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SPECIAL REVIEW

Hydrological connectivity for riverine fish: measurement challenges and research opportunities

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SUMMARY

1. In this review, we first summarize how hydrologic connectivity has been studied for riverine fish capable of moving long distances, and then identify research opportunities that have clear conservation significance. Migratory species, such as anadromous salmonids, are good model organisms for understanding ecological connectivity in rivers because the spatial scale over which movements occur among freshwater habitats is large enough to be easily observed with available techniques; they are often economically or culturally valuable with habitats that can be easily fragmented by human activities; and they integrate landscape conditions from multiple surrounding catchment(s) with in-river conditions. Studies have focussed on three themes: (i) relatively stable connections (connections controlled by processes that act over broad spatio-temporal scales >1000 km² and >100 years); (ii) dynamic connections (connections controlled by processes acting over fine to moderate spatio-temporal scales ~1–1000 km² and <1–100 years); and (iii) anthropogenic influences on hydrologic connectivity, including actions that disrupt or enhance natural connections experienced by fish.

2. We outline eight challenges to understanding the role of connectivity in riverine fish ecology, organized under three foci: (i) addressing the constraints of river structure; (ii) embracing temporal complexity in hydrologic connectivity; and (iii) managing connectivity for riverine fishes. Challenges include the spatial structure of stream networks, the force and direction of flow, scale-dependence of connectivity, shifting boundaries, complexity of behaviour and life histories and quantifying anthropogenic influence on connectivity and aligning management goals. As we discuss each challenge, we summarize relevant approaches in the literature and provide additional suggestions for improving research and management of connectivity for riverine fishes.

3. Specifically, we suggest that rapid advances are possible in the following arenas: (i) incorporating network structure and river discharge into analyses; (ii) increasing explicit consideration of temporal complexity and fish behaviour in the scope of analyses; and (iii) parsing degrees of human and natural influences on connectivity and defining acceptable alterations. Multiscale analyses are most likely to identify dominant patterns of connections and disconnections, and the appropriate scale at which to focus conservation activities.

Keywords: migratory fish, movement barriers, river network, spatial structure

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Connectivity plays a major role in riverine landscapes, although this phenomenon has not been afforded the attention it deserves. Detailed analysis of connectivity in diverse river systems should provide considerable insight into structural and functional attributes of riverine landscapes, including a greater understanding of the factors structuring biodiversity patterns.

- Ward *et al.* (2002)

Introduction

The concept of connectivity underlies many core questions in ecology because it defines linkages among ecosystem elements in space and time. Ecological studies routinely seek to understand how ecosystems elements are connected and what factors influence those connections (e.g. fire and fluxes of water or sediment). Conservation efforts are often interested in reconnecting habitats to influence the viability of target species (Crooks & Sanjayan, 2006; Pringle, 2006). As awareness of ecological connectivity has grown, the concept has become more prevalent in the ecological literature, including in aquatic ecology (Fig. 1) where it is particularly relevant for rivers (Wiens, 2002).

Although ecological connectivity has been widely studied in riverine systems (Gardner, 1989, 1997; Naiman, DeCamps & Pollock, 1993; Pringle, 2001, 2003; Amoroso & Bornette, 2002), these are difficult systems to explore the concept, given the high spatial and temporal complexity. Organisms and their habitats in rivers are potentially connected in three spatial dimensions - along longitudinal, lateral and vertical pathways (Ward, 1989, 1997). Water flow is a dominant driver of connectivity among these riverine pathways (Wiens, 2002) and, as such, 'water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle' was highlighted and defined as hydrologic connectivity (Pringle, 2001). Geomorphic processes and channel characteristics often vary with spatial position in a river network. For many rivers, these features are broadly predictable from headwaters to the river mouth (Fig. 2), but are disrupted by topographically controlled discontinuities (Stanford & Ward, 2001; Miller, Burnett & Benda, 2008; Rice, Roy & Rhoads, 2008a). Confluences juxtapose channels of potentially different flow regime and provenance, with associated changes in bed texture,

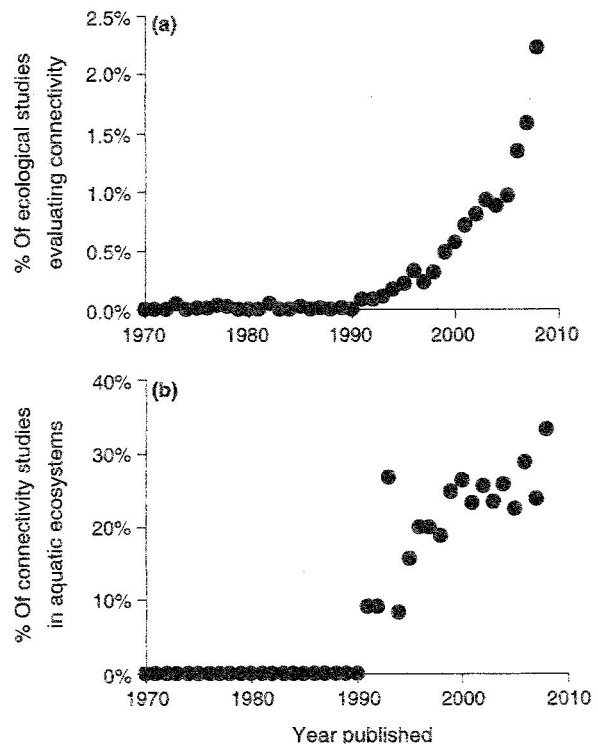


Fig. 1 (a) Percentage of all publications in ecology-oriented journals ($n = 35$; see Appendix S1 for a list of titles) that investigated connectivity. The y-axis is the count of studies in each year where 'connectivity' was in the title, abstract or keywords, standardized by the total number of studies published in that year. (b) Percentage of all studies that investigated connectivity (from above) that involved aquatic systems (the terms 'aquatic', 'freshwater', 'river', 'stream', 'lake', 'reservoir' or 'pond' appeared in the title, abstract or keywords).

channel morphology and water chemistry. Accordingly, the arrangement of confluences can affect the availability and spacing of certain habitat types (Benda *et al.*, 2004a,b; Rice, Greenwood & Joyce, 2001; Rice *et al.*, 2008b). Physical connections are repeatedly formed and broken in rivers, and thus ecological connectivity can fluctuate frequently in time and space to influence the distribution of the biota throughout a river network.

Knowledge about how riverine habitats are connected spatially and temporally is key to answering questions among several levels of biological organization (genes, individuals, populations, communities and ecosystems) and is therefore applicable to sustainable land management and effective species conservation (Primack, 1993; Crooks & Sanjayan, 2006; Kondolf *et al.*, 2006). Both classic theory (e.g.

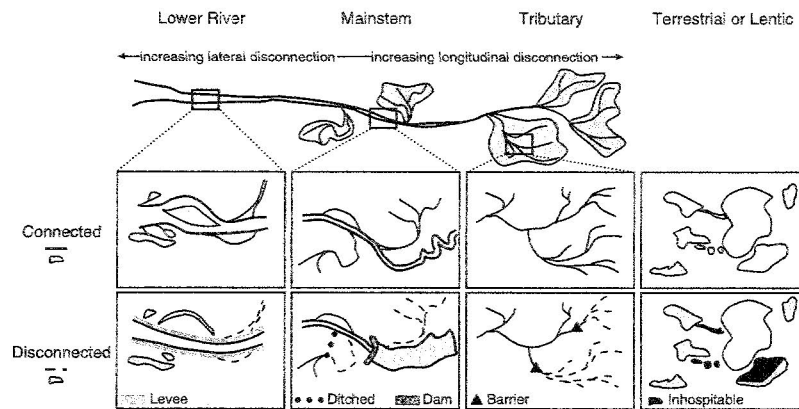


Fig. 2 Schematic illustrating connections and disconnections along a typical North American river. Connections present naturally (top panels), and potential disconnections caused by anthropogenic actions (bottom panels) exhibit distinct spatial patterns depending on network position. Owing to channel width and gradient, disconnections among habitats in tributaries are often longitudinal; whereas disconnections among habitats in lower rivers are often lateral (between main channel and off-channel habitats). Terrestrial examples are provided for contextual comparison.

the River Continuum Concept, Vannote *et al.*, 1980; Minshall *et al.*, 1985; the hierarchical classification of streams, Frissell *et al.*, 1986; Pickett *et al.*, 1989) and alternative hypotheses about river evolution and structure (e.g. the River Discontinuum, Poole, 2002; the Network Dynamic Hypothesis, Benda *et al.*, 2004a; the Riverine Ecosystem Synthesis, Thorp, Thoms & Delong, 2006) provide foundations on which to build new insights about how physical structures and dynamics of connectivity might influence ecological processes in rivers. In this review, we take a first step toward synthesizing the state of knowledge regarding ecological connectivity as experienced by organisms in rivers. Because of the breadth of the topic, we focus on riverine fishes and, in particular, on species that can move a long way. Migratory species, such as anadromous salmonids, are good model organisms for understanding ecological connectivity in rivers because (i) the spatial scale over which movements occur among freshwater habitats is large enough to be easily observed with available techniques; (ii) they are often economically or culturally valuable with habitats that can be easily fragmented by human activities; and (iii) they integrate landscape conditions from multiple surrounding catchment(s) with in-river conditions. Based on our review, we propose eight challenges to analysing and understanding ecological connectivity for migratory riverine fish, and identify potential approaches for advancing knowledge in this arena.

A synthesis of the literature

Our review of the literature revealed three dominant themes (Table 1): the influence on riverine fish of (i) connections that are relatively stable over broad spatio-temporal horizons; (ii) connections that are broken and reestablished in localized areas; and (iii) anthropogenic alterations to natural connections.

Relatively stable connections

This theme encompasses studies that evaluated connections experienced by riverine fish over broad areas (one or more large river basins) and long time frames (centuries to millennia) (Currens *et al.*, 1991; Reeves *et al.*, 1995; Table 1). These relatively stable connections in rivers are controlled by natural physical processes that are slow over many generations of the focal organism or are punctuated disturbances of relatively low frequency and high magnitude (e.g. glaciations, volcanic eruptions; Waples, Pess & Beechie, 2008).

The most common studies have evaluated the influences of relatively stable connections on diversity of assemblages. Presumably such patterns are driven by biotic processes, such as dispersal, adaptation and speciation, that are influenced by relatively stable connections among habitats. Many studies found that species richness was directly related to relatively stable connections. For instance, Matthews & Robison (1998) showed that similarities in composition of fish faunas among upland catchments of the Mississippi

Table 1 General themes in the literature relating to hydrological connectivity experienced by riverine organisms (primarily fish)

Theme/scope	Research questions	Analytical tools	Ecological process	Temporal extent	Spatial extent	Selected references
Relatively stable connections Connections over broad spatial extents that are controlled by long-term ecosystem processes	How does connectivity influence species, community, or population diversity and spatial structure?	Genetics, morphology, or abundance of organisms from different locations throughout distribution; models	Adaptation and dispersal	Evolutionary time scales	Basin or coarser	Matthews & Robison (1998), Honnay <i>et al.</i> (2001), Grenouillet <i>et al.</i> (2004), Wong <i>et al.</i> (2004), Finn & Poff (2005), Cook <i>et al.</i> (2007), Vale'rio <i>et al.</i> (2007), Lubinski <i>et al.</i> (2008) and McClure <i>et al.</i> (2008)
Dynamic connections Connections over fine temporal extents and localized spatial extents that are transient, as influenced by temporally shifting resources	What role does connectivity play in meta-population dynamics and population persistence? How do temporally fluctuating habitat conditions structure populations?	Genetics, morphology, or abundance of organisms from different locations throughout distribution; models Observations in the field (sampling in different habitats, radiotelemetry, or mark-recapture)	Dispersal, migration Small-scale movement and passive drift	Seasons to decades Seasons to decades	Multi-basin to sub-catchment Catchment or smaller	Le Boulenger <i>et al.</i> (1996), Dunham & Rieman (1999), Keymer <i>et al.</i> (2000), Fagan <i>et al.</i> (2005), Hänfling & Weetman (2006), Schick & Lindley (2007), Schtickzelle & Quinn (2007), Muneepeerakul <i>et al.</i> (2007) and Olden <i>et al.</i> (2008a,b) Eby <i>et al.</i> (2003), Fritz & Dodds (2005), Franssen <i>et al.</i> (2006), Gosset <i>et al.</i> (2006), Gortazar <i>et al.</i> (2007) and Tetzlaff <i>et al.</i> (2007)
Anthropogenic alterations to connectivity Disrupted connectivity: severed by habitat fragmentation (often via barriers such as dams)	How do migration or dispersal barriers disrupt population processes?	Genetics, morphology, or abundance of organisms from different locations throughout distribution; models	Dispersal and migration; divergence among isolated populations since fragmentation occurred	Decades to centuries	All scales	Charles <i>et al.</i> (2000), Morita & Yamamoto (2002), Herbert & Gelwick (2003), Cumming (2004), Wofford <i>et al.</i> (2005), Beechie <i>et al.</i> (2006), Gosset <i>et al.</i> (2006), Gresswell <i>et al.</i> (2006), Jager (2006), Lowe <i>et al.</i> (2006a,b), Merritt & Wohl (2006), Sheer & Steel (2006), Fukushima <i>et al.</i> (2007) and Zitek <i>et al.</i> (2008)
Enhanced connectivity: increased connections caused by humans	How do increases in connectivity influence pathways for the spread of nonindigenous species or pathogens?	Field observations, experiments, and genetics	Dispersal, inter-species interactions	Typically annual to decadal	All scales	Adams <i>et al.</i> (2001), Peacock & Kirchoff (2004), Puth & Allen (2004), Campos <i>et al.</i> (2006), Falke & Gido (2006), Benjamin <i>et al.</i> (2007), Bertuzzo <i>et al.</i> (2007), Fukushima <i>et al.</i> (2007), Rahel (2007) and Spens <i>et al.</i> (2007)

(b)

River, U.S.A. were predictable from the hierarchical pattern of drainage connectivity; faunal richness increased with stream size. Hitt & Angermeier (2008a,b) found that species richness in stream fish assemblages in the mid-Atlantic Highlands, U.S.A., depended on network structure. For streams of similar size and local environmental conditions, they found greater species richness in streams that were in close proximity to mainstems compared to headwater streams lacking connections. Thus, the shorter the distance to other fish-bearing streams (i.e. higher connectivity), the more species were likely to be present. These studies illustrate that the present-day spatial organization of biota can be strongly related to semi-permanent features of the landscape that were formed by geological and climatic controls.

Some studies have also suggested that the present-day distribution of species may be related to past connections. For example, Poissant, Knight & Ferguson (2005) found that genetic relationships among 12 brook trout (*Salvelinus fontinalis* Mitchell, 1814) populations better reflected historical hydrologic structure and landscape features than present conditions. Pusey & Kennard (1996) suggested that drainage capture might be responsible for the structure of fish assemblages in eastern Australia. Diversity of Australian land crayfish (*Engaeus sericatus* Clark 1936; Schultz *et al.*, 2008) and freshwater mussels (*Velesunio* spp.; Hughes *et al.*, 2004) was related to both present and past drainage patterns.

Dynamic connections

This theme comprises studies that have evaluated connections experienced by riverine fish over finer spatio-temporal scales (microhabitats to catchments, and seasons to several decades) (Currens *et al.*, 1991; Reeves *et al.*, 1995; Table 1). Short-term changes in geomorphic and hydrological conditions can alter connectivity among surface water habitats, as physical habitat connections are created and broken by processes that are more frequent and localized than those that drive relatively stable connections. Such processes include evolution of structures created by ecological engineers, such as ponds by beaver (*Castor canadensis* Kuhl 1820); and fluctuations in sediment depths because of landslides or in water level because of floods and droughts.

Fish can be structured as metapopulations (Cooper & Mangel, 1999; Dunham & Rieman, 1999; Schtick-

zelle & Quinn, 2007), possessing traits that enable them to exploit resources that vary in space and time. True metapopulations depend more on connectivity than do panmictic or patchy populations (Levins, 1969; Schlosser & Angermeier, 1995). For metapopulations, reductions in connectivity among individual populations may reduce fitness and weaken the ability to resist catastrophic change. Stochastic sequences of fires and storms (climatic drivers) can create abrupt changes in sediment and water flowing into streams, leading to a shifting mosaic of disturbed and recovering stream channels. This disturbance mosaic was demonstrated for the intermountain western USA, (Reeves *et al.*, 1995; Benda *et al.*, 2004a) and can define the spatial pattern of potential habitat offered at different points in time (Bigelow *et al.*, 2007). Disturbances can severely deplete, even extirpate, local fish populations; however, if connectivity to neighbouring populations is maintained; then, affected streams can recover within several years (Rieman *et al.*, 1997; Howell, 2006).

Short-term fluctuations in hydrographs can also drive changes in spatial connections. Magalhaes *et al.* (2007) found that fish assemblages in Mediterranean streams recovered quickly from short-term fluctuations in water level but warned that exacerbated disruptions in longitudinal connectivity caused by low water could negatively influence sensitive species. Ephemeral connections enabling local fish movement among habitat units provide a wider variety of habitats for feeding, sheltering and reproducing. For example, Ebersole *et al.* (2006) found improved winter growth and survival of juvenile coho salmon (*Oncorhynchus kisutch* Walbaum, 1792) in coastal Oregon (U.S.A.) streams that used intermittent tributaries (dry in summer, flowing in winter). However, Bunn *et al.* (2006) suggested that, although a certain degree of surface water connectivity was necessary to enable movement among ephemeral waterholes in Australian dryland rivers, the flow pulses associated with high connectivity can stress fish by reducing their food resources. Thus, connectivity among diverse seasonal habitats can enhance growth and survival during unfavourable conditions, but there may be trade-offs at different levels of connectivity - 'higher growth at low connectivity but higher dispersal capability at higher connectivity.

Biological controls, including rood web connections (Polis, Anderson & Holt, 1997; Power & Dietrich, 2002;

Power, 2006), can spatially structure populations. Temporally dynamic population abundances of predators, competitors and prey directly influence spatial structure of riverine biota. For example, Fraser *et al.* (2006) found that the presence of two predatory fish in Trinidadian streams influenced the spatial distribution of habitats used by the killifish *Rivulus hartii* (Boulenger, 1890). Kawaguchi, Taniguchi & Nakano (2003) found spatial distributions of stream salmonids in Japan to depend on prey sources. When they experimentally excluded terrestrial insects, fish shifted to a diet of aquatic invertebrates and used different habitats. Feyrer, Sommer & Hobbs (2007) suggested that habitat availability, as mediated by flow, controlled food sources for splittails *Pogonichthys macrolepidoius* (Ayres 1854) in a California (U.S.A.) coastal catchment. They postulated that fish growth was therefore limited by physical connections among habitats. Spatial connections can also change rapidly because of biologically driven modifications in geomorphological conditions. For example, Schlosser & Kallemeyn (2000) observed changes in fish assemblages with abandonment of beaver dams and the collapse of associated impoundments. These examples show that physical connections among habitats can be modified by biological interactions and that explicitly considering both may facilitate understanding of dynamic connectivity.

Anthropogenic influences on connectivity

Many anthropogenic activities alter connectivity for fish in fluvial systems (Fig. 2). In our review, we found articles addressing two opposing aspects of anthropogenic influences: (i) disruptions or interruptions to natural connectivity; and (ii) enhancements to natural connectivity.

Studies focussing on disrupted connectivity often addressed effects of habitat fragmentation on fish populations. Many dealt with barriers to movement, such as dams, and how dispersal barriers can disrupt population processes (Fukushima *et al.*, 2007). Although similar in concept to habitat fragmentation in other ecosystems, disconnections in rivers are particularly damaging because the structure of stream networks restricts movement pathways, making it more difficult to avoid barriers (Fagan, 2002; Fagan *et al.*, 2002). A single barrier can obstruct a large proportion of available habitat because alternative

dispersal routes are absent. Cote *et al.* (2009) found that barriers placed lower in a river network most affected diadromous fishes, whereas barriers located further upstream affected potadromous fish. Beechie *et al.* (2006) suggested that migration barriers have reduced the intraspecific diversity of Chinook salmon (*Oncorhynchus tshawytscha* Walbaum 1792) in Puget Sound catchments in WA U.S.A. by blocking breeding ground access for predominantly one life-history type. Sheer & Steel (2006) showed that dams and road culverts prevent access to high quality habitat by populations of steelhead (*Oncorhynchus mykiss* Walbaum 1792) and Chinook salmon in catchments of the Willamette River basin in OR, U.S.A. Moreover, their modelling attributed the reduced viability of Chinook salmon populations to the presence of migration barriers. Schick & Lindley (2007) found that the viability of Chinook salmon in coastal basins of CA, U.S.A. was compromised by drastic reductions in connectivity among populations. As some populations were lost through the construction of hydro-power dams, others remaining became more independent, with less movement of individuals between them.

In addition to direct impacts on connectivity caused by physical barriers, hydromodification can also disrupt connectivity by dewatering habitats or altering thermal regimes. Cumming (2004) found fish community diversity to be significantly affected by downstream dams in WI, U.S.A., but decreases in connectivity resulting from dams had less impact than did altered flow and thermal regimes. Disruptions to connectivity may interact; for example, a culvert may be passable during high flows but not when water withdrawal demand is high. Human actions can also reduce lateral connections with floodplains (Amoros & Barnette, 2002) because of active ditching, water withdrawals that lower the water table and cause channel incision, diking (creation of levees along river banks) and eradication of biological engineers such as beaver that create and maintain impoundments (Butler & Malanson, 2005).

Articles that focussed on enhancements to connectivity caused by anthropogenic actions such as canalization, removal of natural barriers and interbasin transfers, primarily examined how such actions could have unintended consequences for the spread of non-indigenous species (Rahel, 2007; Olden, Kennard & Pusey, 2008a; Fausch *et al.*, 2009) and pathogens

(Pringle, 2006) into native ecosystems. The Saint Lawrence Seaway, which connected the Laurentian Great Lakes (North America) to the Atlantic Ocean, is a well-known example of canalization with devastating consequences to the native ecosystem. Construction of the fish ladder at Willamette Falls, OR, U.S.A. in the early 1900s (Myers *et al.*, 2006) increased the number of anadromous fish passing upstream of the falls and illustrates how removing a natural barrier can facilitate range expansion of a native species. Sometimes, increased connectivity is a targeted conservation action, as when anthropogenic barriers are removed to facilitate species recolonization (Pess, Morley & Roni, 2005; Kiffney *et al.*, 2008). Adams, Frissell & Rieman (2001), Dunham *et al.* (2002) and Benjamin, Dunham & Dare (2007), in evaluating the role of connectivity in the spread of non-indigenous brook trout in the western U.S.A and potential impacts on native fishes, found that increased connections to source populations of non-natives could increase the rate of invasion. Spens, Englund & Lundqvist (2007) modelled the likelihood that a non-indigenous predatory fish would colonize new habitats based on channel gradient and spatial proximities of the lakes into which the fish were stocked. Fukushima *et al.* (2007) found that fish assemblages in Hokkaido, Japan were influenced by dams, but not always negatively. For three of 41 taxa examined, downstream dams increased the probability of occurrence because these species are put into reservoirs. Furthermore, biological interactions with non-indigenous species (predation and/or competition; Harvey & Kareiva, 2005; Sanderson, Barnas & Rub, 2009) can alter connections perceived by native fishes and can have evolutionary consequences (Mooney & Cleland, 2001). These studies illustrate the ecological significance for fish of increased, as opposed to reduced, connectivity in aquatic systems.

Confronting challenges to evaluating connectivity for riverine fishes

Based on our literature review, we identified three research foci and associated challenges to advancing understanding of hydrologic connectivity for wide-ranging riverine fish. Although these topics have been studied in other contexts, we highlight their specific significance to understanding connectivity for fish in rivers. Building on some published approaches for dealing with these challenges, we identify opportuni-

ties for advancing existing analytical approaches and developing new techniques.

Addressing the constraints of river structure

Riverine ecosystems are hierarchically structured by the physical template of nested catchments that contain an interrelated network of streams (Rodriguez-Iturbe & Rinaldo, 1997). Stream networks consist of functional habitats that are hierarchically nested across scales, ranging from stream segments (10^2 m) down to microhabitats (10^{-1} m) (Frissell *et al.*, 1986). This physically imposed hierarchical structure distinguishes streams from most other terrestrial and aquatic ecosystems. Physical factors that control connectivity in river networks may occur over a variety of scales (Table 1). Learning how these controls operate within and across scales is essential to evaluating connectivity for riverine fish. Although the importance of multiscale analysis is not unique to rivers, a key research frontier is to describe and understand how the hierarchical physical structure of rivers influences responses by fish to hydrologic connections over several spatio-temporal horizons.

Challenge 1: network topology. Fish living in river networks may be especially susceptible to decreases in connectivity because few possible pathways exist for dispersal and recolonization (Fagan, 2002; Campbell Grant, Lowe & Fagan, 2007; Muneeppeerakul *et al.*, 2007). In contrast to organisms living in terrestrial or marine systems, fish in a river cannot disperse in all directions from a point; movement is typically limited to upstream or downstream and possibly into a tributary if the point happens to be at a confluence. Networks come in many shapes (e.g. trellis, pinnate, rectangular) (Benda *et al.*, 2004a; Labonne *et al.*, 2008). The physical structure of classic bifurcating dendritic (branching architecture) networks, however, dictates that connections (and associated disconnections) typically shift from predominantly longitudinal (upstream versus downstream) in headwaters to increasingly lateral (mainstem versus floodplain habitats) and vertical (surficial versus hyporheic) in lower rivers (Fig. 2). The structure of stream networks is more complex, and therefore more difficult to analyse, than two-dimensional or linear frameworks (Fagan, 2002; Flitcroft, 2007; Campbell Grant *et al.*, 2007). Therefore, classic terrestrial connectivity metrics often

cannot be directly applied to fish in stream networks because the analytical assumptions of two-dimensional space are invalid (Ver Hoef, Peterson & Theobald, 2006).

Opportunities are dear for directly incorporating the unique aspects of stream networks into analytical tools. Two adaptations of existing spatial statistics and landscape connectivity metrics are key for applying these in river networks (many example applications are listed in Table 2). The first requires addressing the difference between Euclidean (straight-line) distance used in classic metrics and distance as experienced by organisms in a watered stream channel that incorporates sinuosity. Isaak *et al.* (2007) adapted a class of metrics that accounts for focal patch size and distances to all potential source populations (derived from the Incidence Function Model; Hanski, 1994) to quantify connectivity in a study of habitat use by spawning Chinook salmon in ID, U.S.A. They substituted stream distance for Euclidean distance and a measure of population abundance (count of redds) for habitat area. Urban *et al.* (2006) transformed stream distances into Euclidean distances to meet statistical assumptions for a multivariate redundancy analysis in evaluating the effect of network structure on stream

invertebrate community composition along a gradient of urbanization.

The second adaptation is explicitly to incorporate network structure in connectivity measures and analyses. Connectivity metrics for planar space may be modified or new metrics developed for rivers. For example, Cote *et al.* (2009) developed a new distance-based metric for stream networks (the 'dendritic connectivity index'). This metric describes longitudinal connectivity for diadromous or potadromous fish moving throughout a river network. In essence, it is the proportion of stream length accessible to fish, given assigned permeabilities of barriers. Leibowitz & White (2009) used randomly generated stream networks for modelling salmon population dynamics, an approach that explicitly addressed the potential importance of the complex structure of networks on population performance. Torgersen, Cresswell & Bateman (2004), Canio, Torgersen & Cresswell (2005) and Cressie *et al.* (2006) all explicitly incorporated network structure into their measures of population spatial structure in rivers. With increased computing power, it is increasingly feasible to evaluate the influence of complex spatial structures (such as dendritic or fractal networks) on

Table 2 Approaches used to quantitatively evaluate connectivity in freshwater ecosystems (classes after Fagan & Calabrese, 2006). Studies that expressly incorporated stream network structure are marked with an asterisk (*)

Approach	Class	Selected references
Distance-based metrics	Structural	Dunham & Rieman (1999) and Puth & Allen (2004)
Patch-to-patch stream distance		Honnay <i>et al.</i> (2001)*
No. of links upstream/downstream		Hitt & Angermeier (2008b)*
Stream volume (length/drainage area)	Potential	
Adapted Incidence Function Model measures (<i>sensu</i> Hanski 1994)		Isaak <i>et al.</i> (2007)
Spatial statistics	Structural /potential	Dunham & Rieman (1999), Demars & Harper (2005)*, and Urban <i>et al.</i> (2006)
Multivariate, correlative models		Cote <i>et al.</i> (2009)*
Dendritic connectivity index		Torgersen <i>et al.</i> (2004, 2006)*, Canio <i>et al.</i> (2005)*, Cressie <i>et al.</i> (2006)*, and Flitcroft (2007)*
Semivariograms and wavelet analysis		Ver Hoef <i>et al.</i> (2006)* and Peterson <i>et al.</i> (2007)*
Moving-average spatial covariance model incorporating stream distance and flow		Le Pichon <i>et al.</i> (2006)
Models incorporating behavioural elements	Potential	Kocik & Ferreri (1998), Charles <i>et al.</i> (2000)*, Jager (2006), Labonne & Gaudin (2006), and Leibowitz & White (2009)*
Least-cost movement		Bertuzzo <i>et al.</i> (2007)* and Spens <i>et al.</i> (2007)*
Population viability		Johnson <i>et al.</i> (1995)*
Nonindigenous species invasion	Potential	Schick & Lindley (2007)
Diffusion processes (passive behaviour)		McGlashan <i>et al.</i> (2001), Olsen <i>et al.</i> (2004), Poissant <i>et al.</i> (2005), Wofford <i>et al.</i> (2005), Lowe <i>et al.</i> (2006), Neville, <i>et al.</i> (2006b), Cook <i>et al.</i> (2007) and Hughes (2007)
Graph-theoretic	Potential	
Molecular genetic analysis	Potential	Horan <i>et al.</i> (2000), Johnston (2000), Schrank & Rahel (2004) and Homel & Budy (2008)
Movement studies (observational)	Actual	

connectivity (Convertino *et al.*, 2007). For instance, Labonne *et al.* (2008) evaluated the ramifications of river network connectivity, or 'branchiness', on metapopulation demographics using an individual-based modelling approach. They found higher levels of connectivity increased local isolation and decreased time to extinction at low dispersal rates and reduced metapopulation size at high dispersal rates. Both findings are contrary to expectations under classic metapopulation theory, and generated ideas for productive research directions (Labonne *et al.*, 2008). Riverine fishes must contend with the challenge of network structure; thus, advances in our understanding of connectivity will need to consider network structure directly.

The ecology of organisms other than fish should also benefit from approaches that explicitly consider the nature of network connections within streams. Although organisms such as aquatic insects (Macneale, Peckarsky & Likens, 2005; Downes & Reich, 2008), salamanders (Lowe *et al.*, 2006a), muskrats (Le Boulenger *et al.*, 1996), some crayfish (Schultz *et al.*, 2008) and beaver (Collen & Gibson, 2000) are not restricted to aquatic environments, their populations are influenced by the spatial structure of stream networks. The spatial structure of networks may also be an appropriate template for the study of riparian flora (Muneepeerakul *et al.*, 2007) or other animals, such as birds or bats, that seek or avoid riparian corridors for travel. Species living in lakes, wetlands and ponds may also show spatial structure related to stream networks, as they are all part of the same hydrologic cycle. For instance, several comparative studies suggest that physical, chemical and biological characteristics of lakes depend on landscape position relative to one another in the drainage network (Kratz *et al.*, 1997; Soranno *et al.*, 1999; Martin & Soranno, 2006).

Challenge 2: unidirectional flow of water. River ecosystems are controlled by the unidirectional downstream flow of water. Ecosystem processes such as the transport of sediment or nutrients, and organisms or life stages with little to no volitional mobility, can be strongly affected by the force and direction of flow (Hart & Finelli, 1999; Olden, 2007). Despite a lack of spatial overlap, ecosystems downstream can be affected by processes occurring upstream. Physical and chemical characteristics of headwater basins can dictate conditions observed at lower altitudes (Frissell

et al., 1986; Kiffney *et al.*, 2006; Rice *et al.*, 2001); organisms that never travel to headwater streams may be directly affected by processes occurring there (MacDonald & Coe, 2007; Nadeau & Rains, 2007). In addition, the food available to fish in pools can be provided by energy produced in upstream riffles (Rosenfeld & Boss, 2001). The force of flow can directly influence mobility of fishes under certain conditions (e.g. scouring flows). Thus, the force and flow of water is a strong control on hydrologic connectivity for fish in lotic systems and requires new approaches for incorporating its effects into quantitative analysis.

Parametric statistical models assume that observations are independent, yet stream data may not meet this assumption. Sample points in streams are widely believed to be spatially autocorrelated because upstream points may influence downstream points via water flow (Underwood, 1994). However, Lloyd, Macblally & Lake (2005, 2006) found that spatial autocorrelation of benthic communities in relatively unaltered rivers in southeastern Australia was related to spatial scale (and absent or even more similar at larger scales) and unique to the river studied. For streams with demonstrated autocorrelation caused by flow, analytical techniques can include a term to account for this effect. Thus, many existing spatial statistics could be adapted for lotic environments (Fortin, Dale & Ver Hoef, 2002). Ver Hoef *et al.* (2006) outlined a conceptually strong approach for stream networks that incorporates the direction and force of flow and stream distance with a moving window technique. The authors demonstrated the approach to evaluate sulphur concentrations along a river network in MD, U.S.A. Peterson, Theobald & Ver Hoef (2007) built on this approach by outlining methods for generating spatial data in stream networks that meet geostatistical assumptions. Another avenue could be to use diffusion models to estimate dispersal as affected by water flow and physical connections (Johnson, Hatfield & Milne, 1995). For example, Bertuzzo *et al.*, 2007 added a flow-biased element to a reactive-diffusive transport model. Flitcroft (2007) suggested that statistics similar to time series analyses may develop where the flow of water substitutes for the flow of time. A point in the past (upstream) can influence a point in the future (downstream) but not *vice versa*. These analytical techniques would work well for understanding connectivity of non-mobile

organisms, or organisms with limited motility, but will need to be further developed to account for counter-current (upstream) movement of many stream fish. Ignoring the consequence of discharge in rivers could skew interpretations of connectivity for fish and therefore must be addressed directly.

Challenge 3: scale-dependence of connectivity. Crooks & Sanjayan (2006) argue that connectivity is an entirely scale and target dependent phenomenon - definitions, metrics, functionality, conservation applications, and measures of success depend on the taxa or processes of interest and the spatial and temporal scales at which they occur.' Yet connectivity for fish in riverine ecosystems has rarely been evaluated across spatio-temporal scales, or over a scale sufficient to capture important complexities (Fausch *et al.*, 2002). Most research in rivers occurs at either very fine or very broad spatio-temporal scales (both extent and resolution) because of limitations of existing analytical techniques (e.g. intensive field sampling at few locations or coarse datasets available for broad geospatial modelling). The conclusion of Fausch *et al.* (2002) about the importance of research at intermediate scales to understanding ecological phenomena in rivers is especially appropriate to connectivity. For example, when Fagan *et al.* (2005) evaluated extinction risk of desert fishes across spatial scales ranging from 5 to 2500 stream km, they found that risk was highest at intermediate scales (~100 km) of habitat fragmentation. Molecular genetic techniques have proved useful for evaluating the spatial structure of populations over intermediate timeframes (Winans *et al.*, 2004; Neville *et al.*, 2006a; Cook, Bunn & Hughes, 2007). Studies at intermediate spatio-temporal scales may offer context to the projected impacts of both natural and anthropogenic disturbances to connectivity for riverine fish (Waples *et al.*, 2008).

Although an intermediate spatio-temporal scale may be appropriate for many questions, Lowe *et al.* (2006a,b) suggested that empirical research that exploits the hierarchical nature of streams will improve understanding about ecological connections across spatial scales. Schlosser & Angermeier (1995) noted that the appropriate scale of inquiry should be strongly tied to the taxa of interest and may even differ among life stages (rearing, breeding). Thus, it seems reasonable that the spatial constraints of connectivity in river fish should also vary across life

stages. For example, juvenile rearing in salmon often occurs at a much smaller extent (10^1 to 10^2 m) than migration and breeding ($>10^2$ m). Similarly, studying spatial patterns of connectivity over short time frames (one season or year) may yield erroneous conclusions about the structure of populations or assemblages (Lind, Robson & Mitchell, 2006). Metapopulation theory captures this well: populations that are sources at one point in time may become sinks at another. Connectivity may be influenced by interacting spatial and temporal scales, as is the case when organisms feed in different habitats during different seasons.

It is impossible to quantify empirically connectivity at all spatio-temporal scales that might be important to population structure, but approaches are available for analysing empirical data to help identify the range of scales over which connectivity structures populations. Advances in spatial statistics, such as semivariograms applied to rivers (Sinsabaugh, Weiland & Linkins, 1991; Canio *et al.*, 2005), highlight ranges of spatial scales appropriate for studying connectivity. Wavelet analysis (Canio *et al.*, 2005) is an approach for identifying appropriate temporal scales at which to focus analysis. Wavelet analysis can uncover periodicity in spatial connections and can identify temporal scales at which dominant connectivity patterns emerge. Because a variety of ecological questions has been evaluated with these statistical tools, the infrastructure is in place for adaptation to analysing connectivity in rivers. However, analytical techniques may need to be improved to properly account for the uneven spacing of stream data. Hierarchical analysis can also be used to evaluate connectivity over a range of scales (Beechie, Moir & Pess, 2008; Flitcroft, 2007). For instance, Dunham & Rieman (1999) used logistic regression at nested spatial scales to evaluate the relationship between bull trout (*Salvelinus confluentus* Suckley, 1859) metapopulation structure and connectivity of habitat patches in a fragmented landscape. Le Pichon *et al.* (2006) employed least-cost modelling across a hierarchy of scales ranging from 10 s of metres to 100 s of kilometres (individual habitat units, extents used daily to forage and shelter, and subpopulation areas defined by dispersal capabilities) to study spatial structure of a cyprinid population in the River Seine, France. Regardless of the approach taken, we echo Ward, Malard & Tockner (2002a) in calling for the inclusion of a spatio-temporal component when planning connectivity studies in rivers, because

interpretation of connectivity is influenced by scale and probably differs among species.

Embracing temporal complexity in connectivity

River systems are particularly dynamic, often with ecosystem processes and associated habitats that rapidly shift in rates or composition and position through time (Reeves *et al.*, 1995; Beechie, Collins & Pess, 2001; Flitcroft, 2007). Temporal shifts in spatial connections can have huge implications for population viability. The rate at which habitats become disconnected may outpace the rate at which populations become unviable (Taylor, Fahrig & With, 2006). Organisms living in ephemeral habitats may be more sensitive to the rate of habitat change than to the total quantity or spatial arrangement of habitat (Keymer *et al.*, 2000). Further, a completely different picture may emerge when connectivity is compared between periods of low flow and periods of higher precipitation. For example, Lind *et al.* (2006) found that hierarchical spatial patterns in macroinvertebrate assemblages differed between seasons of adequate flow and seasons of drought and that this was only evident from sampling over several seasons. If sampling occurs (or models are run) only once, then understanding that is relevant to conservation will be limited, possibly to one life stage, overlooking connections among habitats needed for fish or other organisms to persist under different conditions. Given these considerations, developing new tools and approaches to better analyse and understand dynamic connectivity for fish in rivers is an important research frontier.

Challenge 4: shifting boundaries. Integral to connectivity is the concept of boundaries (edges or transitional zones) separating elements in space and time. The ability of an organism to move freely among habitats necessary to complete its life cycle implies that boundaries do not impede movement. Boundaries are not always discrete or permanent; rather most fall along a permeability gradient (Puth & Wilson, 2001; Wiens, 2002), where permeability may change over time. For example, natural influences on hydrographs (tidal cycle, floods, seasonal flows, ice-over) and anthropogenic influences (water withdrawals, reservoirs) can alter longitudinal, lateral and vertical boundaries for stream fish. Habitats that are con-

nected at one time may become disconnected at others. Lateral connections caused by animals moving into off-channel habitats can blur boundaries between aquatic and non-aquatic zones, especially in areas with extensive floodplains (Ward & Wiens, 2001). Aquatic biota and habitats may be affected by intrinsic and extrinsic processes that change as a function of distance from a stream channel, and which may be temporally dynamic. For example, the structure and boundaries of the hyporheic zone can vary tremendously over space and time, profoundly affecting the stream channel (Boulton *et al.*, 1998). Defining clear spatial boundaries for the hyporheic zone is challenging; quantifying its temporal influence over connections within a stream network is a far greater challenge.

River ecologists understand that physical boundaries shift temporally (Rice *et al.*, 2001; Benda *et al.*, 2004a). Many studies in rivers address the effect of patch boundaries on biota in some way, usually during one life stage (examples described in Wiens, 2002). Yet many existing connectivity metrics treat habitats as discrete patches (Table 2). While useful, these metrics may be less appropriate for studying connectivity in dynamic systems where boundaries shift rapidly. Better are metrics and approaches that incorporate the temporal variability of spatial patterns. For example, the metric devised by Cote *et al.* (2009) allows the user to define different levels of permeability to instream barriers. Another option might be to simulate many habitat configurations through time and model the response of fish (individuals, populations) to the different levels of connectivity. Because boundaries are integral to understanding dynamic connections for fish, we urge researchers to focus on clarifying the importance of shifting boundaries to movement among resource habitats.

Challenge 5: the behavioural component of connectivity. Most of the research evaluating connectivity for fish has been unable to untangle patterns and processes. To address this holistically, novel tools are needed that explicitly incorporate behaviours such as daily movement, migration and dispersal (Belisle, 2005) into measures of connectivity for riverine fish. Indeed, behaviour is one of the key components of connectivity (Taylor *et al.*, 2006). Consideration of this component can change interpretations of connectivity

at different times. Because of behavioural differences in the way that individuals relate to their environment, connectivity can even differ for the same species in the same landscape at different times (Kindlmann & Burel, 2008).

The most direct approach to understanding connectivity for wide-ranging fish is to empirically monitor behaviour. Fish movement and habitat use can be assessed directly by sampling animals in various habitats (electroshocking, seining or trapping; Horan *et al.*, 2000) or by observing movement visually (snorkeling; Johnston, 2000). Individual movements can be tracked using passive integrated transponder tags (Homel & Budy, 2008), radiotelemetry (Schrank & Rahel, 2004) or other methods (hydroacoustic surveys; Duncan & Kubecka, 1996). Although many studies have evaluated the behaviour of river organisms, few have done so with the express purpose of understanding behavioural influences on the spatial structure of populations. Such studies can shed light on mechanisms structuring populations and suggest new research directions. For example, Brenkman & Corbett (2005) found with radiotelemetry that bull trout migrate over several coastal catchments, instead of single ones as previously believed. The diversity of habitats experienced and behaviours exhibited by these fish could enhance population resilience to environmental disturbance, given the higher likelihood that some individuals will persist in the face of catastrophic change (McIlhenny *et al.*, 2000; Greene *et al.*, 2009).

Aside from dam-removal studies (Doyle *et al.*, 2005), experimentally manipulating connectivity is difficult over larger spatial and temporal scales. Thus, finer-scale empirical studies or modelling may be needed to understand large-scale behavioural influences on connectivity. Insight into large-scale processes can emerge from behavioural experiments, in the laboratory or field, that identify mechanisms operating at finer scales (Romero *et al.*, 2009). Conceivably, ecologists can then determine when it is advisable to extrapolate predictions over broader areas (Urban, 2005). Models and spatial connectivity indices can also include behavioural components (see Table 2). For example, a new connectivity metric, capable of evaluating several fish life histories (resident, anadromous and catadromous), incorporates movement probabilities (Cote *et al.*, 2009). Least-cost modelling (Le Pichon *et al.*, 2006; Wang *et al.*, 2008) directly addresses the costs of moving, such as energy

loss or mortality, by attributing a resistance or permeability value to each stream habitat. Leibowitz & White (2009) described a model of salmon population dynamics that predicts movement of both juvenile and adult fish. Metapopulation models could conceivably be adapted from those developed in terrestrial landscapes (e.g. Hanski, 1994; Schumaker, 2009) to evaluate population interactions for riverine fish. For example, one could constrain spatial extents inhabited by populations to individual subcatchments (or sets of subcatchments) within a stream network and restrict migration pathways to reaches connecting those populations. Then, classic metapopulation modelling constructs could help evaluate how changes in connectivity among populations would affect the metapopulation. Behaviour is an essential component of connectivity. Studies linking the existing wealth of experience in observing fish behaviour with connectivity theory should yield valuable insights about its role in structuring populations, and how its influence changes with time.

Challenge 6: complex life histories. The complex life histories of many species interact with spatio-temporal dynamics to impede our understanding of, and ability to manage, connectivity in riverine environments. Even for single species, connectivity requirements may differ among life stages. Anadromous fish such as salmon or lamprey occupy freshwater tributaries as juveniles, migrate into estuarine and nearshore areas as they mature, and spend the majority of their adulthood in the ocean before returning to freshwater to spawn. Other river fish have complex life histories, rearing, foraging or sheltering in different habitats than those where spawning occurs. Although non-aquatic organisms also experience ontogenetic shifts in habitat, the highly dynamic nature of rivers may exacerbate transitions between habitats, increasing the difficulty in understanding how connectivity affects population and metapopulation dynamics. Different life stages may require different habitat types and have different dispersal capabilities. Even within a single life stage, species may require a number of complementary resources in different habitats; food may be located in fast-flowing water, whereas shelter may be located in marginal habitat (Dunning, Danielson & Pulliam, 1992; Schlosser, 1995). Despite this knowledge, few studies have examined how connectivity between habitats used by different life stages or

differences in connectivity between particular life stages (connectivity may be high at one life stage but low at another) affects freshwater production (Kocik & Ferreri, 1998; Amoros & Bornette, 2002).

One approach to understanding how life stage complexities influence the temporal dynamics of spatial connections might be to add a connectivity component to life-cycle models. Spatial connections experienced by an organism could be quantified at each life stage. These metrics of connectivity within and among life stages could act as stage-dependent gatekeepers limiting the number of fish passing on to the next stage (i.e. bottlenecks). Furthermore, individual-based models (Grimm, 1999) could be developed to evaluate spatial structure for fish in a river, as has been performed in a terrestrial system (Tracey, 2006). Otolith microchemistry, stable isotope analyses (Kennedy *et al.*, 2002, Kennedy *et al.*, 2005) and molecular techniques (Winans *et al.*, 2004) are rapidly developing tools that show promise for identifying different habitats used by species at different times. Because riverine fishes exhibit complex life histories, explicit consideration should be given to how connectivity may change for a fish throughout its life cycle. These tools should help bridge that gap.

Managing connectivity for riverine fishes

Humans have often settled close to water (Paul & Meyer, 2001; Brown *et al.*, 2005; Grimm *et al.*, 2008). Pringle (2001) argued that hydrologic connectivity is often inadequately considered when planning human activities and strongly urged conservation planners and resource managers to address potential implications of connections among elements in the hydrogeologic cycle. An essential research frontier is thus to understand how human activities alter natural connections experienced by fish in riverine ecosystems, and what this means for managing these connections.

Challenge 7: quantifying impacts of humans on connectivity. Few aquatic studies have explicitly evaluated connectivity as influenced by both anthropogenic and natural factors; however, Bunn *et al.* (2006) illustrate how the two influences are intertwined. Human activities are often constrained by the same environmental controls (geology, topography, climate) as those operating on ecological phenomena and, there-

fore, their impacts can be difficult to isolate (Yates & Bailey, 2006; Steel *et al.*, 2010).

A good starting place for distinguishing human and natural influences is to compare existing connectivity patterns with patterns of connectivity in the absence of anthropogenic effects (either in a reference system or in the same system before human alteration). Graph (or network) theory (Urban & Keitt, 2001; Rozenfeld *et al.*, 2008) shows promise for evaluating this issue in rivers. Graph theory has been applied successfully to conservation dilemmas in terrestrial ecosystems (Pascual-Hortal & Saura, 2006; Bodin & Norberg, 2007) and is ripe for adaptation to river environments. The only such application we found evaluated riverine connectivity on past and present population structure of endangered Chinook salmon in CA, U.S.A. by constructing graphs and evaluating the stability of graphs to deletions in connections caused by hydropower dams that act as migration barriers (Schick & Lindley, 2007). By considering connectivity as a dependent, rather than as an independent, variable (Goodwin, 2003), this approach effectively evaluates the impact of habitat change on connectivity. This type of analysis can point to mechanisms by which habitat alterations affect fish, and whether amount is more or less important than spatial arrangement and connectivity. For example, Neville *et al.* (2006a) found that homing in endangered Chinook salmon females (the ability of adults to locate their natal habitats in which to spawn) is sensitive to small-scale fragmentation of stream habitat.

If humans are viewed as integral ecosystem components that contribute to forming and maintaining aquatic habitats (Otte, Simmering & Wolters, 2007; Wu & Hobbs, 2002), then much of natural disturbance theory should apply and existing tools can be adapted to include anthropogenic perturbations. Modelling change scenarios that directly incorporate anthropogenic processes (e.g. climate change, Battin *et al.*, 2007; urbanization, Urban *et al.*, 2006) may help envisage ways that future stressors could affect the spatial arrangement and amount of habitat available. Existing scenario planning in aquatic systems (Baker *et al.*, 2004; Rieman *et al.*, 2007; Fullerton *et al.*, 2009) could be improved by including measures of connectivity and expected effects of connectivity on fish population performance. Humans undoubtedly influence natural connections experienced by riverine fish; these influences should therefore be considered alongside

natural drivers of connectivity for these organisms and their habitats.

Challenge 8: differing management goals. Because management goals for riverine landscapes are complex and often conflict, analytical tools are needed to evaluate and plan for connections needed by fish and other biota. Such tools can help planners assess trade-offs and prioritize among competing management goals. For instance, impacts of conservation actions, such as maintenance of barrier-free corridors intended to benefit native species, could directly impede actions intended to control the spread of pathogens or non-indigenous species, and *vice versa* (Rahel, 2007). Given the potential for negative effects on native ecosystems by non-indigenous species, Fausch *et al.* (2009) and Lodge *et al.* (2006) suggested that increasing connectivity should be carefully considered when devising management and conservation decisions. Jackson & Pringle (2010) suggested that, in urban landscapes, reduced connectivity may be 'better' than increased connectivity, given the greater risk of negative impacts on biota resulting from increased access, for instance, to toxins. Another conflicting management goal involves environmental flows released from reservoirs. Flow releases are typically designed to optimize water available for human consumption, yet decisions about timing and volume of releases can influence connectivity experienced by river organisms (Lind, Robson & Mitchell, 2007).

Management decisions often affect many species, but connectivity studies typically focus on the spatial structure of single populations. The duration that connectivity must be maintained to fulfil life-history requirements differs among species, thus complicating any attempt to understand target levels of connectivity needed to manage whole aquatic systems. A fruitful area of research will be to develop metrics of connectivity that can address successfully many species simultaneously. An initial avenue might be to assess functional redundancy in ecosystem services provided by many species. If present, then evaluating connectivity for one species might yield insight about connectivity for other similar species. Modelling provides an excellent platform for evaluating the spatial relationships among many species living in the same environments (Greene & Pess, 2009). Vos *et al.* (2001) adapted structural connectivity metrics in terrestrial ecosystems to be 'ecologically

scaled' to the species of interest. This approach could be applied in rivers to standardize connectivity measures so that they are comparable across species.

Finally, it may be practical to identify situations in which it is important to consider connectivity. Abundant populations may be less susceptible to the influence of spatial dynamics (With & King, 1997), but connectivity could become important if the species are projected to become rare. Wiens (2006) suggested focussing on conserving habitat quantity if it is either abundant (conserve existing high quality habitat) or rare (conserve or rehabilitate additional habitat), but to focus instead on connectivity (spatial structure of habitats as opposed to habitat amount) if habitat is intermediate in availability. Because it has proved difficult to evaluate habitat size and connectivity independently (Fahrig, 2003; Koper, Schmiegelow & Merrill, 2007), theoretical models may suggest which of these conditions applies under existing population abundances. Recognizing those species that may be more or less susceptible to spatial processes could help simplify multiobjective management. For susceptible species that are the focus of conservation efforts, an important question becomes how to reconnect and maintain connections among important habitats without also introducing negative effects of increased connectivity, such as pathways for non-indigenous species, pathogens and contaminants. Molecular techniques can inform where to place restoration projects. For example, Hughes (2007) used molecular methods to evaluate connectivity for a variety of resident stream-dwelling organisms and suggested that species other than insects and lowland fishes could recolonize habitats only within the same stream. This information could prevent unnecessary expenditure of limited funds available for restoration. Because connectivity needs vary among fish species, it is essential to consider how conflicting management objectives will affect species targeted for conservation.

Concluding remarks

Research that incorporates connectivity among riverine habitats should continue to clarify understanding of how spatial processes structure fish communities in rivers. Our review of the literature highlights substantial progress toward understanding elements of the puzzle, yet significant gaps remain. Management applications in rivers may differ fundamentally

from those in terrestrial systems. Conservation in terrestrial ecosystems has focused on either active (management of matrix habitat) or passive (establishing reserve networks) approaches that strive to promote essential movement corridors. These applications derive from modernized island-biogeography theory explaining biodiversity, species and population persistence. It is less clear how applicable these approaches are in aquatic ecosystems. Riverine environments require an approach that incorporates the temporally dynamic nature of these ecosystems (*sensu* Ward, 1989). To accomplish this, interdisciplinary approaches will be necessary (Thompson *et al.*, 2001; Tetzlaff *et al.*, 2007; Cooke *et al.*, 2008) that borrow theory and techniques from diverse fields such as genetics, physiology, hydrology, telemetry, infrastructure planning, neural sciences and mathematical network theory. Studies of riverine connectivity that build on work in these disparate fields and across spatio-temporal scales will help us discern when and how connections influence biota and will be essential for developing effective riverine conservation plans and efficient management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix 51. Titles of ecology-oriented journals found in the Web of Science ($n = 35$) on 24 September 2009 that contained at least 25 studies published from 1965 to 2008 that investigated connectivity.

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