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Source: Journal of the North American Benthological Society, 29(1) : 245-263

Published By: Society for Freshwater Science

URL: <https://doi.org/10.1899/08-166.1>

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Linkages among aquatic ecosystems

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Abstract. Aquatic ecosystems are almost invariably connected to other ecosystems because the dominant force of water movement facilitates physical, chemical, and biological exchanges among ecosystems. In this sense, we define an *ecosystem linkage* as any persistent or recurring process or attribute that connects different ecosystems in some manner. We argue that such linkages are integral, even defining, components of aquatic ecosystem structure and function, and therefore, should be evaluated in the course of ecological studies. *J-NABS* has made significant contributions to our understanding of such linkages. The percentage of all publications in *J-NABS* addressing some ecological linkage has approached 10% in recent years. Historically, emphasis was placed on upstream–downstream linkages in flowing waters, and theory (e.g., river continuum, nutrient spiraling) has evolved largely around this phenomenon. However, other linkages among ecosystems have received increased attention in the past 20 y. These linkages include surface–subsurface, lake–stream, river–floodplain, and, more recently, marine–freshwater. We contend that many ecological processes, including primary production, nutrient cycling, organic matter processing, and secondary production, are driven by such exchanges because of the donor-controlled nature of many aquatic ecosystems. Exchanges of materials from aquatic ecosystems to terrestrial systems, caused by flooding, nutrient translocation, or insect emergence, can be substantial. Movement of energy and nutrients from the ocean to freshwaters, such as in the migrations of anadromous fishes, also can be dramatic. Despite increasing evidence of the importance of such linkages, considerable impediments to research, such as journal specialization, lack of interdisciplinary study teams, and limited funding of sufficient duration for such research, exist. Such obstacles are surmountable if investigators continue to emphasize that aquatic ecology will be advanced by the study of such linkages, and that environmental problems are better understood and solved in the context of that knowledge.

Key words: freshwater, terrestrial, marine, resource subsidy, connectivity, linkage, energy flow, nutrient dynamics.

We define an *ecosystem linkage* as any persistent or recurring process or attribute that connects different ecosystems in some manner. Such interecosystem exchanges are fundamental components of virtually all ecological systems because ecosystems are rarely closed (i.e., noninteractive with other ecosystems). These linkages can affect ecological compartments ranging from the smallest (e.g., individual organisms) to the largest (e.g., entire ecosystems) scales. Furthermore, ecologists have become increasingly cognizant over the last decade of the pervasiveness and

importance of such linkages to ecosystem function. For example, such linkages can provide the conduit for vital resources from one ecosystem that subsidize the functioning of another ecosystem.

Aquatic ecologists have long recognized that materials move across ecosystem boundaries, and have postulated that such exchanges have profound ecological implications (Hynes 1975, Gorham 1996 [Fig. 1], see Vanni et al. 2004 for a more recent perspective). However, reviews by Gary Polis and colleagues (e.g., Polis and Winemiller 1996, Polis et al. 1997 [Fig. 1]) brought together examples from many different ecosystems, illustrated the prevalence of such resource linkages in nature, and cited the importance of understanding the patterns and conse-

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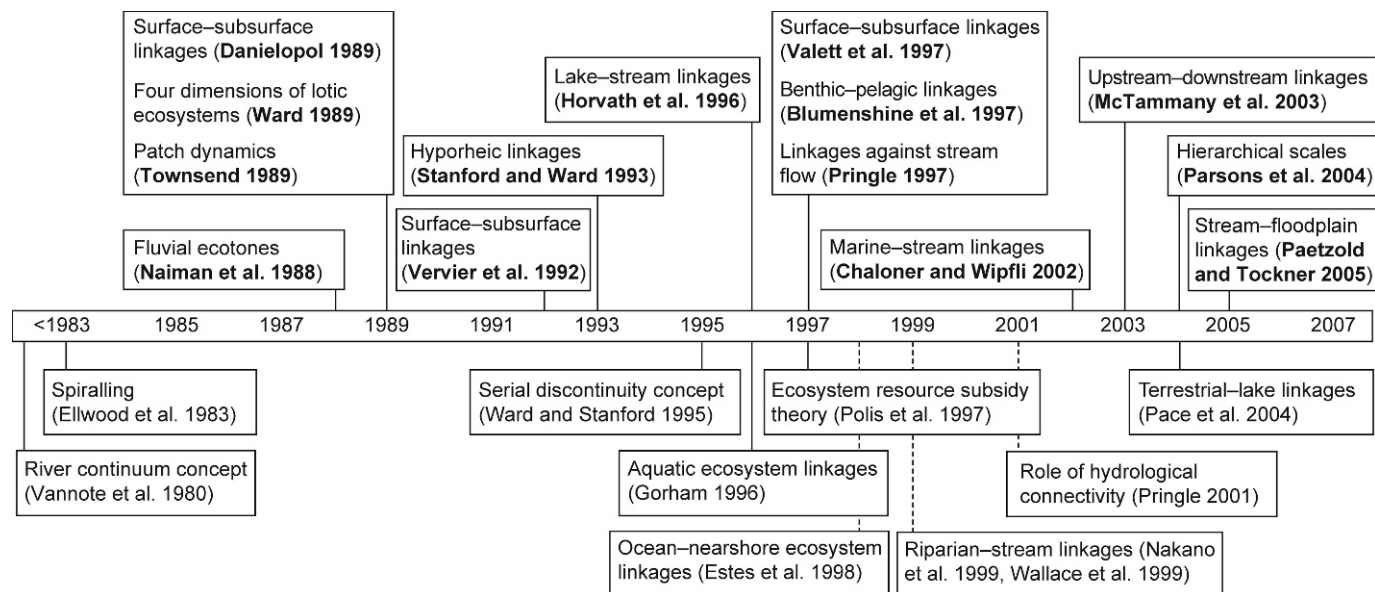


FIG. 1. Timeline illustrating major (i.e., cited on average ≥ 3 times/y since publication) publications concerned with the study of ecological linkages. Dashed lines are used for clarity when a connecting line passes behind a box. Boldface indicates papers published in *J-NABS*.

quences of such ecosystem linkages. These reviews initiated many studies on ecosystem linkages (e.g., Estes et al. 1998, Nakano et al. 1999, Wallace et al. 1999, Pace et al. 2004; Fig. 1). More recently, Polis et al. (2004) synthesized ecosystem linkage research to date and provided a future research agenda, especially in the context of environmental change and resource management challenges. They contended that few, if any, ecosystems or habitats exist that do not benefit from or provide resources to other ecosystems or habitats and that those systems can become impaired by the loss of such linkages. We argue that aquatic ecosystems are no exception and, in some instances (e.g., rivers), can exemplify the broad extent and fundamental nature of such exchanges.

Our goal was to assess ecosystem linkages in the context of aquatic ecosystems, with special attention given to linkages not covered elsewhere in this issue (see Boulton et al. 2010¹ for groundwater linkages, Holomuzki et al. 2010 for foodweb linkages, Poole 2010 for hydrologic linkages, and Tank et al. 2010 for terrestrial organic matter linkages). By aquatic, we refer primarily to freshwater ecosystems (lakes, ponds, rivers, streams, wetlands, and ground water) and the marine-influenced ecosystems in close proximity to them (estuaries, coastal areas). We do not consider the open ocean, except in the context of coastal linkages that ultimately might influence the open ocean and vice versa (e.g., Estes et al. 1998). We

also do not consider terrestrial–aquatic linkages per se because these are covered elsewhere in this issue (see Johnson and Host 2010 for landscape linkages).

We have 3 objectives in this paper. First, we use a topical assessment of published papers in 3 leading aquatic journals, including *J-NABS*, to evaluate the extent to which ecosystem linkages have been studied by aquatic ecologists and the possible reasons for gaps in such research. Second, we provide an overview of ecosystem linkage research as it pertains to aquatic environments. Throughout, our intent is to highlight contributions to this topic from research published in *J-NABS* in the past 25 y, while also citing significant papers from other journals. Third, we make the case for why ecosystem linkages should play a prominent role in aquatic research and make specific recommendations for the most effective ways to study linkages and disseminate such research. We conclude with recommendations on how *J-NABS* could enhance its contribution to this important area of ecological research.

To what extent do aquatic ecologists study linkages and why?

To establish the extent to which aquatic ecologists study linkages, we reviewed the contents of *J-NABS*, *Freshwater Biology (FWB)*, and *Limnology and Oceanography (L&O)*. These journals have overlapping aquatic focus and a relatively small difference in journal impact factor (JIF; ©Thomson Reuters) of ~ 1 (2.4, 2.7, and 3.7, respectively, for 2008). More broadly based

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

journals, such as *Ecology* (JIF = 4.9), *Science* (28.1), and *Nature* (31.4), also have published linkage papers but are not comparable to *J-NABS*, *FWB*, and *L&O* in terms of their disciplinary coverage. We evaluated the contents of *J-NABS*, *FWB*, and *L&O* for the 3-y period from 1995 to 1997 (972 total publications) to gain insight into the state of ecosystem linkage research at a time when interest in linkages was building. The broad similarities in conclusions drawn from our initial survey of these 3 journals and the objectives of this issue led us to review the complete contents of *J-NABS* for the period 1990 to 2007 (868 publications). For both literature reviews, we compiled: 1) the habitat(s) studied in each publication, 2) whether evidence of study of ecosystem linkages was present, and 3) the nature of the linkage(s).

J-NABS publications focused primarily on *lotic* (i.e., flowing) freshwaters, *L&O* emphasized *lentic* (i.e., standing) freshwaters and marine ecosystems, and *FWB* considered lotic and lentic freshwaters about equally (Fig. 2A). Studies of wetlands and estuaries were uncommon in all of these journals, possibly because journals exist that focus almost exclusively on those ecosystems (e.g., *Estuaries*, *Wetlands*). Most (>60%) papers in *J-NABS* addressed lotic ecosystems, whereas a smaller proportion was concerned with lentic ecosystems, including wetlands (<20%), and a very small proportion considered marine and brackish ecosystems (<1%); the remainder were exclusively laboratory studies.

Prior to 1997, few publications in any of the 3 journals were concerned with linkages (~2% overall), and during the period 1995 to 1997, the largest percentage (~6%) of linkage publications was published in *J-NABS* in 1996 (Fig. 2B). However, most of those studies evaluated linkages *within* a particular system, such as physical–chemical and biotic interactions, rather than *among* ecosystems, such as between lotic and lentic ecosystems (data not shown). Even when we considered any type of linkage as contributing to the pool (e.g., trophic interactions, terrestrial inputs), <5% of all papers in *J-NABS* was explicitly concerned with linkage research, with notable exceptions in several years, such as 2001 and 2006 (Fig. 2C).

One conclusion from our literature review is that journal specialization on specific types of ecosystems results in obvious gaps in linkage studies, and thus, relatively few studies treat the connections *among* ecosystems. Of the explicit linkage-type studies published in *J-NABS*, the most prominent were those of surface–subsurface linkages (e.g., Danielopol 1989 [Fig. 1], see also Boulton et al. 2010) and organic matter input and fate (e.g., Webster and Meyer 1997, see also Tank et al. 2010), a terrestrial–freshwater linkage.

Studies of linkages among aquatic ecosystems (e.g., marine–freshwater, lake–stream) and of benthic–pelagic linkages have been relatively rare in *J-NABS*. We catalogued 30 *J-NABS* papers that legitimately could be considered to be ecosystem linkage papers (Table 1). Both Gorham (1996) and Fisher (1997) emphasized the importance of ecosystem connections as a topic of study. Some contributors to *J-NABS* have heeded this appeal (Fig. 2C), but overall the literature shows that investigators have been slow to respond.

Why the slow progress in studying ecosystem linkages?

We perceive several reasons why ecologists who publish in aquatic-focused journals have generally understudied linkages as compared with other ecological processes. To some extent, investigators might be more likely to publish cross-ecosystem studies in general ecological journals, but other explanations also could apply. These reasons reflect the historical emphases of aquatic ecology, limitations imposed by career-building and funding sources, and the relatively recent emergence of theory framing the importance of linkages in aquatic ecosystems.

The 1st reason is that historical research emphasis, and consequently publication, has been placed on ecological interactions within an ecosystem or linkages within a single watershed. In limnology, the concept of stratification and mixing, an inherently within-ecosystem process, drove early research on lakes because of its profound biological implications (Wetzel 2001). In stream ecology, longitudinal patterns within a river system dominated early investigations. For example, European concepts of longitudinal zonation (Illies and Botosaneanu 1963) laid the groundwork for important conceptual developments including the river continuum concept (RCC; Vannote et al. 1980 [Fig. 1]) and nutrient spiraling (Webster and Patten 1979, Elwood et al. 1983 [Fig. 1]). Upstream–downstream linkages remain a subject of considerable interest in stream ecology (e.g., Mulholland and Rosemond 1992, McDowell et al. 1995, Mulholland et al. 1995, Pringle 1997 [Fig. 1], McTammany et al. 2003 [Fig. 1]). This perspective led to consideration of the influence of terrestrial habitats, such as riparian zones, on lotic ecosystems, as pioneered by H. B. N. Hynes (1975) and formalized in the RCC. In terms of linkages, the RCC succeeded by integrating changing terrestrial influences along the stream course while explicitly linking upstream and downstream environments, but failed to incorporate many types of linkages, such as surface–subsurface connections, tributary junctions, and reciprocal freshwater-to-terrestrial linkages (Statzner and Higler 1985). Newer concepts in stream ecology, such

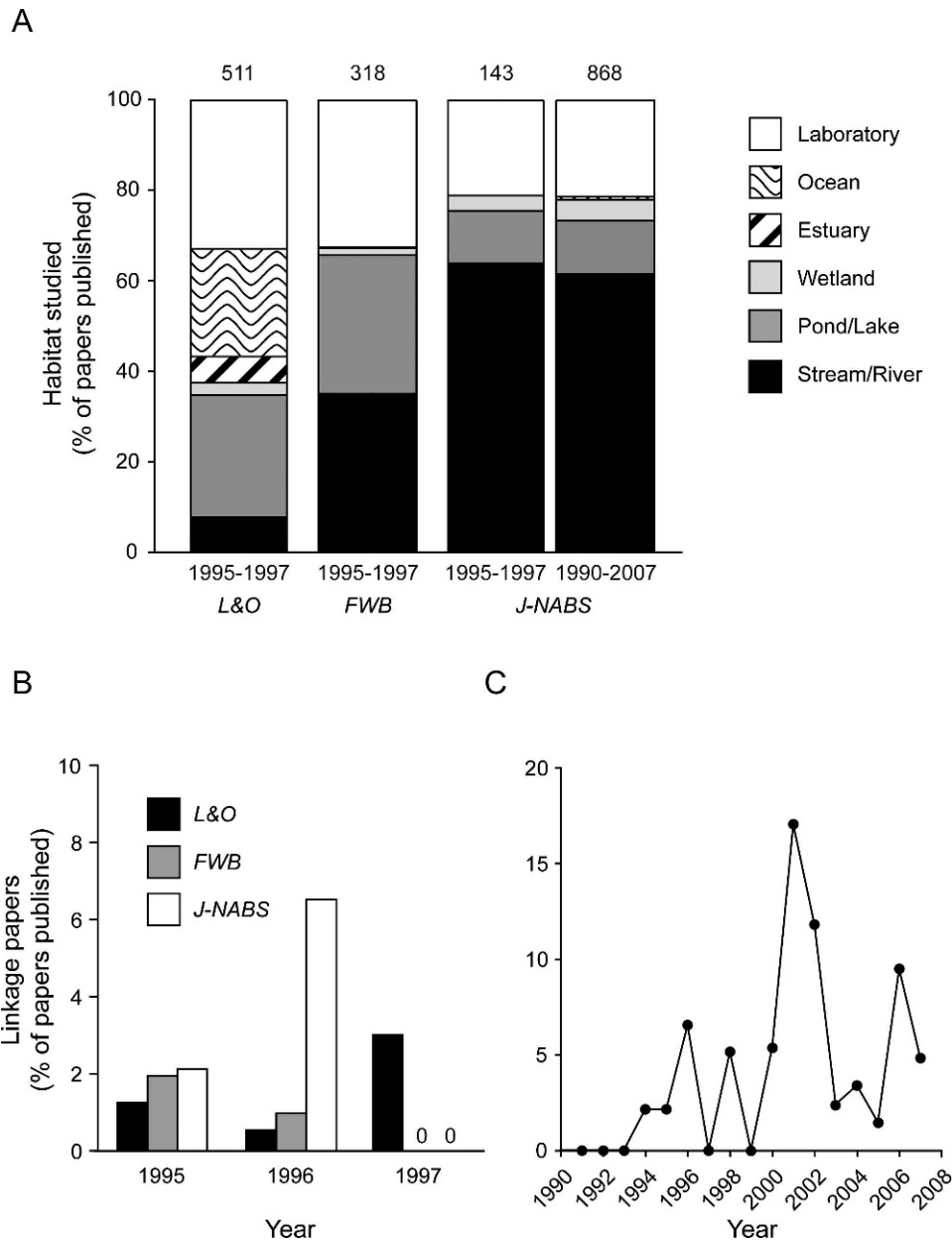


FIG. 2. Results from a survey of research papers on ecological linkages published in *Limnology and Oceanography* (L&O), *Freshwater Biology* (FWB), and the *Journal of the North American Benthological Society* (J-NABS) showing the percentage of published papers dealing with each of several major habitats (number of papers noted above each block; years included shown on the x-axis) (A), with some linkage component in each of the 3 journals over a 3-y period (B), and in J-NABS over an 18-y period (C).

as the flood pulse (Junk et al. 1989), have attempted to incorporate such linkages. Last, ecologists might have been most comfortable studying the interactions of organisms within the context of their immediate environment, and consequently, much is known about those physical, chemical, and biological interactions, such as predator-prey interactions (e.g., Peckarsky 1980) and the response of periphyton to grazing (e.g., Lamberti and Resh 1983; see Holomuzki et al. 2010).

The 2nd reason might be the pragmatic necessity (from a career perspective) of studying a single ecosystem or process. Particularly for young investigators, ecological questions that can be tested in a single ecosystem (e.g., stream) or ecosystem type (e.g., several streams) might be more tractable than questions that consider linked but functionally different ecosystems (e.g., stream and lake). Indeed, given the steep learning curve associated with study of just

TABLE 1. Citation history of 30 *J-NABS* articles dealing with aquatic ecosystem linkages. Citation frequency was determined through early 2008 using the citation search function in Web of Science®. Under the column “Linkage”, the 1st ecosystem listed usually is the donor ecosystem and the 2nd ecosystem is the recipient. Articles are listed in ascending order of citations/y.

Reference	No. times cited	Citations/y	Linkage
Parkes et al. 2004	1	0.3	Lake–stream
Benenati et al. 2000	3	0.4	Reservoir–river
Steinman and Rosen 2000	3	0.4	River–lake
McDowell et al. 1995	8	0.6	Upstream–downstream
Vadeboncoeur 1994	10	0.7	Lake–stream
MacIntyre and Melack 1995	15	1.2	Lake benthic–pelagic
Chauvet and Decamps 1989	27	1.4	Floodplain–river
Smock 1994	20	1.4	Stream–floodplain
Blanco and Scatena 2006	3	1.5	River–marine
Garman and Macko 1998	15	1.5	Marine–stream
D’Angelo et al. 1997	17	1.5	Hierarchical scales
Bott et al. 2006	4	2.0	Stream–reservoir
Mulholland et al. 1995	26	2.0	Upstream–downstream
Velinsky et al. 2006	4	2.0	Reservoir–stream
Stagliano et al. 1998	21	2.1	Stream–riparian
Mulholland and Rosemond 1992	39	2.4	Upstream–downstream
Paetzold and Tockner 2005	8	2.7	Stream–floodplain
Horvath et al. 1996	33	2.8	Lake–stream
McTammany et al. 2003	15	3.0	Upstream–downstream
Parsons et al. 2004	13	3.3	Hierarchical scales
Blumenshine et al. 1997	45	4.1	Lake benthic–pelagic
Danielopol 1989	82	4.3	Surface–subsurface
Valett et al. 1997	48	4.4	Surface–subsurface
Vervier et al. 1992	74	4.6	Surface–subsurface
Chaloner and Wipfli 2002	28	4.7	Marine–stream
Naiman et al. 1988	118	5.9	Lateral and longitudinal
Pringle 1997	67	6.1	Downstream–upstream
Stanford and Ward 1993	172	11.5	Floodplain–river
Ward 1989	258	13.6	Lateral, vertical, longitudinal
Townsend 1989	349	18.4	Lateral and longitudinal

a single ecosystem, many conceptual and logistical challenges can be encountered when studying multiple systems. For example, most stream ecologists probably began their careers (e.g., during PhD research) by focusing on a single system (e.g., Big Sulphur Creek; Lamberti and Resh 1983); studying >1 was unusual (e.g., **McDowell et al. 1995**, **Parkes et al. 2004**), and studying >3 was heroic (e.g., **Valett et al. 1997** [Fig. 1], **Blanco and Scatena 2006**). Recently, the number of multisystem studies conducted, especially at the graduate level, has begun to increase (e.g., 13 streams studied by Bernhardt et al. 2002). Some level of momentum or notoriety can build when an ecologist, or team of ecologists, studies a single system continuously, and thus, their research program becomes strongly associated with that stream. Notable examples of this phenomenon in stream ecology include the long-term studies of Walker Branch, Tennessee, USA (e.g., **Mulholland and Rosemond 1992**) and Sycamore Creek, Arizona, USA (e.g., Fisher et al. 1982). Linkage processes are not easily studied over a short time frame, but require

multiyear effort, which is rarely available to early-career ecologists who must be productive quickly for promotion. Other risks that are inherent in cross-disciplinary work, such as issues related to publication, individual recognition, and institutional limitations, might prevent the formation of truly interdisciplinary teams of investigators. The net effect is that a relatively small window of professional time exists during which linkages can be studied effectively.

The 3rd reason is that the importance of studying ecosystem linkages has been widely recognized only recently. This fact is clear from our review of the study topics published in *J-NABS*. Historically, aquatic ecosystems were considered to be relatively closed systems (Wetzel 2001). However, many external and internal linkages can be identified for a given ecosystem, and some might be hierarchically organized (**D’Angelo et al. 1997**, **Parsons et al. 2004** [Fig. 1]). For example, within a single drainage system, we can identify numerous linkages, including subsurface–surface, lentic–lotic, wetland–fluvial, and river–estuarine (Fig. 3). Over the last decade, subsur-

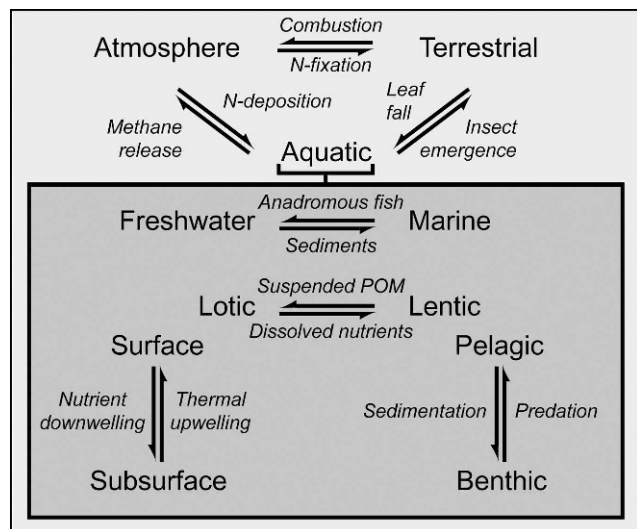


FIG. 3. Conceptual diagram illustrating major linkages within and among freshwater ecosystems and other ecosystems. A linkage example is provided in italics next to each arrow. POM = particulate organic matter.

face–surface (i.e., hyporheic) linkages have been the most intensively studied of these linkages, no doubt because of interest stimulated by the seminal paper of Stanford and Ward (1993; Fig. 1). However, other aquatic habitats, such as springs that reflect groundwater inputs (e.g., Robinson et al. 2000, Barquin and Death 2006) and lake outlets that rapidly transform from lentic to lotic conditions (e.g., Vadeboncoeur 1994, Parkes et al. 2004), also are dominated by external linkages. Physical and chemical characteristics of these habitats are determined by the nature of the linkages, and these characteristics, in turn, influence the associated specialized biota. Even aquatic systems, such as alpine lakes (Gregory et al. 1990), that were once thought of as being closed still have linkages to other systems through stream inputs and outputs and via groundwater and atmospheric inputs (Vervier et al. 1992; Fig. 1). The net consequence is that virtually no aquatic ecosystem is completely disconnected from other ecosystems (but see Sarbu et al. 1996). Perhaps the most common but understudied aquatic linkages are those associated with riverine wetlands and floodplain lakes (Welcomme 1988). *J-NABS* has published comparatively few studies of floodplain habitats and associated organisms (but see Stagliano et al. 1998, Paetzold and Tockner 2005 [Fig. 1]).

The Nature and Ecological Relevance of Aquatic Ecosystem Linkages

Linkages among ecosystems can be separated broadly into those that are largely physical, chemical,

or biological in nature. *Physical linkages* involve the exchange of nonbiological material, such as water, sediments, heat energy, and gases. Such linkages play a major role in shaping the physical template of aquatic ecosystems, and in some ways, can serve as a framework on which other linkages depend. For example, water movements can carry the biological material that constitutes a resource subsidy. *Chemical linkages* include interecosystem movement of inorganic nutrients and other dissolved ions. Water flow provides the normal transport mechanism, but air also can be important (Caraco et al. 1992). Ecologists have become increasingly concerned about contaminant movement via water (Culp and Baird 2006) and in biological vectors, such as migrating Pacific salmon (Gregory-Eaves et al. 2007). *Biological linkages* include the movements of organisms and their products, including feces, chemical signals, exoenzymes, and other exudates. Water flow can transport organisms and their products passively, or purposeful migrations might occur over short daily cycles or longer seasonal periods. Many organisms undertake seasonal or daily migrations, especially to reproduce (e.g., Garman and Macko 1998) or to colonize more productive environments (Kohler 1984).

A diversity of aquatic ecosystem linkages can be identified (Fig. 3), and many more doubtless exist. The context for understanding such interactions stems from seminal papers, some of which have been published in *J-NABS*. These papers include the foundational concepts of patch dynamics (Pringle et al. 1988, Townsend 1989 [Fig. 1]), ecotones (Naiman et al. 1988; Fig. 1), and ecological dimensions (Ward 1989; Fig. 1) as they apply to aquatic ecosystems. *Within* a particular aquatic ecosystem, major linkages include benthic–pelagic, subsurface–surface, and upstream–downstream. *Among* aquatic ecosystems, examples of linkages include lentic–lotic, wetland–lake (or river), and marine–estuarine–freshwater. Strong linkages also exist between aquatic and terrestrial ecosystems (Chauvet and Decamps 1989, Pringle 2001 [Fig. 1]), but these linkages will not be emphasized in our paper (but see Johnson and Host 2010). A related topic is trophic interactions (Power et al. 1988), also covered by other authors in this issue (see Holomuzki et al. 2010).

Within ecosystem linkages: benthic–pelagic coupling

For standing waters, benthic and pelagic components of a given lentic ecosystem most often have been treated separately by investigators, even though these components are often in direct contact. However, benthic–pelagic linkages recently have become the

focus of considerable interest, in part because of differential responses expressed during manipulative (Blumenshine et al. 1997; Fig. 1) and observational studies (Vadeboncoeur et al. 2006). Unfortunately, strictly pelagic studies fall outside the usual scope of *J-NABS*. Therefore, *J-NABS* contributions that deal only with benthic aspects of lentic systems or with benthic–pelagic linkages might escape notice by the broader limnological community.

The effect of nutrient enrichment on pelagic systems is well studied and is the subject of considerable management concern. The effects of lake eutrophication on benthic invertebrate communities also have been well studied by benthologists (e.g., Jónasson 1972). Studies of the effects of nutrient enrichment on benthic communities at levels lower than those that lead to eutrophication have lagged, although this topic has seen some coverage in *J-NABS*. For example, nutrient enrichment increased the chlorophyll content of algae on hard substrates but not on fine sediments (Blumenshine et al. 1997). Nutrient addition also resulted in species shifts in benthic invertebrate communities (Hershey 1992, Blumenshine et al. 1997) but had inconsistent effects on densities. Blumenshine et al. (1997) reported increased zoobenthos densities during a 9-wk limnocorral experiment, but Hershey (1992) found no density effect over 5 y in a divided arctic lake. Sedimentation of particulate organic matter (POM) also provides a potentially important resource for benthic consumers. Lake morphometry determines depositional sites, which have higher zoobenthic biomass compared to nondepositional sites (Rasmussen and Rowan 1997).

Fluxes of nutrients, energy, and materials within lentic ecosystems are bidirectional. Fish feeding on benthic prey has been studied extensively from the perspective of benthic community structure, but fish also have a significant effect on pelagic productivity by returning benthic P to the water column (Schindler and Scheuerell 2002). Several *J-NABS* papers have contributed to our understanding of the reciprocal nature of benthic–pelagic linkages. In a bioturbation study, Caliman et al. (2007) showed that benthic species composition and richness affected the flux of P to the water column. Furthermore, Burks et al. (2001) showed that the direction of energy flow during predator–prey interactions sometimes goes toward the benthos rather than toward the pelagic zone. In this case, odonates in littoral zones had a large effect on zooplankton, but the effect decreased when macrophytes were very dense. This pattern is similar to that reported for effectiveness of fish foraging in macrophyte beds (e.g., Crowder and Cooper 1982). Benthic P generally is not returned to the water column by chemical processes in oligotrophic

lakes, but internal loading of P from the sediments to the water column is very important in eutrophic lakes and maintains a stable eutrophic state (Wetzel 2001). P loading to the water column can be managed through alum addition, but external P loading also must be reduced for the benefit of alum treatment to be sustained (Steinman et al. 2006). Resuspension of benthic nutrients to the pelagic zone also can occur through internal waves; such wave generation depends on wind speed, basin morphometry, and density gradients, which are determined by the rate of heating and convective heat loss (MacIntyre and Melack 1995). Benthic meiofauna also disperse via water-column transport (Peters et al. 2007).

Among ecosystem linkages: lotic–lentic interactions

Linkages between lotic and lentic ecosystems have received far less attention than have processes and dynamics within each of those ecosystems. However, inflowing lotic ecosystems deliver sediment, organic matter, and nutrients to lentic ecosystems, whereas lentic ecosystems deliver dissolved and particulate matter to outflowing streams, with important ecological consequences, some of which will be discussed below.

Nutrient delivery from tributary streams is often the major factor determining primary production within a lake or reservoir. Most studies of effects of nutrient loading on lake productivity have been published in journals other than *J-NABS*, perhaps because these studies were focused on pelagic rather than benthic components of the ecosystem. However, recent papers published in *J-NABS* have made some contributions in this area. The primary productivity of reservoirs reflects the characteristics of the largest tributary stream, and differences in productivity are associated with land use along tributaries (Bott et al. 2006). Hydrologic patterns of tributary streams also strongly affect lentic productivity. For example, flooding reduces benthic algal biomass directly by increasing light attenuation caused by suspended sediment and indirectly by increasing nutrient supply to phytoplankton (Squires and Lesack 2001).

Few *J-NABS* publications have been concerned with concepts involving lakes, probably because lentic ecosystem studies are less well represented in *J-NABS* than are flowing water studies. However, inflowing streams can serve as conduits to lakes for various organisms, including fishes, that can have a significant impact on lake food webs (Wellborn et al. 1996). One concept of stream connections or linkages determining fish control of lake food webs has been formalized as the geomorphic–trophic hypothesis (Hershey et al. 1999). Hershey et al. (1999) proposed

that benthic community structure in Arctic lakes was determined by the fishes present in those lakes, some of which had access to lakes only via stream connections. The geomorphic setting (e.g., past stream capture) determined, in part, access of fish to lakes. At a regional scale in Alaska, USA, Oswald et al. (2000) found the most similar fish faunas in adjacent hydroregions, a result further illustrating the importance of dispersal barriers.

Understanding the ecological consequences of fish migration barriers also has implications for lake management (Schindler et al. 2001). A fair amount is known about the linkages between reservoirs and rivers, but management strategies for dams have long been a major issue for fisheries (Petts 1984). Effects of climate change on water yield could interfere with stream–lake linkages by drying streams, and thereby, severing routes for fish recolonization following winterkill. The result might be an increase in macroinvertebrate populations (Tonn et al. 2004). For some organisms, migrations between lakes and streams are a critical part of their life cycle. For example, Lake Erie walleye recruit from major inflowing rivers where adults spawn (Mion et al. 1998). However, invasive species, such as sea lamprey that spawn in tributaries to the Laurentian Great Lakes and Eurasian ruffe that migrate from estuaries in Lake Superior to upriver areas to spawn and forage (Fullerton and Lamberti 2006), exploit these linkages as well. Lakes are also a source to downriver habitats of exotic species, such as zebra mussels, whose planktonic larvae (veligers) are easily transported downstream with water flow (Horvath et al. 1996; Fig. 1). Exotic fishes have migrated between Lake Michigan and the Illinois River, which are connected only by human engineering. These migrations triggered construction of an electric barrier in the Chicago Shipping and Sanitary Canal to reduce bidirectional exchanges (Rahel 2007).

Lake outlets are dynamic transitional zones where lentic and lotic habitats merge. These outlets exhibit gradients of physical and chemical conditions and organic matter resource availability. Lake outlets are among the best studied of the aquatic linkages. The characteristic fauna of outflows are well described, although the underlying mechanisms are still debated (see Richardson and Mackay 1991). Lake outflows also are transitional environments in which conditions, such as concentrations of suspended organic C (e.g., Vadeboncoeur 1994), change rapidly over a short distance. These habitats are characterized by the presence of lake-derived particulate and dissolved organic matter (DOM) and nutrients, which decline in abundance or quality along a downstream gradient. Lake supple-

ments to streams typically are seasonal but can be relatively constant within a season. Important aspects of seasonality are determined by thermal stratification within a lake. During summer, relatively deep lakes exhibit thermal stratification. An important consequence of stratification is that stream temperature is warmer for the outlet stream than further downstream or for inflowing streams and does not exhibit diel fluctuations. Furthermore, epilimnetic waters deliver a relatively constant supply of algae and nutrients that reflect the trophic condition of the lake and strongly influence the downstream biota.

Lake outlets have long attracted the interest of benthologists because they often exhibit dense aggregations of filter feeders with very high secondary production (Richardson and Mackay 1991). Lake outlets have strong gradients of periphyton biomass (Cattaneo 1996), seston quality (Valett and Stanford 1987), and nutrients (McHale et al. 2000) with distance from the lake. Authors of *J-NABS* papers have studied lake outlets largely from the perspectives of the fate of lake-derived seston and DOM and the impact of lake seston on invertebrate communities, rather than from the perspective of dynamics of lake-derived nutrients. A strong relationship often exists between biomass of filter feeders (e.g., hydrosychid caddisflies and black flies) and distance from a lake (Morin 1991). For black fly larvae, this relationship appears to be determined largely by feeding on lake-derived algae rather than bacteria (Parkes et al. 2004). However, DOM, especially colloidal exopolymers, also might be a direct and significant food source for larval black flies at outlets (Wotton 1996). Hydrosychid caddisflies exploit algal seston at outlets, but higher temperature at lake outlets compared to further downstream also appears to facilitate hydrosychid populations (Fairchild and Holomuzki 2002). Densities of filter-feeding zebra mussels decline exponentially with distance from invaded lakes, and their presence in streams is best described by a source–sink model (Horvath et al. 1996), whereby invasion of the stream depends on a lake population to supply veligers to the stream outlet (Fig. 4A) because downstream populations are not self-sustaining (Horvath and Lamberti 1999). The importance of lake-derived seston diminishes rapidly with increasing distance from a lake because instream processes begin to control seston dynamics. The distance over which this transition occurs depends on discharge (Vadeboncoeur 1994).

Dams provide an important and special type of linkage between lotic and lentic ecosystems. Large dams moderate variability in discharge and temperature, which can have dramatic and long-term consequences for stream ecosystems (e.g., Adler

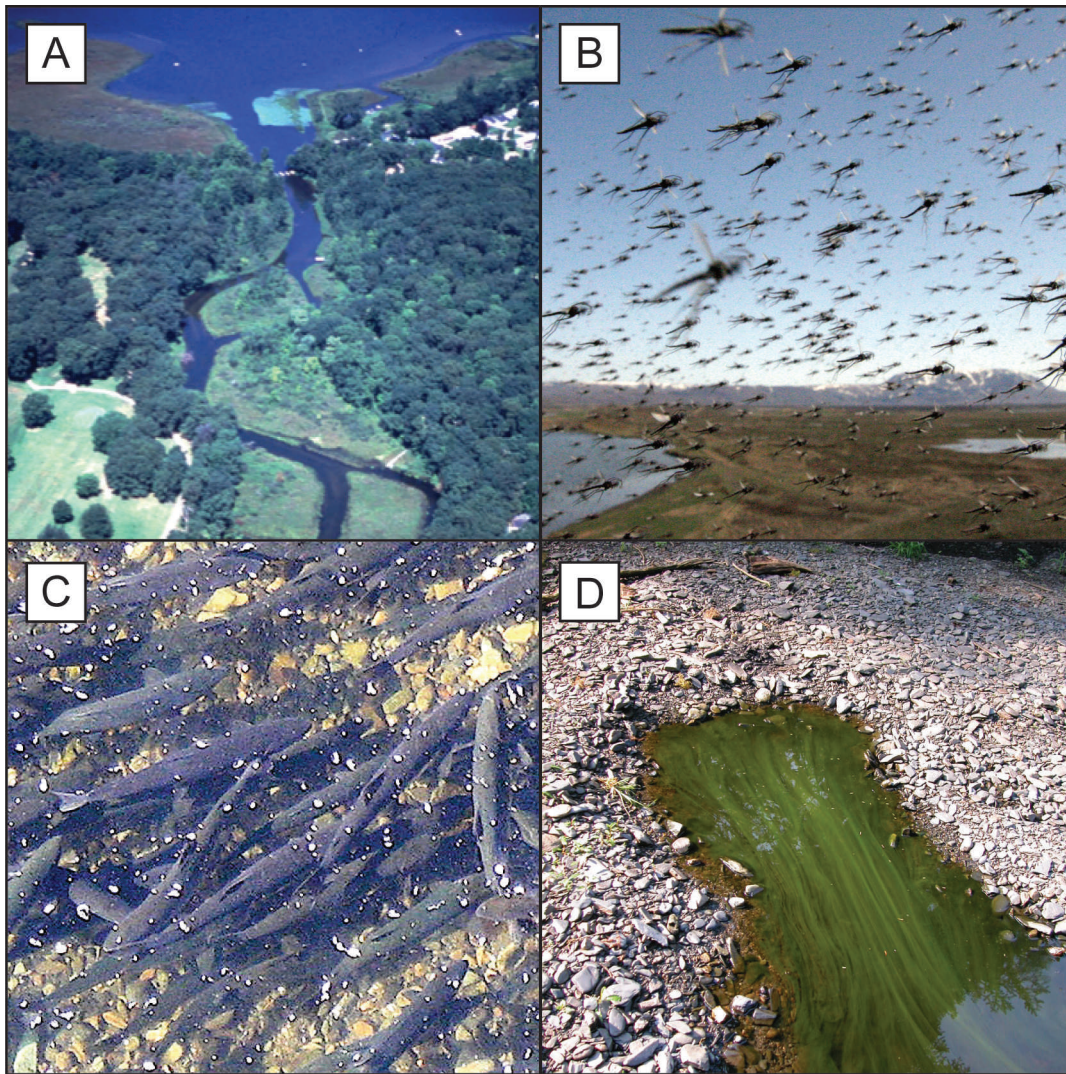


FIG. 4. Examples of ecosystem linkages. A.—Stream–lake linkage illustrated by Christiana Creek flowing out of Christiana Lake, Michigan, where zebra mussel veligers are transported from the lake into the outlet stream (photo credit: GAL). B.—Aquatic–terrestrial linkage illustrated by chironomid midges (Diptera: Chironomidae) emerging from Lake Myvatn, Iceland (photo credit: Árni Einarsson, Myvatn Research Station). C.—Marine–freshwater linkage illustrated by adult Pacific salmon (*Oncorhynchus* spp.) returning to spawn in Maybeso Creek, Alaska (photo credit: Scott Tiegs, Oakland University). D.—Subsurface–surface linkage illustrated by *Cladophora* algal growth in an upwelling zone in an isolated part of Peterson Creek, Alaska (photo credit: DTC).

1996) and can have a major effect on upstream–downstream linkages, such as fish migrations. Even though the serial discontinuity concept (SDC; Ward and Stanford 1995; Fig. 1) made theoretical predictions about ecosystem recovery from regulation by dams, this topic has only recently received detailed attention from freshwater ecologists. For example, studies of the effect of Glen Canyon Dam on the Colorado River have shown that changes to snowmelt-fed discharge altered the phytobenthic community below the dam (Benenati et al. 2000). Studies by Stevens et al. (1997) support the SDC, in that the benthos did not recover over distance

below Glen Canyon Dam and that geomorphological differences in substratum availability mediated these effects. A long-term data set has shown that ecological interactions and colonization patterns can modify the effects of river regulation on aquatic biota usually associated with changes in those physicochemical conditions (Vinson 2001). However, removal of small dams might have limited consequences for downstream ecosystems. P uptake rates increased immediately after removal of 2 small dams in Wisconsin, but uptake length was temporally dynamic, and overall differences in uptake length over a 2-mo period before

and after dam removal were not significant (Orr et al. 2006). Removal of a low-head dam in Wisconsin had relatively minor and short-term effects on channel geomorphology and macroinvertebrate community (Stanley et al. 2002). Removal of a small dam on a Pennsylvania stream also had little effect on C, N, or P concentrations (Velinsky et al. 2006).

The above discussion of *J-NABS* contributions to the study of lotic–lentic linkages suggests that treatment of this topic in the journal has been biased toward lake effects on outflow streams. *J-NABS* has been a leader in publishing studies of the fate of lake-derived seston in outlet streams and the consequences of lake-derived particulate and dissolved materials for benthic communities. The influence of dams and their removal appears to have received relatively balanced treatment in *J-NABS*. However, lotic impacts on *lentic systems* (i.e., stream inflow effects) have received relatively sparse treatment in *J-NABS*, perhaps because the journal is not perceived as an outlet for work on lentic ecosystems and because lentic studies have focused more on pelagic than benthic components of the ecosystem. However, one exception is the study by Bott et al. (2006) of reservoir productivity as a response to incoming stream water quality. The paucity of studies of this linkage suggests an area where *J-NABS* could become a leader. For example, Wall et al. (2005) found that N cycling in an Illinois reservoir was tightly coupled to the biogeochemistry of its incoming streams, which they referred to as the river–reservoir continuum.

One tendency we found in the literature was for investigators to limit studies to a *pair* of ecosystems, such as a single lake and its outflowing stream. Sequential (i.e., multiple) linkages among ecosystems, such as multiple lakes in the same river system that periodically reset the river also have important ecological consequences. An example is provided by the complex hydrological linkages within the highly modified Kissimmee River–Lake Okeechobee–Everglades system of Florida, USA. Steinman and Rosen (2000) reviewed efforts to restore Lake Okeechobee, which has been culturally eutrophied, and emphasized the importance of understanding and incorporating lentic–lotic, lentic–lotic–estuarine, and lotic–wetland linkages into these restoration plans. Similar issues are faced in the regulated Colorado River, Arizona, USA (Stevens et al. 1997, Benenati et al. 2000).

Linkages among freshwater, terrestrial, and marine ecosystems

Linkages between aquatic and terrestrial ecosystems or between freshwater and marine ecosystems

involve the bidirectional exchanges of water, sediments, nutrients, organic matter, and organisms (Fig. 3). Studies of such reciprocal linkages among ecosystems are less common in general, and especially in *J-NABS*, than are studies of donor-driven relationships. Furthermore, *J-NABS* has published few papers in the areas of marine–terrestrial and marine–freshwater linkages. Indeed, the importance of leaf inputs to streams has been recognized for several decades (Hynes 1975), but the broad importance of resource linkages between ecosystems has been recognized only recently (Polis et al. 1997) and then built upon conceptually (Polis et al. 2004). This recognition appears to have stimulated many ecosystem exchange studies that are now appearing in *J-NABS* (Fig. 2C) and elsewhere (e.g., Nakano et al. 1999, Bouchard and Bjorndal 2000, Sabo and Power 2002, Pace et al. 2004).

Given the number of published studies in this area, stream ecologists could be considered leaders in recognizing the importance of donor-control of ecosystems, which characterizes many small streams. Many papers on the role of leaf inputs to streams have been published in *J-NABS* and other aquatic journals (see Tank et al. 2010), and this exchange probably is the best understood of the ecosystem linkages associated with freshwaters. Many published studies have addressed the type of material delivered (e.g., Smock 1994, Vadeboncoeur 1994, McDowell et al. 1995), the fate and consequences of that material (e.g., Garman and Macko 1998, Benenati et al. 2000, Bott et al. 2006), and comparisons across space and time (e.g., Mulholland and Rosemond 1992, McTammany et al. 2003, Blanco and Scatena 2006). However, studies published in *J-NABS* are biased toward streams, with only limited studies of terrestrial inputs to lentic or wetland ecosystems (see Bridgman and Lamberti 2009). Moreover, studies published in *J-NABS* have given little attention to the broader implications of such inputs for downstream ecosystems, such as estuarine and coastal environments, despite an increase in the literature concerned with the influence of rivers on near-shore marine environments (e.g., Hedges et al. 1997, Syvitski et al. 2005). Such research has demonstrated the extent to which freshwater ecosystems can influence marine ecosystems and is highly relevant to understanding the impacts of global environmental change. For example, recent concerns about coastal hypoxia (e.g., Gulf of Mexico dead zone) have focused attention on the role of rivers in nutrient loading of nearshore marine environments (e.g., Royer et al. 2006).

Relatively few studies of reciprocal freshwater-to-terrestrial linkages have been published in *J-NABS*

despite recent recognition of the importance of emerging insects for riparian predators, such as spiders, and the consequences of such predation for those insects (e.g., Nakano et al. 1999, Sabo and Power 2002; Fig. 4B). Stagliano et al. (1998) quantified the substantial insect emergence from 2 wetland habitats in the southeastern US, and Paetzold and Tockner (2005) found that taxon-specific predation by riparian arthropods altered the taxonomic composition of emerging aquatic insects. Considerable research opportunities exist in this arena. Studies are needed that address biotic exchanges and the ecological roles of sediments, nutrients, and water delivered by flood flow into terrestrial habitats.

Marine–freshwater exchanges.—A recent area of interest involves the flows of marine materials into freshwater ecosystems, as exemplified by the dramatic migrations of anadromous and catadromous organisms, such as salmonids and decapods, between marine and freshwater ecosystems (Fig. 4C). Pringle (1997) compellingly described the multitude of processes that can actually move against flow (i.e., upstream), including physical, chemical, and biological fluxes. Hynes (1970) commented on the potential importance of semelparous anadromous fish, which die after spawning, to freshwater ecosystems, although suggestions of their effect can be found in both contemporary (e.g., Hall 1972) and much earlier literature (Juday et al. 1932). Numerous studies have shown that freshwater and estuarine organisms use and respond positively to the resources delivered by the influx of marine fishes (e.g., Garman and Macko 1998, Chaloner and Wipfli 2002 [Fig. 1]). In addition, salmon nutrients stored in subsurface areas can produce impressive algal blooms as they are released to surface waters (Fig. 4D). Nonnative salmon also are an important nutrient source where introduced, such as in Great Lakes tributary streams (Schuldt and Hershey 1995).

The freshwater-to-marine vector of material from rivers, through estuaries, to marine ecosystems, has been studied from both oceanographic and geologic perspectives. Rivers can contribute massive quantities of material, including sediments, dissolved nutrients, and organic C, to marine environments. For example, rivers transport dissolved and biogenic silica (as diatoms) to the ocean. The dissolved silica fraction is 84% and biogenic silica is 16% of ocean silica inputs worldwide (Conley 1997). The contemporary global sediment flux in rivers is estimated to be 12.6 billion metric tons/y (Syvitski et al. 2005). The ecological importance of these fluxes of energy and nutrients for estuarine and nearshore marine environments has been studied intensively over the last 20 y. Evidence, especially from stable isotopes, shows that resources

associated with river plumes can subsidize nearshore benthic (Darnaude et al. 2004) and pelagic (Moline et al. 2008) food webs. However, many factors, including the size of the donor system (Connolly et al. 2009) and connectivity within nearshore food webs (Darnaude et al. 2004) determine the overall influence of these river-plume resource subsidies. Recently, agricultural nutrients entering the Mississippi River from agricultural fields of the midwestern US and flowing into the Gulf of Mexico have been implicated in the development of a hypoxic zone that grows annually (Royer et al. 2006). Similar areas of coastal hypoxia have been identified in other areas around North America, including the Chesapeake Bay (Rabalais et al. 2001). These examples demonstrate the profound effects that freshwater ecosystems can have on estuarine and nearshore marine environments.

Watershed–stream connections.—Linkages between the watershed and its aquatic habitats in natural and human-converted landscapes are an important topic of ecological inquiry and have considerable management implications (see Johnson and Host 2010). Watershed-scale land uses affect nearly all aspects of aquatic ecosystems, and therefore, their connections as well. Substantial contributions have been made by authors of papers published in *J-NABS* to models and indices designed to assess water quality and to link water quality to land use. Thus, *J-NABS* has assumed a leadership position among scholarly journals in the development and the evaluation of approaches to studying landuse impacts on streams and other freshwater ecosystems (e.g., Lenat 1993, Pan et al. 2000, Weigel 2003). Authors of *J-NABS* papers also have evaluated the appropriateness of various metrics for assessing landuse impacts (e.g., Fore et al. 1996, Reynoldson et al. 1997, Fortino et al. 2004). Below, we address effects of 2 major land uses, agriculture and urbanization.

Agricultural land use has large effects on aquatic communities and ecosystem processes. Agricultural land use almost universally increases nutrient loading to streams (e.g., Meyer et al. 1988, McDowell et al. 1995, Schaller et al. 2004). Denitrification is elevated in agricultural streams, but denitrification is not a significant N sink in agriculture-dominated watersheds (Schaller et al. 2004). Reforestation of riparian buffers after agricultural abandonment can lead to recovery of stream gross primary production and community respiration, but these streams continue to support higher nutrient and suspended solid concentrations than do forested streams (McTammany et al. 2007). Agricultural land use has strong effects on algal assemblages (Kutka and Richards 1996, Munn et al. 2002). By altering nutrient loading to streams,

agricultural land use affects periphyton stoichiometry, the stoichiometry of consumers, and nutrient fluxes through consumers (James et al. 2007). Nutrient-enriched streams also can have high invertebrate production, typically of limited or tolerant taxa (Shieh et al. 2002). Agricultural land use also affects dissolved organic C and particulate organic C loading to streams (Kaplan et al. 2006). Agriculture has been implicated in the extinction of native mussel species (Poole and Downing 2004). However, within agricultural catchments, mussel species evenness was greater in streams with forested riparian zones than in streams with grassy riparian zones (Morris and Corkum 1996). Agricultural land use disrupts the role of riparian zones in stream N cycling by simplifying the drainage network of headwater streams (Arango and Tank 2008) and affects shredder distribution, thereby altering leaf decomposition (Sponseller and Benfield 2001).

Urbanization alters hydrologic patterns, amplifies scour of channels and benthic communities, delivers fine sediments and pollutants from various sources, and generally results in an unstable system (Paul and Meyer 2001). The resulting degraded stream condition has been termed “urban stream syndrome” (Paul and Meyer 2001, Meyer et al. 2005, Walsh et al. 2005a). *J-NABS* has published 2 special issues on urban streams, “Symposium on Urbanization and Stream Ecology” (volume 24, issue 3; Feminella and Walsh 2005) and “Second Symposium on Urbanization and Stream Ecology (volume 28, issue 4; Roy et al. 2009). Many aspects of degradation are related to the amount of impervious surface in a watershed (Roy et al. 2005, Walsh et al. 2005b), such that planning boards of many cities and counties use % impervious cover in their development ordinances. Biotic communities are sensitive indicators of urban impacts. For example, Kratzer et al. (2006) reported that urbanization resulted in degraded macroinvertebrate communities, a pattern also found by Lamberti and Berg (1995) in a long-term assessment of an urbanized watershed. Impervious cover affects hydrology and delivery of nutrients and pollutants, all of which can have negative effects on various aspects of stream ecosystems. Scoggins et al. (2007) found a decrease in aquatic community health downstream of coal-tar-sealed parking lots, a result implicating toxicity from polycyclic aromatic hydrocarbons as the cause. Hydrologic variables accounted for 22 to 66% of variation in fish assemblage structure in urban Georgia (USA) streams (Roy et al. 2005). However, effects of urbanization on fish assemblages appear to be spatially variable. Morgan and Cushman (2005) found a greater impact of urbanization on fish

assemblages in the Eastern Piedmont than in the Coastal Plain ecoregion of the US. One *J-NABS* paper showed a negative impact of urbanization on platypus populations in Australia (Serena and Pettigrove 2005).

Urban streams generally have higher nutrient concentrations (Grimm et al. 2005, Meyer et al. 2005) and remove a smaller fraction of total NO_3^- load (Hall et al. 2009) than do undisturbed streams. However, maintenance of geomorphic heterogeneity is very important for N processing in urban streams and provides balance between processes that produce and consume NO_3^- (Groffman et al. 2005). Nonpoint-source pollution from urban areas is reflected in stable isotope signals and C:N ratio of seston (Ulseth and Hershey 2005), and enzyme activity can be used to assess impacts of urbanization on organic C bioavailability (Harbott and Grace 2005).

Widespread degradation of stream ecosystems caused by landuse effects has prompted stream restoration efforts in recent years. Unfortunately, far less investment has been made in monitoring effectiveness of restoration than in implementing engineered structures designed for restoration purposes (Bernhardt et al. 2005). *J-NABS* is one of the few aquatic journals to have addressed this topic. For example, Moerke et al. (2004) showed that after 5 y, algal and macroinvertebrate abundance and habitat quality had recovered in a restored urban stream, but macroinvertebrate diversity and fish abundance showed limited recovery. Moerke et al. (2004) attributed these results to the overwhelming effects of watershed degradation that negated the positive influence of the spatially limited restoration. Eliminating pollutants and reversing hydrologic damage might not be feasible in some urban areas because of high costs (Booth 2005). However, drainages can be redesigned to reduce effective imperviousness by routing rainfall to areas other than a stormwater drainage system (Walsh et al. 2005a).

Dodds and Welch (2000) and Biggs (2000) called for establishment of nutrient criteria for streams and highlighted the critical need for sound scientific data for doing so. The same might be said for other measures, such as biological metrics, of effects of land use on receiving waters. Despite the many contributions that *J-NABS* authors have made to understanding watershed-stream linkages and in assessing landuse impacts on stream water quality, the science is far from providing practical sustainable solutions. *J-NABS* probably will continue to be an important outlet for research on watershed-stream linkages for the foreseeable future, and we urge investigators to continue their work in this important arena.

Ecosystem Linkages as a Frontier for Aquatic Science

We argue that ecosystem linkages should play a prominent role in future aquatic research agendas. Our assessment suggests that aquatic linkages are garnering more attention among ecologists, and that aquatic journals, including *J-NABS*, have made significant contributions to improving our understanding of those linkages. However, much opportunity remains to study interactions among ecosystems that historically have been studied by different groups of scientists. For example, more research is needed on the linkages between natural riparian wetlands and adjacent waters (i.e., streams, rivers, or lakes), especially with respect to hydrology, C budgets, nutrient and toxin exchanges, biodiversity, and nutrient cycling. The discipline of aquatic ecology also could benefit from more interdisciplinary linkage studies involving toxicologists, conservation biologists, and climate change scientists. Interdisciplinary teams could provide insights that would help us more fully understand the implications of human activities for aquatic ecosystems. We suggest that much potential exists for *J-NABS* authors to contribute to this area of inquiry.

Understanding linkages is important for protecting ecosystems and for restoring impaired ecosystems. For example, in urban stream restorations, reach-scale projects can have limited success because linkages, especially between upstream and downstream areas, are not appreciated. Furthermore, restoration of critical habitats might require restoration of natural linkages before ecosystem structure and function return. For example, introduction of endemic organisms, such as native riparian plants, might be prerequisite to large-scale structural changes, such as the introduction of large wood or reestablishment of channel sinuosity.

Several actions might alleviate impediments to studying ecosystem linkages. *First*, we need to accelerate the recent trend, encouraged by funding agencies, to conduct interdisciplinary research and cross-ecosystem investigations. For example, research teams could be formed that specifically address ecological linkages, thereby removing historical barriers to interdisciplinary research at institutional levels. *J-NABS* could contribute to this effort by dedicating an editorial, a journal section, and perhaps even an entire issue, to the topic of ecosystem linkages.

Second, we need to train students in a more integrative fashion. This goal could be met by encouraging broad training to study linkages, such as with training grants. For example, the National Science Foundation Integrative Graduate Education

and Research Traineeship (NSF-IGERT) program specifically funds graduate training programs in the US that are interdisciplinary in nature. Linkages could be incorporated explicitly into existing courses or new courses that emphasize linkages could be developed. The North American Benthological Society (NABS) could link to other societies under the auspices of NSF-funded programs similar to Eco-DAS (Ecological Dissertations in the Aquatic Sciences, formerly known as DIALOG) of the American Society of Limnology and Oceanography to foster exchange of information among ecologists working in different but potentially linked ecosystems. Furthermore, aquatic ecologists could foster an intellectual atmosphere in which knowledge of ecological exchanges is essential to understanding ecosystems and, thus, to solving environmental problems. This outcome would require that freshwater ecologists work actively with terrestrial and marine ecologists, probably to the benefit of all 3 groups.

Third, funding agencies should allocate resources specifically for studying aquatic linkages. Such agencies include traditional government funding agencies, but also foundations and organizations that support less traditional research. A critical step in this process will be to convince program directors, panels, and reviewers that cross-ecosystem research is important and should be supported, especially in the context of global environmental change. Increased publication of such research in venues like *J-NABS* would support this effort by making such research more visible.

Fourth, appropriate outlets for publication of linkage research should be developed. Such research sometimes falls between the scopes of mainstream journals and, therefore, might not have an obvious "home." For example, by the very nature of their names, *J-NABS*, *L&O*, or *Wetlands* might select for research focused in specific areas. In contrast, other established journals (e.g., *Ecology*, *Oecologia*) are not ecosystem-specific and might embrace cross-ecosystem research but could have difficulty finding appropriate reviewers for those papers. Some developing journals, such as *Aquatic Sciences - Research Across Boundaries*, emphasize cross-ecosystem research. *J-NABS* could compete in this expanding arena. Journal editors should be open to devoting more space to linkage-related papers. Within specialized journals, new journal sections that emphasize cross-ecosystem processes might be useful.

J-NABS can vault to the forefront in this arena by encouraging the submission of papers with a broader view of aquatic ecology that goes beyond lotic ecosystems to the broader landscape (cf. Polis et al. 2004). Our analysis indicates that neither *FWB* nor

L&O have been especially prone to publishing papers concerning ecosystem linkages. We think that *J-NABS* could make that contribution, especially for those linkages involving flowing waters. For example, *J-NABS* could encourage study of lotic ecosystems in the context of stream and river networks that drain variable landscapes (e.g., urban, agricultural, pristine) to help better manage and restore systems within a broader landscape perspective. Stream ecologists already have pioneered integrative concepts, such as the River Continuum Concept (Vannote et al. 1980) and the Serial Discontinuity Concept (Ward and Stanford 1995), which were then promoted by various publications in *J-NABS*. Stream ecologists also should remember that the paper published by Ward (1989) in *J-NABS*, which identified the importance of various linkages (i.e., lateral, longitudinal, and vertical), helped to develop the broad notion of a stream as an integral part of the watershed. Thus, *J-NABS* has a history of publishing papers on important concepts, such as ecosystem linkages, and should seek ways to enhance this role.

Fifth, we need to develop new ideas and generate intellectual excitement related to ecosystem linkages. We can use symposia and workshops at society meetings for intellectual exchange, or propose workshops to funding agencies for independent support. In particular, meetings that bring together different groups of scientists are likely to be the most effective forum in which to encourage interdisciplinary discussion. The ultimate goal of these efforts should be to attract the best teams of scientists to study ecosystem linkages. As a consequence of such efforts, aquatic ecology will be advanced, and solving the planet's daunting environmental problems, which almost invariably involve multiple ecosystems, probably will become more tractable.

Acknowledgements

We are extremely grateful to the many individuals who contributed to the ideas and content of this paper. In particular, we thank Jason Keller and Susanne Hebbeler for their heroic efforts in painstakingly examining the published literature and assembling the data that contributed to Fig. 2. We are greatly indebted to them. This manuscript sprang from a NABS Presidential Address delivered by GAL at Prince Edward Island in 1998, but the ideas contained in that address remained dormant for some time. We thank Al Steinman for encouraging us to resurrect them in this paper. A graduate seminar held at the University of Notre Dame contributed substantially to the ideas contained in that address, and Aimee Fullerton assisted with the graphical content of that address. The students

and postdoctorates in the University of Notre Dame Stream Ecology Laboratory have, over the past 10 y, generously shared ideas and made suggestions that greatly improved the final manuscript during its considerable gestation period. Robert Hall, Pamela Silver, and 2 anonymous referees made valuable comments on a previous version of this paper, for which we are grateful. Research leading to this paper was supported by the US Department of Agriculture-Cooperative State Research, Education, and Extension Service National Research Initiative Competitive Grants Program (Managed Ecosystems Program 2006-35101-16566), the NSF (DEB-0516043), and the Great Lakes Fishery Trust (Project 2007.857).

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Received: 7 November 2008

Accepted: 21 October 2009