PERSPECTIVE / PERSPECTIVE

Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream–lake networks

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Abstract: Lakes and rivers are intimately connected in an alternating series of lentic and lotic reaches in many regions. The study of lakes and their outlets in hierarchical and branching river networks has not gained the attention of stream ecologists, and little effort has been focused on synthesizing the ecology of lake–stream interactions within a drainage network. Rapid and predictable changes in the ecological characteristics of streams occur at the interface with lakes. The influence that a lake might have on a stream is dependent on its position within the stream, stream type and size, lake size and shape, and the inlet and outlet positions. Little is known about the influences of multiple lakes within stream–lake networks and how these influences are determined by network shape and pattern. Fruitful collaborations and novel insights will come from the combined efforts of limnologists, stream ecologists, and landscape ecologists. Geographic information systems and network analyses will play an important role in summarizing aquatic landscape characteristics and creating a predictive science of aquatic networks. Lakes need to be more explicitly incorporated into ecological concepts in stream ecology, and reciprocally, streams need to be incorporated into ecological concepts involving lakes for the successful management and conservation of our aquatic resources.

Résumé : Dans plusieurs régions, les lacs et les rivières sont intimement reliés par une succession en alternance de sections lentiques et lotiques. L'étude des lacs et de leurs émissaires dans les réseaux fluviaux hiérarchiques et ramifiés n'a pas suscité l'intérêt des écologistes des eaux courantes et peu d'efforts ont été déployés pour faire la synthèse des interactions entre les lacs et les cours d'eau dans un même bassin versant. Il se produit des changements rapides et prévisibles dans les caractéristiques écologiques des cours d'eau à la rencontre des lacs. L'influence que peut avoir un lac sur un cours d'eau dépend de sa position dans le cours d'eau, du type et de la taille du cours d'eau, de la taille et de la forme du lac et de la position du tributaire et de l'émissaire. On sait peu de choses sur l'influence de lacs multiples dans les réseaux de lacs et de rivières et sur l'effet de la forme et de l'organisation du réseau sur ces influences. La combinaison des efforts de limnologistes, d'écologistes des eaux courantes et d'écologistes du paysage pourrait produire des collaborations intéressantes et ouvrir de nouvelles perspectives. Les systèmes d'information géographique et les analyses de réseaux joueront un rôle important en synthétisant les caractéristiques du paysage aquatique et en créant une science prédictive des réseaux aquatiques. Il est essentiel d'incorporer de manière plus explicite les lacs dans les concepts de l'écologie des eaux courantes et, réciproquement, les cours d'eau doivent être incorporés dans les concepts écologiques reliés aux lacs pour une gestion et une conservation réussies de nos ressources aquatiques.

[Traduit par la Rédaction]

Introduction

Stream ecologists typically see the landscape in terms of a network of streams that inevitably empty into another stream or lake, whereas limnologists typically see bodies of water dotted on the landscape. Stream ecologists have largely ignored stream networks punctuated with lakes. Similarly, limnologists have largely ignored streams connecting lakes (cf. Kling et al. 2000; Arp and Baker 2007; Marcarelli and Wurtsbaugh 2007). Soranno et al. (1999) examined spatial variation and ecological organization among lakes within chain lake systems across North America. They noted that although limnologists have long been interested in regional patterns in lake attributes, only recently have they considered lakes connected and organized across the landscape, rather than spatially independent entities (Martin and Soranno 2006). A similar perspective on the ecology of stream

Received 17 July 2009. Accepted 4 June 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 28 July 2010. J21309

Paper handled by Associate Editor Jordan Rosenfeld.

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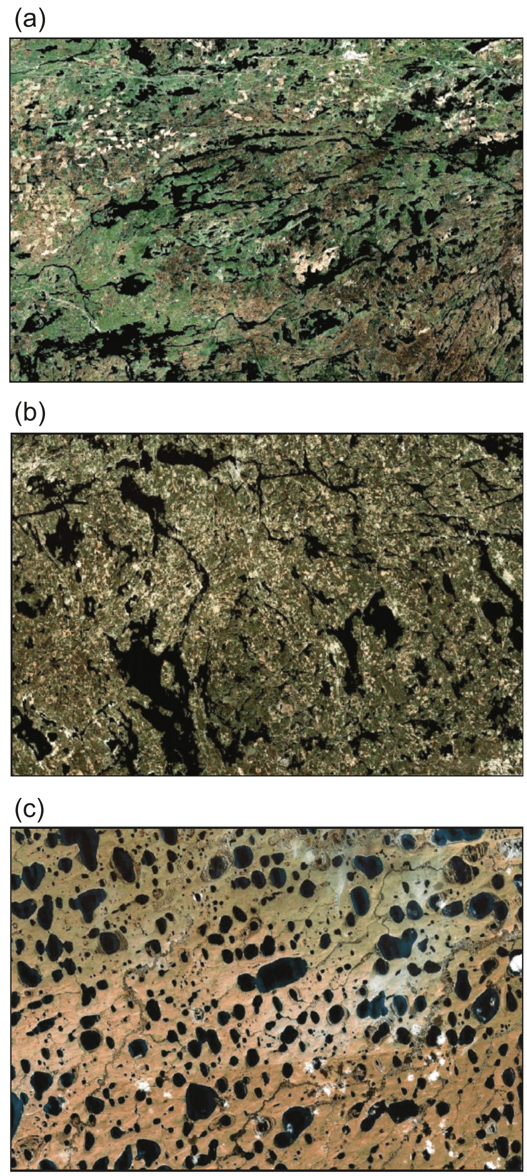
reaches connecting lakes in stream–lake networks has not been articulated.

Streams are typically envisioned as long channels of continuously moving water that drain watersheds, yet for many parts of the world (e.g., Canada, United States (US), Sweden, Finland, Norway, Russia, Argentina), streams and lakes are intimately connected (see Kratz and Frost 2000; Fig. 1). For example, the Canadian Shield occupies an area of 4.6 million km^2 or nearly half the land area of Canada and is densely populated with lakes and interconnecting streams (Fig. 1*a*). Portions of the Shield are also found in Minnesota, Wisconsin, Michigan, and New York. In Ontario, this Shield region has many lakes (35 000 lakes > 20 ha) and an even greater number of streams. For instance, the mainstem of the Petawawa River has 26 lakes on its 200 km length. In central Canada, the Churchill River has 52 large lakes on its 1300 km length and many unnamed lakes representing wider reaches of the river. In addition, ephemeral beaver (*Castor* spp.) ponds within watersheds are often not mapped. In Alaska, Canada, and Russia, streams flow through small shallow thaw lakes that are abundant in lowland ice-rich permafrost (Fig. 1*c*).

The river continuum concept (RCC; Vannote et al. 1980) provides a conceptual framework for understanding the fluvial system as an integrated series of physical gradients and associated biotic adjustments along the stream. This view of the river represents one of the most influential conceptual works in river ecology as evident in the many concepts it has spawned, many of which challenge this linear view (e.g., Rice et al. 2001; Poole 2002; Benda et al. 2004). More recently, stream ecologists have taken a view of the river that incorporates ideas from landscape ecology and the influence of tributaries to develop the hierarchical patch dynamics concept (Poole 2002) and network dynamic hypothesis (Benda et al. 2004). However, as Poole (2002) notes, the river discontinuum view does not dismiss the older continuum view so much as "subsume" it: gradual transitions between habitat patches do occur, resembling a continuum. Poole (2002) noted that the "river discontinuum" is comprised of hierarchically nested patches and individual stream segments arranged longitudinally in space, many of which might have unique and dynamic structures and functions over time. In this network view, the river is a population of channels and confluences, each of which generates unique streams. Benda et al. (2004) developed the network dynamics hypothesis, providing a structural basis for predicting how disturbances or watersheds interact with the spatial structure of river networks to generate spatial heterogeneity in habitat along river profiles and throughout watersheds. This view emphasizes variation rather than the average state in stream character and, thus, complements the concept of hierarchical patch dynamics.

Ward and Stanford (1983) advanced the serial discontinuity concept as a theoretical perspective of regulated rivers that predicts and explains the effect of reservoirs along the river continuum. In this linear perspective, reservoirs disrupt the continuum and cause upstream–downstream shifts in abiotic and biotic parameters and processes. The effect is related to the position of the dam along the continuum. For example, a bottom-draw dam in the lower reaches of a river may sharply decrease water temperature. Although there have been numerous studies on the influence of reservoirs on river structure and function, there has been much less investigation focused on the influence of natural lakes.

Fig. 1. Satellite imagery from 2007 of contrasting stream–lake networks found around the world (Google Maps, http://maps.google.ca/maps?hl=en&tab=wl): (*a*) a typical area of the Canadian Shield north of Thunder Bay, Ontario; (*b*) 60 km northeast of Helsinki, Finland, showing strong geologic control; and (*c*) thaw lake systems generating regular circular lakes on the North Slope of Alaska. Black areas and lines indicate water.



Despite the abundance of stream–lake networks, the ecology of streams connecting lakes and stream–lake networks taken together has been largely ignored (cf. Kling et al. 2000; Marcarelli and Wurtsbaugh 2007; Luecke and MacKinnon 2008). Hence, the available literature is limited for review. Concepts in stream ecology have advanced our understanding of streams for many areas of the world, yet a theoretical perspective synthesizing the ecology of stream–lake networks is lacking. The structure and ecology of stream–lake networks have important implications for the way in which we view river ecosystems, thus influencing how we design studies, interpret data, and manage our natural resources.

In this synthesis, I begin by considering the local effects of a lake on a downstream stream segment. This initial discussion explores the influence of lake position in a watershed on the outcome of a lake's effect and takes a linear perspective for illustrative purposes. I then describe how characteristics of lakes and their inlet and outlet streams (size, shape, configuration, and serial juxtaposition of multiple lakes) might modify expected influences on downstream segments. In the second section of this paper, I explore the broader perspective of lakes within stream networks. This larger-scale whole-network perspective strives to incorporate the interactions among lakes and between lakes within contrasting network patterns. Lastly, I discuss lake effects on fish distribution and community structure in stream–lake networks. Lakeless streams are not discussed here because they should follow predictions of the river continuum concept or have variability not due to lakes. Other sources of variability creating discontinuities include confluence points (Benda et al. 2004), beavers (Collen and Gibson 2001), geology, land use, and anthropogenic factors, e.g., culverts, forestry, and hydropower.

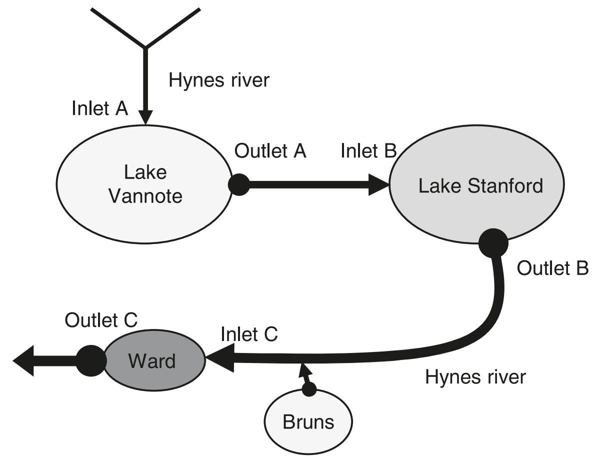
Terminology

For the purposes of this synthesis, streams draining the landscape without lakes on their drainage network will be called lakeless streams (Hynes River before it enters Lake Vannote; Fig. 2), whereas lake-effect streams have one or more lakes on their drainage network (Hynes River downstream of Lake Vannote; Fig. 2). Overall, the collection of streams and lakes are called a stream–lake network or, sometimes, "chain lakes". An outlet stream (outlet A) drains Lake Vannote and becomes an inlet stream (inlet B) where it empties into Lake Stanford (Fig. 2). Stream segments between lakes are identified by the lake flowing into the stream and the lake receiving the stream, e.g., Vannote-Stanford segment of the Hynes River (Fig. 2). The influence of the upstream lake on the outlet stream is called the lake effect.

The influence of lakes on outlet streams: a linear perspective

Lakeless streams in forested regions may exhibit continuous downstream trends in energy inputs and habitat structure as predicted by the RCC (Vannote et al. 1980), but many will express a discontinuous pattern (Poole 2002). In headwater streams, we can expect that stream characteristics will be influenced by riparian vegetation that shades the stream and provides coarse particulate organic matter (CPOM) input. Here, heterotrophy will be more prevalent than autotrophy. Benthos belonging to the shredder and collector functional feeding groups and coolwater fishes that feed mainly on invertebrates will likely dominate. In midreaches, riparian vegetation has less influence on the wider stream. Sunlight now reaches more of the stream, and periphyton and macrophytes become the primary energy sources. Benthos dominance shifts from shredders to grazers, and fishes shift from coldwater to piscivorous, coolwater species. In lower reaches, increasing turbidity and depth cause the river

Fig. 2. Schematic representation of a stream–lake network illustrating some of the different configurations of lake size and location within a drainage area. Downstream ecological impacts of different lakes are illustrated in Fig. 5.



to become more heterotrophic, although phytoplankton and macrophytes will be present. Invertebrates that use fine particulate organic matter (FPOM) dominate the benthos. Warmwater and planktivorous species of fish may be present. Exceptions to these longitudinal gradients described in the RCC are many and include streams in biomes where tall riparian vegetation is absent (e.g., grasslands, desert, and the Arctic), regulated streams, and stream–lake networks, the focus of this paper.

Ward and Stanford (1983) hypothesized relationships among physical, chemical, and biological variables as functions of stream order (distance) along a stream continuum. They illustrated the influence that reservoirs can have on the continuum depending on their position (headwater, midreach, and lower reach) in the stream network. In this model, Ward and Stanford assume that a reservoir releases cold oxygenated hypolimnetic water during summer. Despite obvious differences between reservoirs and lakes, many of the relationships that they hypothesized for reservoirs may hold true for natural lakes. In the following section, relationships between stream order and various parameters were derived from key sources in the literature (e.g., Vannote et al. 1980; Ward and Stanford 1983; Naiman et al. 1987). The point of this discussion is to illustrate the influence of a lake located in the headwaters, midreaches, and lower reaches of a river. For the purpose of illustrating chain-lake systems, I do not consider other influences such as confluences or tributaries, which form the basis of the discontinuous view of rivers as described above (Poole 2002).

Lake effects on physical attributes of outlet streams

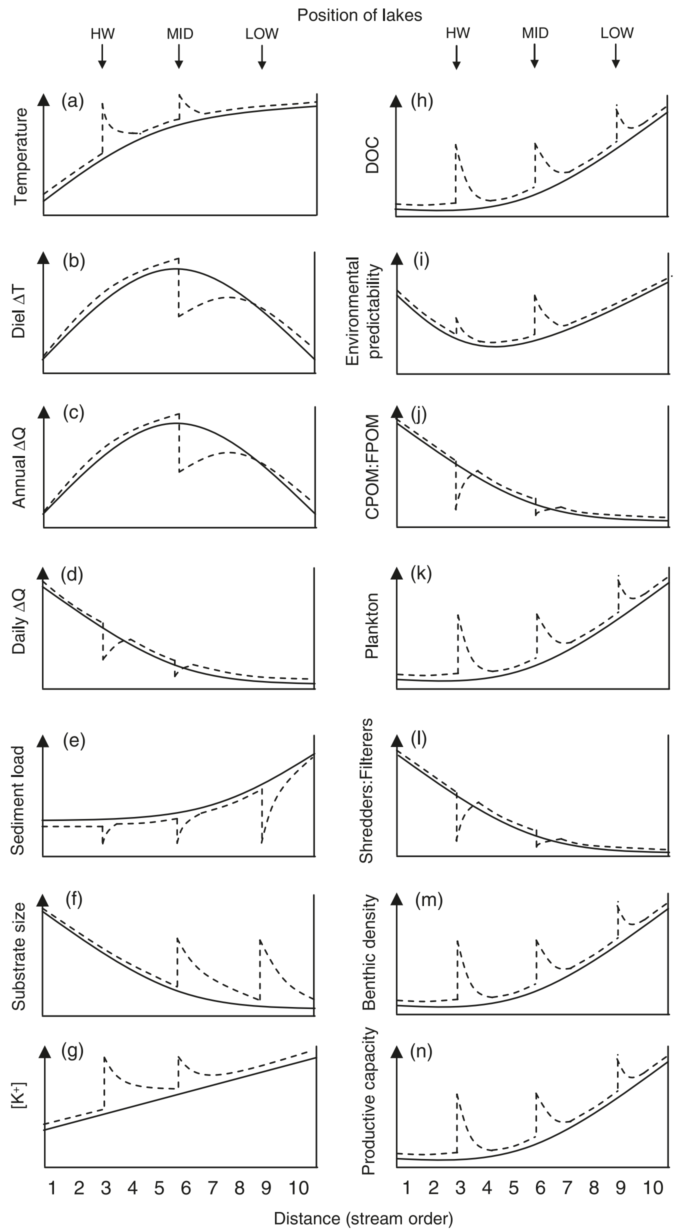
The storage capacity of lakes tend to stabilize the thermal and flow regime characteristics of outlet streams. During summer months, a lake will provide warm (Fig. 3*a*) epilimnetic water to the outlet stream (Wotton 1995; Dorava and Milner 2000; Luecke and MacKinnon 2008). In headwater streams, the lake effect decreases progressively downstream as warm, epilimnetic water cools in the presence of increased riparian shading and groundwater inputs. Some streams may not be able to shed added heat during the summer, and downstream water temperatures may continue to warm as a result of normal stream heating processes. As stream size increases, the influence of lakes on water temperatures will likely decrease (Fig. 3*a*) because larger streams are typically warmer already. Because of the large thermal inertia of lakes, these warmer temperatures may persist well into the fall season (Fukushima and Smoker 1997; Hieber et al. 2002; Luecke and MacKinnon 2008) but are cooler in the spring. During winter, ice formation and transport in the outlet stream may be reduced, resulting in less scouring and damage to biota and their filter-feeding structures.

The large thermal inertia of a lake also results in less diel variation in water temperatures (Fig. 3*b*) than would be observed in most lakeless streams except those with high inputs of groundwater (Hieber et al. 2002; Jones et al. 2003*a*; Luecke and MacKinnon 2008). Decreases of the diel range will be most dramatic below a lake in the middle reaches where the greatest daily thermal range is normally observed (Caissie 2006). Less diel variation and warm epilimnetic water temperature can result in more degree-days that increase rates of decomposition and nutrient turnover, stimulate the growth of primary and secondary producers (e.g., algae, benthic invertebrates, and fish), and enhance ecosystem productivity (Jones et al. 2003*a*; Dorava and Milner 2000). During the warm summer months, fishes may leave the outlet stream and move into the lake or downstream to cooler locations if the outlet temperature increases above their preferred temperature or water levels become exceedingly low.

The flow regime of an outlet stream will be partially dictated by water levels in the upstream lake. Lakeless streams flowing into a lake are influenced by the nature of the watersheds they drain and may vary from highly variable and unpredictable to very stable flow regimes (Poff and Ward 1989). Regardless of the flow characteristics of lakeless streams draining into a lake, the lake will dampen or moderate flow fluctuations (ΔQ; Figs. 3*c*, 3*d*) such that outlet flows may be sustained during periods of drought or freezing (Dorava and Milner 2000; Arp et al. 2006). The damping effect of lakes on the runoff hydrograph can prevent small runoff events from maintaining a measurable flood wave through the basin (Spence 2006). The location at which a runoff event is interrupted in the watercourse is a function of lake size relative to upstream runoff inputs. Runoff is more susceptible to evaporative losses in large receiving lakes where inflow per unit area is less. These processes may cause intermittent streamflow in small outlets (Spence 2006).

The sediment load (Fig. 3*e*) in outlet streams is generally low because most sediment in inlet streams will settle out before reaching the outlet stream (sediment sink; Dorava and Milner 2000; Arp et al. 2007). If the continuity of sediment transport is interrupted by lakes, the flow in the outlet may become sediment-starved (Kondolf 1997) and prone to erode the streambed and banks, producing channel incision (down-cutting), coarsening of bed material (often called armouring; Myers et al. 2007; Luecke and MacKinnon 2008), and loss of spawning gravels (as smaller gravels are transported without replacement). Bed sediments in lake outlet segments are likely less mobile during bankfull flows in

Fig. 3. Relative changes in physical and chemical variables as a function of stream order in lakeless streams (continuous lines; based on Vannote et al. 1980; Ward and Stanford 1983; Naiman et al. 1987). The postulated effects of lakes in forested headwaters (HW), midreaches (MID), and lower reaches (LOW) of a river are illustrated with broken lines (modified from Ward and Stanford 1983). Lakes are illustrated as points for simplicity, and the influences of other factors (e.g., tributaries) along the discontinuum are ignored. ΔT, temperature change; ΔQ, change in flow; DOC, dissolved organic carbon; CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter.



contrast to sediments at lake inlets (Myers et al. 2007). The coarsening of substrate (Fig. 3*f*) will be less pronounced in headwater streams where substrate sizes are generally large, whereas in lower reaches, fine substrate may be removed. In a mountain lake district, Arp et al. (2007) noted 50% recovery of sediment characteristics 1–5 km downstream, but for some streams, full recovery required 10–20 km. Outlets are typically wide and shallow with coarse sediment, whereas inlets are narrow and deep with finer sediment (Arp et al. 2007; N.E. Jones, personal observation). In contrast, Dorava and Milner (2000) found that lakes lead to narrower channels, more stable banks and riparian areas, and more diverse and stable habitat in contrast to glacial streams (braided, anastomosing streams) without lakes. This difference suggests that the response of the outlet stream may be predictable if the context, i.e., catchment and sediment characteristics, are considered (Montgomery 1999). Dorava and Milner (2000) also observed that lakes reduced suspended sediment dramatically in glacier-fed systems in Alaska.

Lake effects on chemical attributes of outlet streams

There is surprisingly little information in the literature concerning longitudinal changes in water chemistry in lake outlet streams (but see Kling et al. 2000; Arp and Baker 2007). In general, the similarity in chemical characteristics between lake surface waters and outlet streams will decrease with distance downstream. Tributary streams and groundwater may deliver water of contrasting chemical composition that alters water chemistry in the outlet stream (Bruns et al. 1984). Kling et al. (2000) noted that streams tend to have higher concentrations of major anions and cations than lakes within the same network, which had higher concentrations of particulate carbon, nitrogen, phosphorus, and chlorophyll *a*. Kling et al. (2000) observed predictable differences in water quality parameters measured at the inlet versus the outlet of lakes and in parameters measured at upstream versus downstream sites in the stream-reach connecting lakes. In-lake processing tended to consume alkalinity, conductivity, H^+, dissolved inorganic carbon (DIC), Ca^{2+}, Mg^{2+}, CO_2, CH_4, and NO_3^-, and produce K^+ and dissolved organic carbon (DOC). In-stream processing resulted in the opposite trends (consumption of K^+ and DOC; Figs. 3*g* and 3*h*), and the magnitudes of change were often similar to those measured in the lakes but with the opposite sign (Kling et al. 2000). Arp and Baker (2007) found that there was very little nitrate uptake in most lake outlet streams, whereas PO_4^{-3} uptake was higher at outlets in comparison with reference and lake inlet reaches. They also noted that the best predictor of patterns in nutrient demand was the proportion (%) of watershed area not routing through a lake. They estimated that NO_3 and PO_4^{-3} uptake returned to 50% of above-lake conditions within 1–4 km downstream of a small headwater lake but required considerably greater distances for larger lakes positioned lower in the watershed.

Lake effects on biological characteristics of outlet streams

Combined changes in the thermal, flow, and sediment regimes observed at lake outlets creates an environment or habitat template (sensu Southwood 1988) that is less variable or harsh (Fig. 3*i*) than lakeless streams (Dorava and Milner 2000; Hieber et al. 2002; Jones et al. 2003*a*). In this environment, species with life histories more suited to low variability environments will be favoured over those with life histories suited to environmental instability. Stable flow regimes and low amounts of sediment moderate the disturbance regime in the outlet stream (see Wootton et al. 1996; Myers et al. 2007), likely reducing the magnitude of periphyton scour following spates and perhaps allowing a greater accrual of biofilm and mosses that provide food and habitat for benthic invertebrates and, subsequently, fishes (Haraldstad et al. 1987; Dorava and Milner 2000). The influence of a lake will decrease downstream to a point where stream attributes resemble lakeless streams, thereby increasing the diversity of habitat types within the watershed as a whole.

Organic matter

Lakes act as transducers along the river network that alter the quantity and quality of organic matter delivered to stream reaches. A lake may supply an outlet stream with a rich source of organic carbon ranging from dissolved to CPOM (Fig. 3*j*), including coarse woody debris (Kownacki et al. 1997). Richardson and Mackay (1991) noted that large aggregations of filter-feeding invertebrates, each with a particular particle size preference (Harding 1997), will selectively ingest particles that are more likely to enhance growth (high quality foods), reducing their availability downstream. The consumption of DOC by invertebrates may explain the in-stream decrease of DOC as noted by Kling et al. (2000). In turn, invertebrate fauna alter the DOC size spectrum and, thus, the assemblage of invertebrate species downstream (Wotton et al. 1998; Parkes et al. 2004). Vadeboncoeur (1994) observed that although initial concentrations of suspended organic carbon are determined by the lake within a short distance (<3 km), concentrations become regulated by in-stream processes (including sedimentation and consumption by filter-feeding invertebrates). In addition to the large amount of energy flowing into the outlet, outlet streams likely have higher proportions of phytoplankton providing a source of labile DOC as opposed to residual refractory carbon of terrestrial origin from similarly sized lakeless streams.

Plankton

Phytoplankton, zooplankton, and bacterioplankton are abundant in epilimnetic lake waters (Fig. 3*k*) delivered to the outlet (Haraldstad et al. 1987; Parkes et al. 2004) where dramatic changes occur within the biological community. The morphology of the littoral zone influences the transport of zooplankton into outlet streams (Walks and Cyr 2004). Once in the outlet stream, water velocity, depth, and likely width-to-depth ratios are the principle factors influencing particle transport downstream (Paul and Hall 2002; Walks and Cyr 2004). The extent of lake influence on seston density expands and contracts longitudinally with increases and decreases in discharge on any individual stream (Vadeboncoeur 1994; Campbell 2002). Vadeboncoeur (1994) found a longitudinal decrease in lake-derived phytoplankton that was balanced by an increase in stream algae. Drift in lake outlet streams is typically dominated (>90% by abundance) by planktonic microcrustaceans (Jones et al. 2003*b*) similar in species composition to upstream lakes (Campbell 2002). Depending on the habitat characteristics of the outlet stream (e.g., cascades and riffles), many of the fragile planktonic organisms may be damaged or killed by turbulent flows (Richardson and Mackay 1991). In the lower reaches of rivers, the abundance of planktonic organisms may be relatively high, so plankton-rich lakes may have relatively little influence in lower reaches (Fig. 3*k*).

Benthos

The high density of benthic invertebrates in lake outlet streams (particularly filter-feeding) and their rapid decline downstream has been attributed to gradients in food resources, flow, temperature, and sediment regimes. The high particulate density drifting into outlet streams provides vital energy and nutrients required for the growth of benthic invertebrates (Robinson and Minshall 1990) and mussels (Welker and Walz 1998). This energy transfer from one habitat to another subsidizes the outlet food web (Polis et al. 1997; Doi 2009); the food base for benthic invertebrates can be dominated by lacustrine inputs (>80%) in small shaded lake outlets (Junger and Planas 1994). Filter-feeding organisms (e.g., Simuliidae and Hydropsychidae) typically dominate the benthos of lake outlets (Fig. 3*l*) much like reservoir outlets (Ward and Stanford 1983; Wotton 1988). This filtering of particulate carbon can increase the retention of carbon and decrease nutrient spiralling length (Ensign and Doyle 2006). Dorava and Milner (2000) noted that benthic densities and diversity below Skilak Lake on the Kenai River system were about four times that found in the lakeless glacier-fed Johnson River some 100 km away. The density (Fig. 3*m*) and size of filter-feeding benthos typically decreases with downstream distance from a lake (for a review of mechanisms creating this gradient, see Richardson and Mackay 1991; McCreadie and Robertson 1998). Farther downstream, a large amount of particulate matter has either been filtered out by benthos or has settled to the streambed (Richardson and Mackay 1991; Wotton et al. 1995; McCreadie and Robertson 1998). This nutrient export can be traced downstream for 10 to 10 000 m, depending on the physical characteristics of the stream (see Plankton above).

Dissolved organic matter from lakes may be a significant food source for many benthic groups, including Trichoptera and Simuliidae larvae (Ciborowski et al. 1997). For example, Wotton et al. (1998) observed black fly densities greater than 60 000 individuals·m^{-2} in a lake outlet stream, suggesting that black fly larvae are "allogenic ecosystem engineers" capturing fine and dissolved organic matter from suspension. The egested fecal pellets are then available to the benthic microbial and invertebrate communities.

Fishes

Fishes inhabiting the outlet stream can benefit from the higher densities of benthos and zooplankton drift and higher water temperatures (Irvine and Northcote 1982; Hayes 1995; Jones et al. 2003*b*). Jones et al. (2003*a*) noted that differences in the characteristics of some Alaskan (mainly lakeless streams) and Barrenlands (mainly lake outlets) tundra streams propagate to higher trophic levels, increasing the capacity of outlet streams to support greater benthic invertebrate and fish production (Fig. 3*n*). In an assessment of the importance of small lakes, Irvine and Johnston (1992) determined that coho (*Oncorhynchus kisutch*) fry generally grew fastest in lakes and their outlet streams on Vancouver Island. Similarly, Dorava and Milner (2000) state that sustained summer flows, warmer water temperatures, suitable instream and riparian habitat, and stable coarse substrates led to enhanced salmon (*Oncorhynchus* spp.) productivity compared with purely glacier-fed systems. Luecke and MacKinnon (2008) also found that the growth of Arctic grayling (*Thymallus arcticus*) in a stream–lake network was 50% greater than in an adjacent lakeless stream network. Although several studies have shown that benthic densities are higher near the lake and decrease downstream (Richardson and Mackay 1991), published examples of this longitudinal gradient for fishes in terms of density, biomass, or growth are absent. Jonsson and Sandlund (1979), however, noted that brown trout (*Salmo trutta*) caught 10 km downstream from the outlet had growth comparable with trout from an inlet stream. The characteristics and properties of lake outlets, i.e., resource subsidy and benign environment, may promote higher productivity than would be observed in streams without lakes (Hieber et al. 2002; Jones et al. 2003*a*; Luecke and MacKinnon 2008). Such an understanding could lead to more refined estimates of river production and management of fishery resources (Gibson 2002). Randall et al. (1995) proposed that rivers are generally more productive for fish than lakes. In this review, we see that outlets, or at least the segments of streams near the lake outlet, are perhaps more productive than neighbouring lakeless stream systems.

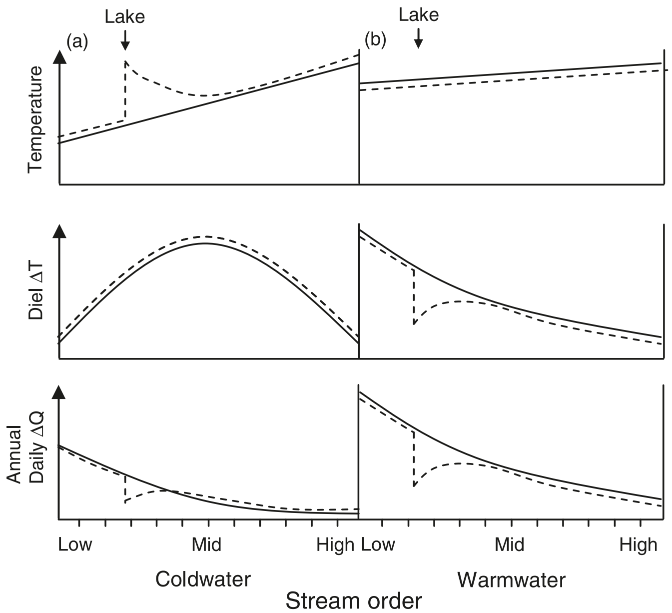
Landscape dependence of lake effects

Lake effects have a strong contextual basis that is influenced by the characteristics of a particular landscape (Montgomery 1999). For example, the effect of a lake on a flashy and turbid warmwater stream dominated by surface flow contrasts sharply with the effect of a lake on a coldwater trout stream. Coldwater streams in forested catchments of temperate latitudes often have groundwater inputs resulting in relatively constant water temperatures and flows, whereas warmwater streams often lack groundwater and (or) surrounding forests resulting in large diel variation in water temperature and variable, perhaps intermittent, flows (Fig. 4). Upon entering a lake, shading is absent and water temperature rises dramatically in the formerly coldwater stream. As a result, the coldwater stream is transformed into a warmwater stream by receiving warm epilimnetic water; however, diel temperature and flow variability remain relatively unchanged and low (Fig. 4*a*). In contrast, water temperatures in the warmwater stream are less variable: flow and diel temperature variability are reduced and perennial base flow may be observed (Fig. 4*b*). Further downstream, the lake effect diminishes even more and the continuum is re-established or perhaps altered by joining a large, contrasting river type (Benda et al. 2004).

Lake size, lake shape, stream size, and inlet and outlet position

The physical, chemical, and biological characteristics of outlet streams are determined, in part, by the characteristics of the source lake and the streams that flow into it. Within a lake, inflowing materials are captured, processed, transformed, and released in the outlet water. The position of inlets and outlets may also determine the degree of lake influence. A lake with inlets and outlets at the opposite ends (Fig. 5*a*) will alter the inflowing stream to the greatest degree, whereas inlets and outlets in close proximity may short-circuit the lake effect, particularly during high flows (Fig. 5*b*). The latter might be particularly true if the tributary angle of entry into the lake points directly to the lake outlet.

Fig. 4. Context dependence of lake effects on three factors: stream temperature, diel stream temperature change (ΔT), and annual and daily variability in discharge (ΔQ) in (*a*) a coldwater stream vs. (*b*) a warmwater stream (modified from Ward and Stanford 1983). Position of the headwater lake is indicated by arrows. Continuous and broken lines represent lakeless and lake outlet streams, respectively.



The degree of influence that the lake has depends largely on the relative size of the stream and lake. For example, the characteristics of a small stream flowing into a large lake with a low flushing rate (Fig. 5*c*) have the potential to be significantly altered, whereas a larger river flowing into a small lake with a high flushing rate may retain many of its physical and chemical characteristics (Fig. 5*d*).

Lake residence time (days to years) is dependent on internal physical processes (Ambrosetti et al. 2003). Lake shape and the presence of islands will influence flow patterns, and simple calculations of inflow to lake volume are inadequate to assess the extent of water mixing. Depending on the water temperature of the stream relative to that of the lake, a stream may move through a lake in a variety of ways: as surface overflow, as intermediate depth interflow, or as near-bottom underflow. High flows at certain times of year influence when most of the mixing and outflow occurs; hence, there is seasonality in the mixing process. Circulation of the lake is further influenced by the Earth's rotation so that incoming rivers flow preferentially counter-clockwise along the shoreline of lakes in the northern hemisphere (Carmack et al. 1979).

Effects of multiple lakes along the river continuum

Ward and Stanford (1983) developed a conceptual model to quantify the linear effects of multiple reservoirs on the continuum. This view of a river shows the compound linear effect of multiple impoundments along a river, which are also manifest in natural lake chains. Reservoirs disrupt the continuum and cause upstream–downstream shifts in abiotic and biotic structure and function. In multiple-lake scenarios, the continuum may never match the characteristics of their lakeless stream relatives. For example, changes in ecological characteristics of a forested stream without lakes (Fig. 6*a*) can be very different from those of a stream with lakes that punctuate the continuum causing up- and down-shifts in expected condition (Fig. 6*b*). Below I expand on Ward and Stanford's linear perspective of lakes punctuating a continuum to develop the idea of a chain lake network including lakes distributed throughout river networks, which generate heterogeneity in river habitat characteristics at a landscape level.

Fig. 5. Effects of discharge and inlet stream configuration on lake effects. A lake with inlets and outlets at opposite ends (*a*) will provide a greater opportunity for transformation of ecological characteristics than if the inlet and outlet are very close (*b*). Similarly, lake effects will be greatest when discharge is low relative to lake volume (*c*) and less when the discharge is high relative to lake volume (*d*). Similarly, arrows indicate the direction and magnitude of river flow.

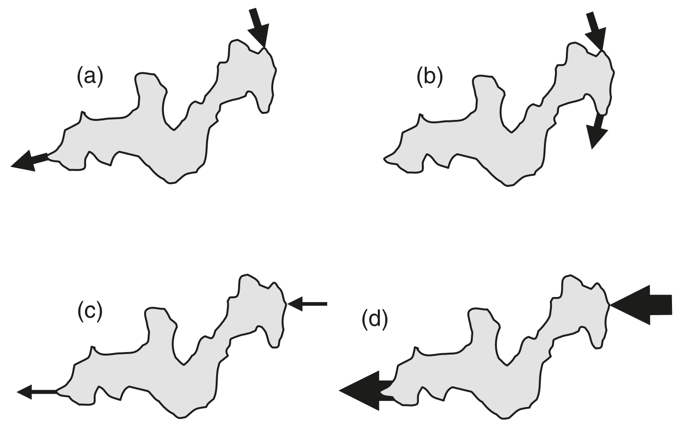


Fig. 6. Hypothesized changes in ecological characteristics of a forested stream as it flows through the stream–lake network represented in Fig. 2. (*a*) Relative changes in temperature and plankton (short-dashed line), ratio of coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) (continuous line), and substrate size (long-dashed line) in a lakeless stream according to the river continuum concept (RCC; Vannote et al. 1980). (*b*) The hypothetical changes from lakes disrupting the continuum as illustrated in Fig. 2.

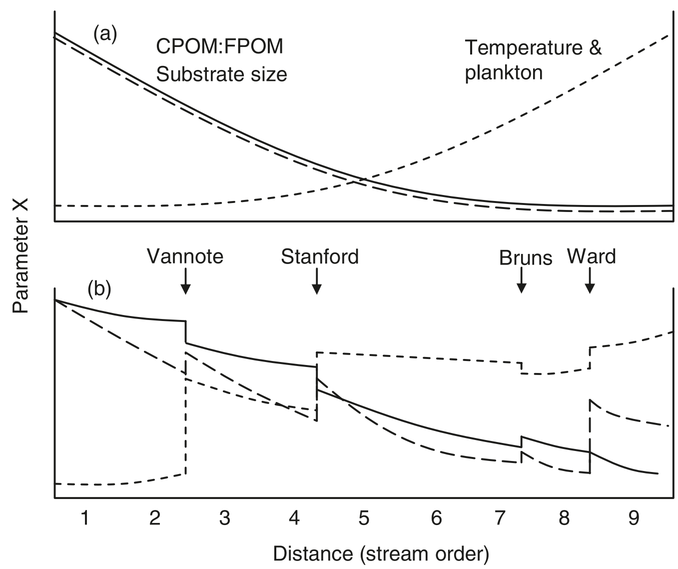


Fig. 7. The influence of a lake is likely to decrease as rivers increase in size down the network.

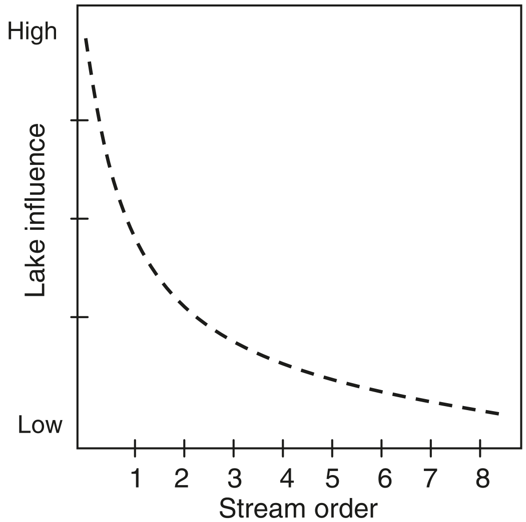


Fig. 8. (*a*) Trellis and (*b*) dendritic network drainage patterns and respective basin shapes illustrate how basin shape influences lake effects. A single lake in the midreaches of a trellis network may alter the ecological characteristics (e.g., flow regime) without dilution from large neighbouring network branches for many kilometres. In contrast, the same placement of a lake in the dendritic

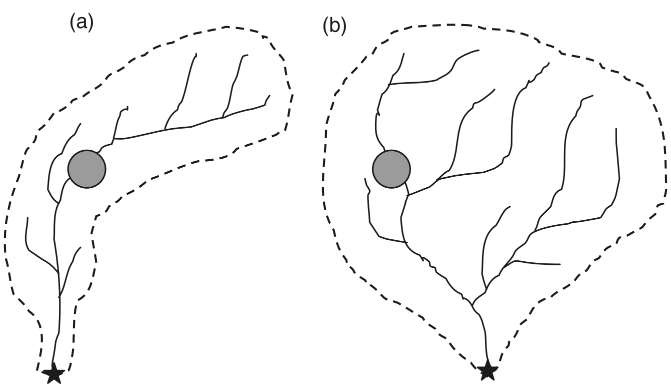
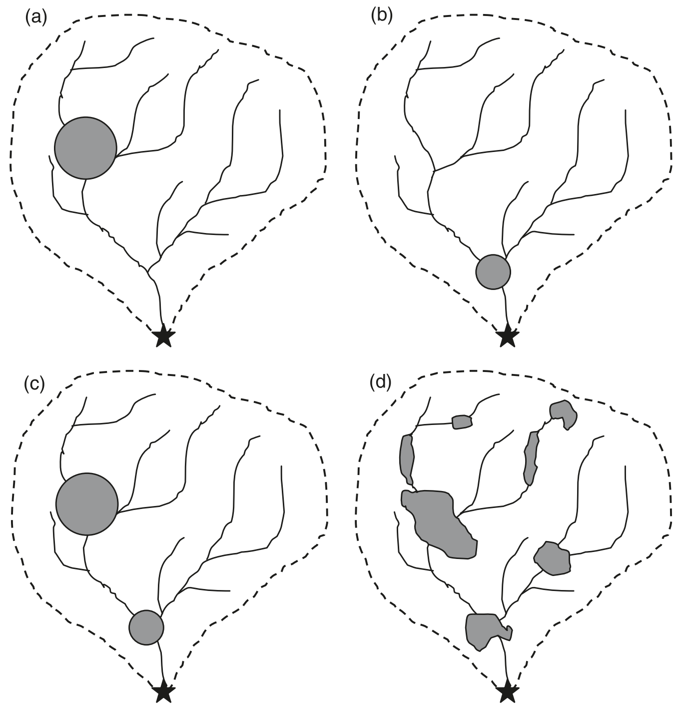


Fig. 9. The position and size of lakes in a river network can have profound implications for the ecological characteristics of streams. The star represents a hypothetical sampling point in the network. (*a*) A relatively large lake in the headwaters of a network may significantly alter the characteristics of the stream. Further downstream, a lakeless tributary dilutes this lake effect. (*b*) A relatively small lake may have little influence on stream characteristics in the lower reaches of a network. (*c*) The combination of two lakes in the network influences the ecological characteristics of both main tributaries. (*d*) The position and size of lakes in a more realistic stream–lake network. The individual and combined influences of lakes on the network are complex and not easily summarized.



Lakes nested within river networks: patch dynamics and hierarchy

Spatial heterogeneity of habitat in streams occurs at multiple scales from grain size to entire catchments (Frissell et al. 1986). Poole (2002) elegantly showed how confluences within stream networks punctuate the river continuum resulting in abrupt changes in stream characteristics and nonlinearities in the expected gradient: a discontinuum network view. Later, Benda et al. (2004) provided a physical basis for predicting how confluences generate longitudinal spatial heterogeneity in habitat. The hierarchical patch dynamics view stresses variation in pattern rather than a continuum. In addition to confluences, there are many other sources of variation, including lakes, which are the focus of this paper. The RCC postulates a gradient in average conditions from the river headwater to lower-order reaches. Lake outlets, as described above, also generate predictable gradients in conditions but at a smaller scale, nested within the larger RCC gradient. In turn, lakes impose obvious spatial heterogeneity within the network that is precipitated downstream (cf. Pringle 1997).

The influence that a lake has on the river is likely to decrease as the river grows larger down the network (Fig. 7). Lake size may increase with landscape position (Kratz et al. 1997); however, in some physiographic regions, large lakes are as likely to be located in headwater areas as lowlands. As river size increases, small lakes on its network path can become a river widening. In many cases, the distinction between a lake and a river is unclear. Functionally, a lake is perhaps defined by its ability to support lake forms of phytoplankton and zooplankton before entering the outlet where conditions are unfavourable for planktonic forms. The downstream distance of the lake effect increases as river size increases such that lake effects extend only metres in small streams to several kilometres in large rivers.

Drainage basin shape may determine the impact that lakes can have on a stream network. Dendritic networks, hierarchically branching and tree-like in form, typically develop in low-relief physiographic regions where relatively homogeneous geology exerts little control over development of drainage networks. Deranged and trellis networks, typical of the Canadian Shield (Fig. 8), are governed by geology and

Table 1. Potential measures and descriptors of stream–lake networks, including summary metrics of whole-watershed conditions, as well as a lake's potential to alter outlet stream characteristics.

Measure	Contributing measures	Rationale
Watershed-scale metrics of lake influence	Percentage of the watershed covered by lakes	High percentage, i.e., >10% of the watershed covered, may indicate a large lake influence on the system. The distribution, however, could be restricted to one large headwater lake.
	Position of lakes in watershed	Surface area or volume of lakes in headwater, midreaches, and lowland areas of watershed
	Percentage of river kilometres flowing through lakes or percentage flowing as river	A measure of overall lake effect
	Size distribution of lakes in the network	Many small lakes likely have less potential to alter streams.
	Cumulative lake-effect score for watershed	A measure of the influence of lakes on streams in the network
A lake's potential to alter downstream characteristics	Surface area or volume of lake relative to the size (width or discharge) of the inlet or outlet stream	Attributes of a small stream have the potential to be significantly altered when flowing into a large lake with a low flushing rate; in contrast, a larger river flowing in a small lake with a high flushing rate may retain many of its characteristics.
	Residence time	Mean time that water spends in a particular lake
	Sizes of inflowing streams	Bankfull width or stream discharge provide an indication of stream size.
	Highest order of stream flowing into lake	Provides an indication of stream size
	Flow path distance between inlet and outlet in lake	A lake with inlets and outlets at the opposite ends will alter the outlet stream attributes to the greatest degree, whereas inlets and outlets in close proximity may short-circuit the lake effect.
	Angle of inlet to outlet	The tributary angle of entry into the lake relative to outlet position
	Number of streams flowing into lake	A large number of streams flowing into a lake may indicate a short residence time.
	Basin shape	The ratio of basin area to the squared value of the basin length
	Distance downstream of a lake	Distance below the lake will determines the magnitude of the lake effect at a downstream sampling site. Coefficients and functional form of the downstream attenuation of lake effects is largely unknown.

can be densely populated with lakes, wetlands, and wandering interconnecting streams. Deranged and trellis networks are often long and rectangular (Briggs 1993), contrasting with round or teardrop-shaped dendritic drainages. A simple assessment of basin shape is the ratio of basin area to the squared value of the basin length. Calculated values of shape can range from near zero (elongated basins) to those approaching one (circular; Strahler 1968). These contrasting basin shapes illustrate how network configuration modifies lake effects. A single lake in the midreaches of a trellis network will alter ecological characteristics (e.g., flow regime) without the dilution from large neighbouring network branches for perhaps many kilometres (Fig. 8*a*). In the dendritic basin, the same placement of a lake will lead to ecological changes that are soon diluted by tributaries (Fig. 8*b*), which also create abrupt changes in the continuum (Benda et al. 2004).

Ecologists often build predictive models to understand how biological characteristics such as species presence or absence and diversity relate to landscape characteristics (e.g., McGarigal et al. 2002; Zorn and Wiley 2006). How well we quantify patterns in river networks will determine how well we can predict and understand their physical and biological attributes (Snelder et al. 2005; Seelbach et al. 2006; Brenden et al. 2008). Lakes connected to river networks present new challenges for deriving meaningful metrics of watersheds. In some cases, simple metrics such as the percentage of the watershed covered by lakes may be adequate to understand the relative influence of lakes on stream networks (Detenbeck et al. 2005). For more detailed metrics, the distance of a biological sampling point from upstream lakes of various sizes may be needed. For instance, what is the relative influence of a small lake 2 km upstream from a sampling point in comparison with a large lake 10 km upstream from a sampling point (Figs. 9*a*, 9*b*)? How does the influence of two or more lakes merge downstream to determine resultant stream condition (Figs. 9*c*, 9*d*)? Quantifying the attributes of stream–lake networks at the watershed-scale is challenging. The degree to which a lake can influence a stream might be estimated by considering lake size relative to the size of an inflowing stream, lake shape, and inlet and outlet position such that each lake in the network could be scored by its potential degree of alteration of stream properties from an otherwise lake-free network. Potential measures that could prove useful in describing stream–lake networks are summarized and postulated (Table 1). Clearly, much work needs to be done in this area to provide measures that are consistent with data availability and that may harmonize with other measures of stream networks and landscape position of lakes (Benda et al. 2004; Martin and Soranno 2006). Hopefully, complex landscape measures will emerge through future collaborations between aquatic and landscape ecologists and the use of geographic information systems and remote-sensing data.

Further advances may be realized by incorporating landscape ecology and network analyses (e.g., graph theory) used in other disciplines such as epidemiology, studies of internet linkages, and transportation networks (Wiens 2002; Ganio et al. 2005; Proulx et al. 2005) to create a predictive science of biological networks. Graph theory provides existing techniques to examine the organization and function of biological systems, e.g., hierarchical branching stream–lake networks containing nodes (lakes and confluences) and edges (interconnecting streams), but has not attracted the attention of aquatic ecologists. Aside from providing a framework for understanding properties of stream–lake networks, other areas of scientific interest may benefit by applying network concepts to metapopulation and invasion ecology, connectivity (Schick and Lindley 2007), material and energy flow, and habitat heterogeneity in stream networks. Fresh ideas may emerge when we expand our view to the study of entire stream–lake networks, surpassing what we might learn from studying the parts (Proulx et al. 2005).

Lakes effects on fish communities in river networks

Piscivory by fish can be a dominant factor in structuring fish communities in both streams and lakes (Jackson et al. 2001). Lakes in stream networks can serve as a reservoir of predators and competitors, whereas streams can provide refuge from predators in the lake (e.g., lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*)). For example, Degerman and Sers (1994) found that the effect of lakes on water temperature, flow regime, drift of plankton, and invertebrates did not influence the stream fish fauna to the same extent as the presence of lentic fish (northern pike (*Esox lucius*); European perch (*Perca fluviatilis*); roach (*Rutilus rutilus*); and burbot (*Lota lota*)) in a zone upstream and downstream of the lakes. Correspondingly, the occurrences of stream fish (brown trout; European grayling (*Thymallus thymallus*); European minnow (*Phoxinus phoxinus*); and bullheads (*Cottus* spp.)) were lower close to lakes. The presence or absence of northern pike in lake networks in Sweden and Canada was a function of stream gradient (Jones et al. 2003*a*; Spens et al. 2007).

Lake inlet and outlet streams provide migratory pathways in a stream–lake network (Olden et al. 2001; Jones et al. 2003*c*; Daniels et al. 2008). This connectivity between lakes may provide colonization routes needed for metapopulations to persist, particularly in Arctic stream–lake networks where small streams and lakes typically freeze solid or in arid-region intermittent streams. Inlets and outlets may also provide critical habitat for spawning and rearing, whereas lakes provide overwintering habitat and refuge during drought (Dorava and Milner 2000; Luecke and MacKinnon 2008). Fishes in lake outlet systems may exhibit a simple adfluvial life history instead of a fluvial life history strategy consisting of distinct and lengthy migrations to spawning, feeding, and overwintering habitats (Northcote 1978; Jones et al. 2003*a*; Luecke and MacKinnon 2008). Based on the movements of fishes in Manitowish Chain of Lakes, Wisconsin, Weeks and Hansen (2009) suggested that walleye (*Sander vitreus*) be managed based on individual lakes and that muskellunge (*Esox masquinongy*) be managed for the entire lake chain. Overall, stream–lake networks provide a diverse array of habitats that may support a wider variety of species than would be present in lakeless steams. The mouths of lake inlets, and possibly outlets, can have relatively high biodiversity associated with different ecotones (Pinay et al. 1990; Willis and Magnuson 2000). Pringle (1997) notes that reservoirs and beavers dams can dramatically influence the spread of non-native fishes and source–sink dynamics in rivers. Although Pringle's focus was on perturbations downstream that have upstream impacts (e.g., dams, urbanization, water withdrawals), lakes on stream networks may have similar upstream consequences.

Challenges collaborations and questions

There are many unanswered questions about stream–lake networks that are fundamental to our understanding of fluvial ecology and our ability to design studies, interpret data, and manage natural resources. For example, what is the spatial and temporal variability of the lake effect and how far downstream is a significant lake effect observed? How does this vary with landscape position? Strong gradients in the physical, chemical, and biological characteristics of outlet streams have large implications for the design of ecological studies and impact assessments. Can lakes in a network "reset" the effects of natural and human disturbances? How do lake residence times, position, morphology, and size relative to stream discharge influence the characteristics of the outlet hydrograph? How important are lake outlet streams for providing migratory pathways and critical habitat (e.g., spawning, overwintering, and rearing) for fishes? And lastly, can the inhabitants of stream–lake networks show metapopulation dynamics?

Fruitful collaborations to resolve these questions will undoubtedly come from the combined efforts of limnologists, stream ecologists, and landscape ecologists. Geographic information systems will play an important role in summarizing landscape characteristics. Lake effects need to be more explicitly incorporated into ecological concepts in stream ecology, and limnologists would likely benefit by incorporating streams into their thinking. This comprehensive approach would help unify the study of aquatic ecosystems needed for the successful management and conservation of our aquatic resources.

Acknowledgements

The author thanks Peter McCart for discussions leading up to this paper. Geoff Poole provided many helpful ideas and edits. Two anonymous reviewers offered helpful advice.

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