discontinuities.

Lake management and conservation programs increasingly are adopting regional approaches for planning, assessment, and monitoring that use landscape and climate as fundamental predictors of lake properties. Climate, geomorphology, and other landscape variables provide overarching constraints on chemical, physical, and biological attributes of aquatic ecosystems. Understanding these constraints provides a context for assessing system responses to human activities or natural disturbances and predicting assemblage structure. To this end, considerable effort has been devoted to classifying lakes, streams, and wetlands in terms of their internal properties (Hawkes 1975, Cowardin et al. 1979, Busch and Sly 1992) and their position within regional landscapes (Higgins et al. 2005). Such classification systems have not been well tested to determine whether the resulting groups of lakes are coherent in their properties (but see Jenerette et al. 2002). Cheruvelil et al. (2007) tested several regionalization frameworks that classified lakes with similar water chemistry and quality to determine the appropriate spatial scale for effective regional monitoring. The best classification systems were those that resulted in smaller divisions and a larger number of classes. Tests with only minimally disturbed lakes captured less variance among regions (discussed below).

Ecoregional boundaries are based on the coincidence of physiographic features, including topography, land form, soils, and climate (Omernik 1987, Host et al. 1996), and rarely coincide with watershed boundaries. They provide a classification that has the potential to capture the broad-scale climatic and physiographic properties that influence aquatic ecosystems. The 2000 special issue of *J-NABS* focused on the role of landscape classification in bioassessment and quantifying various aspects of aquatic biota (**Hawkins and Norris 2000**). Authors examined classification relationships mainly in rivers (**Feminella 2000**, **Gerritsen et al. 2000**, **Hawkins et al. 2000**, **Marchant et al. 2000**, **Rabeni and Doisy 2000**, **Sandin and Johnson 2000**, **Van Sickle and Hughes 2000**, **Waite et al. 2000**), but one article focused on Swedish lakes (**Johnson 2000**). Articles addressed biotic assemblages, including invertebrates (**Hawkins and Vinson 2000**), diatoms (**Pan et al. 2000**), and fish (**McCormick et al. 2000**, **Oswood et al. 2000**). In a synthesis of these studies, Hawkins et al. (**2000**) concluded that landscape classifications alone were not sufficiently resolved to benefit bioassessment efforts, although landscape classifications did account for significant variation in biotic communities (**Hawkins et al. 2000**).

This conclusion was not surprising because factors operating at many scales determine the communities or ecosystem properties of an individual water body. This result led to refinements of ecoregion classification, in which additional landscape variables associated with particular biota were included in the classification framework. For example, the River Environment Classification for New Zealand (**Snelder et al. 2004**) includes climate, topography, geology, land cover, and network structure as classification variables. In a comparison of 5 classification systems based on combinations of ecoregions, geology, digital elevation models, or the geographical distance between sites, Pyne et al. (2007) agreed with Snelder et al. (**2004**) that different combinations (and scales) of classification variables were needed to predict attributes of different assemblages. The results of this and other studies suggest that regional patterns in biotic assemblages can be predicted from broad-scale classification systems, but site-level patterns are controlled by local-scale features (**Hawkins and Vinson 2000**, **Van Sickle and Hughes 2000**, **Snelder et al. 2004**, 2008).

Hierarchical control of habitat structure and communities

The strong hierarchical influence of landscape features (e.g., catchment size, geomorphology) and position in the network on habitat structure (e.g., depth, substrate, water velocity) and biotic assemblages has been acknowledged explicitly for some time (Allan and Johnson 1997). Disentangling the effects of features at different spatial scales has been the topic of many studies (especially of lotic ecosystems) over the past decade (reviewed by Allan 2004). Many studies partitioned variation among factors

occurring at 3 to 4 spatial scales (e.g., landscape with ≥ 1 catchments; stream segment consisting of a valley segment, a shorter stream segment defined by riparian conditions, and a local habitat scale). More researchers are using a network or subnetwork scale that encapsulates conditions within a certain buffer distance of the stream (Burnett et al. 2006, Wang et al. 2006b). Variations in these approaches have been used to examine patterns across very broad areas (nation, state, ecoregions, large drainage basins; Allen et al. 1999, Jones et al. 2001, Johnson et al. 2004, Pan et al. 2004, Sandin and Johnson 2004, King et al. 2005, **Arscott et al. 2006,** Goldstein et al. 2007), or to include smaller units, such as pool/riffle habitats or microhabitat patches (Townsend et al. 2004, Smiley and Dibble 2008, **Winemiller et al. 2010**). In nonlotic systems, authors have examined buffers at various distances surrounding wetlands to assess the influence of landscape phenomena (e.g., Mensing et al. 1998, Brazner et al. 2007a, b).

Robust statistical techniques have become available only recently to partition this variation into constituent parts. The singular and combined effects of variables at different spatial scales can be quantified with *variance partitioning* methods (Richards et al. 1997, Johnson et al. 2004, 2007, Stoffels et al. 2005, Gido et al. 2006, **Kratzer et al. 2006**, Brazner et al. 2007a, b). Another common approach for assessing effects at various spatial scales is to develop regression models based on groups of variables that represent the different scales, with subsequent comparison of the model fit by comparison of the *F*-value, variance explained, or evaluation of Akaike information criterion (AIC; Akaike 1974, **Dow et al. 2006**). Techniques for partitioning variation among stressor and nonstressor variables or among spatial scales are addressed below.

Burnett et al. (2006), Johnson et al. (2006), and Dow et al. (**2006**) used regression to evaluate the influence of catchment-, riparian-, and local-scale variables on habitat. They found distinct regional differences in the spatial scales characterizing dominant predictors of habitat, a strong influence of geomorphic factors, such as catchment area and channel width, on the distribution of large wood, and significant effects of land use/cover at riparian to subcatchment scales. Goldstein et al. (2007) evaluated the relative importance of environmental setting (geology, topography) vs land use on stream habitat variables across the US and found that land use was not a good predictor of stream habitat variables at the scale of the continental US. However, the predictive power of land use increased as the scale decreased to that of level II ecoregions. Hierarchical control over habitat structure has been addressed in relatively few studies, but an increasingly large body of work has addressed geomorphic controls over the structure and function of large floodplains and river channels (**Poole 2010**).

Many studies have examined interactions among spatial scales to explain patterns of biotic diversity and assemblage structure (e.g., **Corkum and Ciborowski 1988**, **Corkum 1991** [Fig. 1], **1992** [Fig. 1]), Downes et al. 1993, Boyero and Bailey 2001, Li et al. 2001). As landscape studies have become more common, effort has shifted to address variation in biotic responses (mainly diversity, species richness, and assemblage structure) along environmental or geographic gradients (Table 3) and to test theoretical relationships regarding the processes responsible for controlling local and regional species richness. Winemiller et al. (**2010**) provide a review of patch-scale phenomena that influence biotic assemblages and populations.

Spatial heterogeneity of riverine systems influences α (within-site) and β (among-site) diversity (Ward 1998, Ward and Tockner 2001, Amoros and Bornette 2002 [Fig. 1], Robinson et al. 2002). Disparities persist with respect to predictions of local vs regional or joint control over fish α diversity (Hugueny and Paugy 1995, Angermeier and Winston 1998, Oberdorff et al. 1998). Local diversity was not associated with regional diversity in 5 Mississippi River drainages (Love and Taylor 2004). Fish assemblage diversity was hierarchically controlled in 2 large tributary catchments of the Mississippi River in Illinois, but disturbance levels influenced diversity patterns (Pegg and Taylor 2007). Patterns of diversity for introduced species differed from those of native species (Angermeier and Winston 1998). Strong seasonal patterns in flow regimes (and habitat structure) in tropical lowland rivers appear to be associated with high α and β fish diversity (Arrington and Winemiller 2004).

Patterns of invertebrate species diversity and richness differ depending on the size of the study streams. In Finnish headwater streams, local macroinvertebrate species richness was linearly related to regional species richness, a result suggesting that local communities were unsaturated and free of local control. Regional factors set the upper limit of local species richness (Heino et al. 2003). Clarke et al. (2008) reviewed macroinvertebrate diversity in headwater streams from around the world and concluded that α diversity in headwater streams was not high, but that β diversity was high within catchments and, thus, contributed to higher regional (γ) diversity. Clarke et al. (2008) also concluded that species richness follows a hump-shaped pattern with increasing stream size, i.e., along the longitudinal gradient. Whether macroinvertebrate diversity was determined by regional or

local features in Swedish lakes and streams was not clear (Stendera and Johnson 2005). α diversity (within sites and within ecoregions) was low, whereas β diversity (between sites and between ecoregions) was high, a result suggesting that regional factors were more important than local factors (Stendera and Johnson 2005). That study suggested that the size of the regions studied might explain differences in results between Finnish and Swedish systems. Their study illustrated the importance of using different diversity indices to account for the contributions of rare and common species (see also Erös 2007, Heino et al. 2008). The distributions of individual species are influenced by species interactions and by life-history strategies and landscape connectivity, which play a role in processes, such as dispersal and colonization potential (e.g., Malmqvist 2002). However, spatial and temporal dynamics affecting connectivity and spatial heterogeneity interact to influence biodiversity at multiple scales (Clarke et al. 2008). Such differences highlight the fact that we have not yet arrived at the full explanation of the factors that control diversity and richness. Genetic data are proving essential for quantifying the spatial patterns of species dispersal patterns (Hughes 2007, Finn et al. 2007) and might lead to some resolution of these issues. *J-NABS* has not played a significant role in this area of research.

Many studies have quantified the relative importance of local and regional variables for predicting assemblage structure. In Table 3, we present a list of representative studies and list the spatial scale of responses for different assemblage types and aquatic ecosystems. The diversity of responses at different scales is notable. One study assessed the spatial scale of responses assemblages of fish, macroinvertebrates, macrophytes, and algae to environmental gradients across relatively undisturbed lowland and mountainous European streams (Johnson et al. 2007). The spatial scales of responses of the 4 assemblage types were unexpectedly similar among assemblages. Most among-site variation was explained by latitude and ecoregion, but when geography was used as a covariate, the greatest variation was explained by local habitat variables reflecting water chemistry and substratum. However, that local habitat largely explains assemblage structure is not universally recognized (Roth et al. 1996, Wang et al. 1997, 2001, Allen et al. 1999, **Mykrä et al. 2008**; Table 3). Different results among studies might reflect differences in study region size or level (possibly also types) of disturbance. The authors of many studies have concluded that scale dependencies in the distribution of biota should be matched appropriately to the scale dependencies in environmental features to understand most effectively the factors controlling biological communities. Understanding such dependencies can inform the selection of appropriate scales for environmental assessments and the choice of summary metrics (**Parsons et al. 2004**, Brazner et al. 2007a, b). Furthermore, variability within and among sampling units at different scales should be addressed in the sample design (Heino et al. 2004, Stoffels et al. 2005, Smiley and Dibble 2008) to ensure that observed patterns are not artifacts.

Influence of spatial heterogeneity and context

Landscape position and connectivity, especially with respect to the type, width, and contiguity of riparian vegetation, affect responses of aquatic ecosystems to local and regional conditions (reviewed by Steinman and Denning 2005). However, the influence of the landscape matrix (the dominant land cover in the catchment) in mediating these relationships is not as well understood. Fish assemblage responses were poorly predicted by land use in catchments under intensive agricultural production (resulting in low landscape heterogeneity) in southern Minnesota (Stauffer et al. 2000) and Iowa (Heitke et al. 2006). Macroinvertebrate assemblage structure and species traits also were poorly predicted in predominantly agricultural catchments in Minnesota and Michigan (Richards et al. 1996, 1997). Richards et al. (1996) found that reach-scale (i.e., local) variables were the best predictors of macroinvertebrate species traits in Michigan catchments with a mixed-landuse landscape (higher heterogeneity) and a pronounced disturbance gradient. Over a larger area that included all of Wisconsin and northern Michigan, Wang et al. (2006b) concluded that local-scale variables were the better predictors of fish assemblage composition, abundance, and presence/absence in the more disturbed regions, whereas catchment-scale variables, including land use, were the better predictors in the less disturbed regions. The predictive power of the intermediate-scale variables (network = riparian zone upstream of sampling point, and riparian zone within sample reach) was similar among disturbance levels. Hughes et al. (2005) observed a similar shift in importance from local- (instream) to network-scale factors along a gradient from more to less disturbed regions. However, in less-disturbed areas of Michigan, Wisconsin, and Minnesota, which are dominated by forested land cover, landuse variables were better predictors of invertebrate traits than were climate, geology, or reach-scale variables (**Weigel et al. 2003**).

These studies (and others) suggest that the influence of landscape variables on biotic assemblages is difficult to predict when disturbances are severe and

widespread or the landscape is relatively homogeneous, a conclusion that is consistent with the results of nutrient-input simulations by Gergel (2005). This problem probably is attributable to the lack of variation in the landscape predictor variables. Depending on the response variables and the size of the study region, the relative influence of landscape and local variables can be distinguished when the landscape is less disturbed. Across very large regions, variation in biotic assemblages in undisturbed streams often is explained mainly by local features once the effect of latitude has been removed (e.g., Heino 2005, Johnson et al. 2007, Mykrä et al. 2007). However, this trend is not universal (e.g., Gido et al. 2006, Urban et al. 2006, **Mykrä et al. 2008**), and a better understanding of the interactions among the size of the study region, the amount of background disturbance, and the role of landscape heterogeneity clearly is needed.

The lateral and vertical dimensions of hydrologic connectivity within a catchment or network have been relatively well studied in aquatic ecosystems (Junk et al. 1989, Ward et al. 2002a). Different types and extents (in space and time) of connections influence variables, such as water temperature, turbidity, nutrient content, and habitat heterogeneity. The timing and duration of connections among riverine habitats affect successive creation and destruction of habitats (Arscott et al. 2002) and habitat refugia (Robinson et al. 2002), with resulting patterns in species richness that vary across biota depending on habitat requirements and life-history stage (Tockner et al. 1998). Ecosystem processes, such as production and transport, also influence organic matter processing during various stages of inundation (Amoros and Bornette 2002). Winemiller et al. (**2010**) discuss resulting patterns of heterogeneity and implications for habitat, biodiversity, and ecosystem processes.

The study of floodplain dynamics has benefitted greatly from the integration of GIS, remote sensing, aerial photograph interpretation, and modelling. A time-series of data collected over 60 y showed that the structure of floodplain systems (i.e., shifting mosaic) was the result of interactions among climate, floods, and plant succession (Whited et al. 2007). Regulation of rivers by humans has profound effects on the geomorphology of a river system because it alters flow regime and sediment deposition (e.g., Surian 1999). These effects also influence riparian (and island) vegetation and other aquatic assemblages (Kollmann et al. 1999, Gurnell et al. 2001). See Bunn and Arthington (2002) for a comprehensive review of the consequences of altered flow regimes for biodiversity, and Stanley et al. (**2010**) for a more general discussion of disturbance.

Habitat patch connectivity strongly influences biological assemblages. Schlosser (1991, 1995) and Schlosser and Angermeier (1995) were among the first to interpret fish assemblage patterns through the lens of habitat patch connectivity. They recognized that fish life-history requirements and availability of refugia depend on the spatial arrangement of habitat patches within a network. Thus, species-specific life-history and habitat requirements dictate responses to disconnected and connected water bodies. α diversity of fish assemblages tends to decrease, whereas β diversity increases when side-channel habitats become disconnected. In contrast, diversity patterns for selected species of amphibians showed an opposite pattern (Amoros and Bornette 2002). Amphibian diversity in wetland complexes varies with respect to wetland connections to permanent water bodies, which generally support predaceous fish (Wells 2007).

Recognition of the importance of spatial arrangement and spatial scale of observations has fundamentally altered stream fisheries management (Fausch et al. 2002). Spatially continuous data collected at intermediate levels of observation provide the most robust relationship assessments between fish-habitat and habitat heterogeneity (Gresswell et al. 2006, Torgersen et al. 2006). Continuous sampling is expensive and prohibitive for regional efforts, but provides invaluable information on species distributions, population survival, and persistence of communities within a stream network in response to local-scale conditions and disturbances. A less expensive approach is to include spatial data about the position of sampling sites within the stream network implicitly by noting the proximity of a sampling site in a tributary to the main stem of the river (e.g., Hitt and Angermeier 2008). Analyses based on graph theory might be useful for examining the effects of fragmentation on riverine fish populations (Schick and Lindley 2007).

In rivers, landscape position along a regional flow path strongly influences many ecosystem properties, including habitat, water quality, nutrient cycling, and assemblage structure and composition. In lakes, position along a regional flow path influences concentrations of cations and other solutes (Kratz et al. 1997 [Fig. 1], Sorrano et al. 1999, Kling et al. 2000, Lyons et al. 2000), thermal properties (Benson et al. 2000), and structure of algae, invertebrate, fish, snail, or crayfish assemblages (Lewis and Magnuson 2000, Riera et al. 2000, Quinlan et al. 2002, Hrabik et al. 2003, Heino and Muotka 2006). Kratz et al. (1997) reported that fish and snail species richness increased from lakes in the upper drainage to lakes low in the

TABLE 3. Examples of recent (post-2000) studies addressing the scale at which environmental factors explain the structure of biotic assemblages in aquatic ecosystems. Spatial scales that explain the most variation are in boldface. Different terms for similar spatial scales make identification of global trends difficult (see Future Challenges above). R = river, L = lake, I = invertebrate, F = fish, D = diatom, M = macrophyte, S = snails, C = clams.

Ecosystem type	Assemblage	Response	Citation
R	I	Assemblages best explained by **local** habitat in highly disturbed region (southern Minnesota, USA)	Dovciak and Perry 2002
R	I	Variability in assemblages of mountainous streams best explained by **longitudinal position**; functional traits best explained by **reach-scale** variables (Colorado, USA)	Finn and Poff 2005
R	I	Caddisfly assemblage distributions best explained by **local and regional** (landuse) features (Oklahoma, USA)	Galbraith et al. 2008
R	I	Functional diversity best explained by **local features**; spatial position (geography) also important (Finland)	Heino 2005
L	I	Taxonomic and functional composition best explained by **habitat** in lake littoral zones; latitude also important predictor (Sweden)	Johnson and Goedkoop 2002
L, R	I	In lakes, among site variation best explained by **habitat** characteristics; in streams, **ecosystem** scale best predictor (Sweden)	Johnson et al. 2004
R	I	**Ecoregion and stream** scales explained most variation in assemblage structure; differences in richness varied among spatial scales (western Oregon, USA)	Li et al. 2001
R	I	Assemblages differ among **ecoregions, drainage systems,** and **stream size class** (in that order) in near-pristine streams (Finland)	Mykrä et al. 2004
R	I	Assemblage structure best explained by **local** features; influence of local features (especially stream size, acidity) increased with decreasing spatial extent (Finland)	Mykrä et al. 2007
R	I	Minor differences in explanatory power of local vs regional attributes (Finland)	**Mykrä et al. 2008**
R	I	Assemblage similarity was greatest among riffles and regions; **region** and **reach** best predictors of assemblage structure (Australia)	**Parsons et al. 2003**
R	I, F	Invertebrate assemblages best explained by natural features at **catchment** scale; fish assemblages best explained by natural features at **local** (bedform) scale (New Zealand)	Townsend et al. 2003
R	I	Local habitat and reach features poor predictors; taxon richness negatively related to household density; assemblage structure predicted by amount of remnant forest in the catchment and in the riparian zone; instream distance (**connectivity**) strongest predictor (Connecticut, USA)	Urban et al. 2006
R	I, D, M	After accounting for spatial factors (geography, ecoregion), **habitat**-scale features best predictors for all assemblages in least-disturbed streams; lowlands and mountains of Europe	Johnson et al. 2007
R	F	**Soils, slope, land use** explained more variation in assemblages than reach or site features (Iowa, USA)	Gido et al. 2006
R	F	Assemblage best predicted by instream **habitat**; land use not a good predictor in highly disturbed landscape (Iowa, USA)	Heitke et al. 2006
R	F	Metric responses to local stressors might be influenced by presence of mainstem connections; **spatial position** in network deemed important (Mid-Atlantic ecoregion, USA)	Hitt and Angermeier 2008
R	F	**Long-term flow regime, catchment and riparian cover** best predictors of occurrence, abundance, biomass (eastern Australia)	Kennard et al. 2007
R	F	Assemblages best predicted by **lithology, stream size,** and **mean rainfall**; spatial factors also influential; increased richness seen at downstream locations (Portugal)	Magalhaes et al. 2002

TABLE 3. Continued.

Ecosystem type	Assemblage	Response	Citation
R	F	Fish diversity at **site** scale contributes to regional diversity; disturbance history is an important explanatory factor in regional diversity (Illinois, Missouri, USA)	Pegg and Taylor 2007
R	F	Spatial, temporal (flow history), and environmental factors equally important in explaining assemblages (Queensland, Australia)	Stewart-Koster et al. 2007
R	F	**Reach-**scale variables explained most variance; influence of reach-scale variables greatest in undegraded areas; **catchment-**scale factors increase in importance with disturbance (Midwestern USA)	Wang et al. 2003
R	F	Assemblage structure best explained by **catchment**-scale features (land use, soils, riparian, bedrock geology) in disturbed regions; as level of disturbance decreased, **local**-scale features better predictors (Michigan, Wisconsin, USA)	Wang et al. 2006b
L	SC	**Landscape position** (along the flow path) and **local habitat** equally important explanatory power for predicting molluscan assemblages (Finland)	Heino and Muotka 2006

landscape. Low-order lakes are isolated from the regional flow path, and thus reflect the basin and precipitation chemistry. Lakes lower in the chain were more directly influenced by ground and surface water and had higher ionic concentrations and more connections to stream networks than did lakes higher in the chain. Complex chemical and biological responses result from the confounding effects of bedrock and surficial geology, hydrologic regime, and geographic location in both lentic (Sorrano et al. 2009) and lotic (**Sweeney et al. 2006**) ecosystems.

Natural dispersal barriers limit the connectivity of lakes, and thus, the distribution of fish within lake chains. Landscape tools have been used to help predict the distribution of fish based on identification of such barriers (e.g., Spens et al. 2007). However, factors other than landscape connectivity also influence fish distributions. Landscape variables, such as lake size, depth, outflow gradient, distance to other lakes, lake order, altitude, river drainage, and age of glacial surface were evaluated as predictors of fish distributions and colonization and survival potential in Alaska. The distribution of fish species was influenced by geologic restructuring of the landscape through time that has altered landscape patterns, especially the extent and location of stream connections (Hershey et al. 2006).

Climate changes can alter landscape connectivity to create remnant populations in areas experiencing drying and to increase the potential for colonization in areas experiencing flooding. Enhanced connectivity can allow range extensions of native and of nonnative invasive species. Predicting changes in biotic assemblages under future climate scenarios will be challenging because anthropogenic disturbances that disrupt natural flow regimes (and water levels) and climate effects are likely to be confounded and because the ability to disperse differs among species. Moreover, physicochemical characteristics of water bodies are likely to change as surficial and groundwater connections change.

Landscape perspectives on the impact of disturbance

Human disturbances must be viewed at the catchment scale to account for cumulative impacts and the underlying constraints of the natural landscape. Effects of large-scale phenomena (including human disturbance) on biota can be inferred indirectly through variance partitioning or mechanistic explanations based on habitat responses (e.g., Richards et al. 1996, 1997, Hutchens et al. 2009). Covariance structure analysis (CSA) can quantify direct and indirect landscape effects. CSA was used to analyze effects of catchment hydrology, stream hydraulics, and stream channel shape on fish assemblages, fish biomass, and stream temperature in southern Michigan streams (Infante et al. 2006, Zorn and Wiley 2006, Wehrly et al. 2006). Catchment agriculture was negatively associated with fish condition (mass), but was positively associated with species richness. Catchment variables (stream size, land use, surficial geology) explained substantial spatial variation (50–80%) in habitat variables, such as depth and flow, which directly affected substrate composition. Local-scale variables (nutrients, substrate) had direct effects on fish biomass, whereas catchment-scale variables (area, land use) had indirect effects (Zorn and Wiley 2006). Thus, CSA can provide causal pathways that can be used to identify targets for management and restoration.

Regional impacts of landscape-scale phenomena, such as urbanization, can be quantified more directly when variation caused by local-scale features is removed from the data set by applying rigorous site-selection criteria. A comparative study of 3 urban centers in the US was conducted using this type of design and urban intensity indices (one applied across all regions and others applied to each region) that incorporated land use, socioeconomic factors, and infrastructure variables (Tate et al. 2005). Predictions of habitat (Meador et al. 2005), algae (Potapova et al. 2005), fish (Meador et al. 2005), and macroinvertebrate responses were confounded by strong regional differences among the cities. The best predictors of macroinvertebrate responses were related to land use at the basin scale (Cuffney et al. 2005), a result that was not surprising, given the strong emphasis on use of site-selection criteria to remove variation at the local scale. Moore and Palmer (2005) found strong linear responses of invertebrates to an urban gradient in the Washington, DC, metropolitan area. However, riparian vegetation cover was associated with increased taxonomic diversity, even in areas with significant amounts of impervious surface cover. Alberti et al. (2007) found that the amounts and configurations of impervious surface and forested land were strong predictors of benthic macroinvertebrate assemblages (IBIs). Few other studies have addressed the spatial patterning of landuse elements, although increasing availability of appropriate tools might increase the frequency of such studies.

Disturbances associated with patterns of housing and roads in urbanized landscapes are one of the important landscape elements affecting aquatic ecosystems. Catchment and lakeshore development have been studied at regional scales to assess their impacts on littoral zone habitat structure, including woody debris (Christensen et al. 1996), aquatic vegetation (Radomski and Goeman 2001), trophic interactions (Jeppesen et al. 2000), macroinvertebrates (Brauns et al. 2007), fish distributions, and cultural eutrophication (Scheuerell and Schindler 2004). In all of the above examples, development of lake shorelines disrupted assemblages, habitat, or processes. Two special symposia on urbanization, one published in *J-NABS* (**Walsh et al. 2005**) and another published as a symposium proceedings of the American Fisheries Society (Brown et al. 2005) have made significant contributions to this body of work.

Landscape perspectives on coastal environments

Coastal areas can contain many hydrogeomorphic formations and ecosystem types, such as cliffs, beaches, and fringing, palustrine, and riverine wetlands (Keough et al. 1999). Thus, coastal areas provide a different set of challenges for linking landscape and response variables. A multiscale assessment designed to disentangle the influence of a human disturbance gradient and nonstressor covariables was implemented for coastal wetlands along the US side of the Laurentian Great Lakes (Danz et al. 2005, 2007, Brazner et al. 2007a, b). Distribution patterns among birds, amphibians, fish, invertebrates, wetland vegetation, and diatoms were better explained by geographic (lake) factors than by geomorphic factors (wetland type) or human disturbance (Brazner et al. 2007a). Environmental variables in this assessment were summarized across a range of spatial scales (100, 500, 1000, 5000 m, and whole catchments). Nonstressor covariables explained more variation in biological response variables than did disturbance variables, and responses were not concordant across assemblages (Brazner et al. 2007a). A human disturbance gradient also has been used to identify reference reaches in streams (e.g., Danz et al. 2005, 2007, Host et al. 2005, Wang et al. 2008).

An increase in landscape-related assessment papers in 2005 and 2006 corresponded with NABS-sponsored symposia at 2 annual meetings (''Determining and Using Reference Condition in Biological Assessments'' and ''Environmental Assessment Meets Landscape Ecology Meets Landuse Planning'' (the latter summarized by Johnson et al. 2007). Many papers published during this period emphasized land use, particularly urbanization and agriculture, as factors regulating biological and chemical responses. An increase in assessment articles coincided with an increase in articles on ecological indicators of ecosystem health that incorporated landscape-scale influences (e.g., 2007 special issue of *Journal of Great Lakes Research* on coastal indicators). See Hawkins et al. (**2010**) and Dolédec and Statzner (**2010**) for discussions of reference approaches and bioassessment.

Landscape perspectives on assessing ecosystem functions and services

J-NABS has been a leader in publication of studies focused on measures of ecosystem function in aquatic ecosystems, and some of these studies have included a landscape component. The link between landscape characteristics and ecosystem functions received relatively little attention until recently, when efforts to understand the mechanisms by which human activities degrade aquatic ecosystems began to be focused on developing measures of ecosystem functions for use in environmental assessment programs.

Many measures of ecosystem function are not well suited for implementation over large regions because of the time and cost of field sampling or sample processing. However, altered ecosystem function is a symptom of human disturbance (Bunn and Davies 2000, **Meyer et al. 2005**, **Sweeney et al. 2006**) and should be included in evaluations of restoration success (Lake et al. 2007). Bunn et al. (1999) were among the first to implement a regional characterization of benthic gross primary production and respiration measures to assess the impact of catchment and riparian disturbance on stream ecosystems in Australia. A special issue of *J-NABS*, "Source-Water Monitoring: Combining Basic and Applied Research," featured a comprehensive study of the New York City water-supply catchments. Sweeney et al. (**2006**) used a broad range of biological and ecosystem function measures, including (in part) macroinvertebrate assemblages (**Kratzer et al. 2006**), organic matter transport (**Kaplan et al. 2006**), primary production and ecosystem metabolism (**Bott et al. 2006a**, b), and nutrient and organic C uptake (**Newbold et al. 2006**) to assess the sources of the New York City drinking-water supply. They integrated these measures in a comprehensive analysis of local and landscape features that included variance partitioning across spatial scales (**Arscott et al. 2006**).

Net ecosystem production measures appear to be strongly controlled by local-scale factors, and are particularly sensitive to riparian cover (Bunn et al. 1999, Young and Huryn 1999, Bunn and Davies 2000, **Bott et al. 2006b**). Bott et al. (**2006a**) found negative correlations between gross primary production (GPP) and indicators of urbanization. In contrast, ecosystem metabolism was not correlated with indicators of urban land use in streams in the vicinity of Atlanta, Georgia (**Meyer et al. 2005**), although lower uptake velocity values for NH_4 and soluble reactive P were found in urban than in forested streams. Increased nutrient removal but reduced efficiency were associated with elevated nutrient concentrations, a pattern consistent with results of Mulholland et al. (2008) from streams across a wide range of land uses and geographic regions.

Runoff from agricultural fields and riparian vegetation alteration are associated with elevated total N and NO_3-N concentrations in nearby water bodies. The proportion of row-crop land use in the catchment can predict up to 86% of the total variation in N content (e.g., Johnson et al. 1997, Jones et al. 2001, Meador et al. 2005, Dodds and Oakes 2007). Such loadings are expected to alter N cycling. Denitrification rates did not differ among agricultural and urban streams in Indiana, USA, but NO_3-N concentrations were higher in the agricultural streams (**Arango and Tank 2008**). Mean annual nitrification and denitrification rates were positively correlated with % agriculture in the catchment and in 100-m buffers. Nitrification rates were best predicted by sediment C content (**Arango and Tank 2008**). Instream structures, such as debris dams and organic-rich gravel bars, were sites of intensive denitrification activities in suburban and urban streams (**Groffman et al. 2005**). Unfortunately, structures, such as debris dams, are among the first habitats removed by well-meaning landowners concerned about potential flood impacts. In addition, increased stream power in channelized urban streams can preclude the persistence of such structures. Increased nutrient loading also directly affects invertebrate consumers. Lower periphyton C:N and C:P ratios were associated with elevated nutrient (NH_4^+ and soluble reactive P) excretion by mayflies (**James et al. 2007**), but body content nutrient concentrations and ratios did not differ across a range of agricultural landuse intensities.

The emerging emphasis on ecosystem functions and services probably will result in increased use of landscape ecology techniques for assessing environmental impacts and the success of restoration projects or ecosystem recovery. McTammany et al. (**2007**, 2008) examined ecosystem recovery from agricultural activity, and found that nutrient levels and suspended particles were higher in recovering streams than in forested streams. In recovering streams with well-developed riparian zones, GPP (**McTammany et al. 2007**) and stream temperatures (McTammany et al. 2008) were similar to those of forested streams, but the elevated nutrient concentrations indicated that the streams in which agricultural activities had ceased for $\geq$50 y had not yet fully recovered. Other ecosystem properties also have long recovery times. For example, abundance of large wood in Pacific Northwest streams is predicted to require $\geq$100 y following harvest in the riparian zones (e.g., Murphy and Koski 1989). Few studies have fully quantified recovery of ecosystem functions following a persistent disturbance, such as change in land use.

Summary

The paradigm that many fundamental components of aquatic ecosystems are regulated by processes operating at landscape scales has evolved. Early aquatic studies with large spatial extents focused on correlative relationships between landscape features and biotic components of stream systems (Table 2). Later studies addressed intermediate causal linkages between landscape and biota, including landscape

influences on hydrology, habitat at various spatial scales, and instream processes (Table 3). Understanding and quantifying these causal linkages paved the way for recent advances in ecological assessment techniques that use GIS and remote sensing technologies to make interpretations of aquatic ecosystem health over broad spatial scales (Kloiber et al. 2000, Brezonik et al. 2005, Wolter et. al. 2005, McKean et al. 2008a).

Increasingly sophisticated tools are available for measuring landscape pattern and context including airborne thermal imaging (e.g., FLIR), high-resolution texture or elevation data (e.g., LiDAR), and computer algorithms for delineating watershed boundaries (e.g., ArcHydro®). Regional landscape context and appropriate classification units are important for quantifying the correct scale of analysis and quantifying responses. However, evaluating results across spatial scales is a challenge. For example, at least 3 terms were used commonly to describe the area within the stream at the reach level, as defined by Frissell et al. (1986). This scale is variously called the habitat, site, or local scale. At larger scales, various authors refer to regional, catchment, watershed, or landscape scales. Such terms are imprecise and complicate development of generalizations about responses to features across spatial scales. The terms used to describe the area included in a spatial scale of interest should be standardized. We recommend that editors insist on clear definitions of the approximate area and spatial extent of a study unit.

Challenges and Future Directions

Considerable progress has been made in applying landscape concepts to aquatic ecology. However, future researchers face a number of key challenges. Foremost among these are the confounded interactions between broad-scale factors that regulate aquatic ecosystems (climate, physiography, regional hydrology) and patterns of human disturbance. Discriminating natural and anthropogenic effects remains difficult despite advanced mapping and statistical tools. Better analytical techniques or high-resolution mapping tools will facilitate detection of key drivers (and stressors) and ecosystem responses. Advanced multisensor systems are generating large amounts of data useful for research applications and monitoring of freshwater systems, but the widespread integration of GIS and remote sensing technologies into landscape analyses has brought both opportunities and challenges. Even with inexpensive data storage and advanced processing capabilities, the sheer amount of data contained in QuickBird, LiDAR, or other types of images poses formidable analysis problems when applied over large spatial scales. Continued availability of consistent data (including river, lake, and wetland watershed delineations) is essential because robust analyses are driven by data, particularly for monitoring purposes.

A relatively recent development is deployment of sensor systems in ocean, lake, and stream systems. Large-scale monitoring efforts such as the National Oceanographic and Atmospheric Administration's Integrated Ocean Observing System (IOOS), the Global Lake Environmental Observing Network (GLEON), and the National Ecological Observatory Networks (NEON, STREON) ultimately will provide spatially extensive fundamental data on aquatic and terrestrial ecosystems. These efforts involve integration of sensing tools with newly developed or refined models, such as those being developed to map dynamic processes in rivers and floodplains. Other efforts range from regional scales, such as the Great Lakes Observing System (GLOS), to local networks of stream and lake sensors, such as those available through www.lakesuperiorstreams.org (Axler and Lonsdale 2003) and related systems in King County, Washington, the Chesapeake Bay, and numerous other locations (Hart and Martinez 2006). The increase in availability of detailed, real-time data on aquatic systems comes with the challenge of making these data meaningful to local decision makers and the public. Advances in on-line visualizations of real-time data (e.g., Host et al. 2000) and increased access to geospatial data through services, such as Google Earth and TerraServer, have brought sophisticated data resources into the realm of elementary and high schools and higher education. This capability has tremendous potential for development of a computer-literate and environmentally aware future workforce that understands the importance of thinking and acting at a landscape scale.

Other opportunities to integrate site-specific measures with remotely sensed data are imminent. Coordinated sensor systems and arrays deployed through national programs, such as NEON and GLOS, will provide opportunities to merge landscape and site-specific data in near real time. The enormous challenge will be how to condense and deliver meaningful data to researchers, appropriate management personnel, and the public.

Despite efforts to expand development and deployment of remote sensing equipment for environmental applications, few researchers have integrated data at molecular scales to landscape scales. One emerging area is use of molecular markers to detect sources of sediments (Mukundan et al. 2009), contaminants (**Aufdenkampe et al. 2006**), microbes (Ishii et al.

2007), and specific environmental conditions, such as hypoxia (Brouwer et al. 2005). Further effort could be made to develop environmental indicators based on physiological measures, such as fish growth (see Wagner et al. 2007) or development. Integration of data derived from studies that include mesocosms, small-scale field experiments, and broad-scale landscape analyses would be even more informative (e.g., a study by Rohr et al. 2008 that linked herbicides, fertilizers, and frog malformations). However, such studies require many investigators and robust funding. *Landscape genetics* is an emerging field that combines landscape ecology and population genetics to understand interactions between landscape features and genetic processes, such as gene flow, natural selection, and genetic drift. Such techniques have been used to address interactions between landscape connectivity and the distribution of species in aquatic ecosystems (see Hughes 2007, Kalinowski et al. 2008).

The ultimate scaling question is how to refine and down-scale climate-change models to help us better understand the potential effects of climate change on aquatic environments. In our opinion, many of the issues discussed above are critical to both research and management/policy communities. We need: 1) robust statistical and sampling techniques to discriminate among multiple stressors (e.g., climate and land use) and among anthropogenic and natural stressors, 2) mechanistic and empirical models linked to multi-sensor systems, 3) cross-sensor integration to expand the temporal and spatial density of data collection, and, 4) sustained communication between researchers and managers to ensure rapid deployment of mitigation and adaptation strategies. *J-NABS* publishes a broad range of topics and types of communications (opinions, broad perspectives, papers on topics ranging from management to theoretical concepts) and is likely to continue to play a significant role in disseminating ideas based on landscape concepts.

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