

A new measure of longitudinal connectivity for stream networks

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Received: 18 January 2008 / Accepted: 22 September 2008 / Published online: 4 October 2008
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Abstract Habitat connectivity is a central factor in shaping aquatic biological communities, but few tools exist to describe and quantify this attribute at a network scale in riverine systems. Here, we develop a new index to quantify longitudinal connectivity of river networks based on the expected probability of an organism being able to move freely between two random points of the network. We apply this index to two fish life histories and evaluate the effects of the number, passability, and placement of barriers on river network connectivity through the use of simulated dendritic ecological networks. We then extend the index to a real world dendritic river system in Newfoundland, Canada. Our results indicate that connectivity in river systems, as represented by our index, is most impacted by the first few barriers added to the system. This is in contrast to terrestrial systems, which are more resilient to low levels of connectivity. The results show a curvilinear relationship between barrier passability and structural connectivity. This

suggests that an incremental improvement in passability would result in a greater improvement to river network connectivity for more permeable barriers than for less permeable barriers. Our analysis of the index in simulated and real river networks also showed that barrier placement played an important role in connectivity. Not surprisingly, barriers located near the river mouth have the greatest impact on fish with diadromous life histories while those located near the center of the river network have the most impact on fish with potadromous life histories. The proposed index is conceptually simple and sufficiently flexible to deal with variations in river structure and biological communities. The index will enable researchers to account for connectivity in habitat studies and will also allow resource managers to characterize watersheds, assess cumulative impacts of multiple barriers and determine priorities for restoration.

Keywords Aquatic connectivity · Barriers · Connectivity indices · Dendritic ecological networks · Fish passage · Fragmentation · River networks · Watersheds

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Introduction

Decades of research have highlighted the critical importance of habitat connectivity in ecology and conservation within terrestrial ecosystems. However,

little of this work has been translated into aquatic systems, despite the fact that landscape and riverine ecology share many attributes and organizing principles (Benda et al. 2004), including the concept of connectivity (Wiens 2002). Alteration to this defining structural element has undoubtedly resulted in considerable short-term and long-term shifts in the aquatic community.

Terrestrial landscape connectivity is manifested in two dimensions, as animals in one patch can often cross a gap to another patch, usually following one of several alternate paths. Landscape ecologists are familiar with conceptualizing such patches and connections as a lattice network (Watts and Strogatz 1998), and have made use of graph theory to describe and analyze such networks (Urban and Keitt 2001). In contrast, movement between habitat patches in aquatic systems is longitudinal along the river channel (at least for obligate aquatic species such as fish) (Fagan 2002). In addition, the geometry of river and stream networks presents challenges to applying terrestrial landscape indices. Grant et al. (2007) characterize rivers and streams as dendritic ecological networks (DENs) and suggest that these are a unique subset of spatially structured networks that merit special attention. While graph theory has been usefully applied to DENs (Schick and Lindley 2007), Grant et al. (2007) maintain that statistical indices describing connectivity of lattice networks obscure unique ecological processes associated with DENs. These differences result in a state of knowledge of aquatic network connectivity that lags far behind that in terrestrial landscapes (Wiens 2002).

What is well-known is that humans are a significant source of alteration to aquatic habitat connectivity—one to which aquatic communities have had less time to adjust (Stanford et al. 1996). Human impacts typically decrease aquatic connectivity by creating barriers in river networks (e.g., dams) but may also increase aquatic connectivity by providing routes around natural barriers (e.g., navigation canals). Barriers, such as dams and culverts, alter current velocity, water depth and create vertical drops at outflows that change the hydrology and thermal regimes of aquatic systems (Berkamp et al. 2000) and impede the movement of aquatic species (Warren and Pardew 1998; Wheeler et al. 2005). These alterations are widespread and have had repercussions ranging from drastic alterations to the ecology of the

Great Lakes of North America (Mills et al. 1993), to species declines and extirpations in major rivers of Europe (Porcher and Travade 1992), Australia (Barry 1990; Mallen-Cooper and Harris 1990), Asia (Zhong and Power 1996; Morita and Yamamoto 2002), and North America (Quiros 1989; Baum 1994; Meyers 1994; Stolte 1994). Although a great deal of attention has been given to analyzing the effects of barriers, especially on fish (e.g., Jungwirth et al. 1998; Peter 1998; McLaughlin et al. 2006), surprisingly little attention has been given to the cumulative effect of barriers at the scale of river networks. Methods to measure effects of multiple barriers at the extent of the entire landscape are in their infancy; hence management and land use decisions are often made in the absence of adequate information on hydrological connectivity (Pringle 2003).

Recent work by Schick and Lindley (2007) provide an elegant example of an empirical method to characterize population connectivity at a larger scale for an aquatic dendritic system. There is a need, however, for a simple, general framework that can be easily applied in multiple contexts with limited biological information. In this paper we propose a new method, the Dendritic Connectivity Index (DCI), to quantify the longitudinal connectivity within river networks. We take the definition for habitat connectivity used in the terrestrial sense, where it is used to describe and measure the “spatial continuity of a habitat or cover type across a landscape” (Turner et al. 2001, p. 3) and explore how it can be explicitly applied to measure longitudinal river network connectivity. Here, longitudinal connectivity refers to connections between upstream and downstream sections of a river network, as opposed to vertical (benthic to pelagic) or lateral (bank to bank) connections (see Kondolf et al. 2006). Our intent is that this metric will provide an analogous means of quantifying aquatic habitat connectivity to the myriad of terrestrial landscape metrics, and will provide a useful indicator of aquatic ecosystem integrity. We explore this method to assess longitudinal connectivity from the perspective of diadromous (migrations between marine and freshwater) and potadromous (migrations within freshwater) fish life histories and to evaluate the effects of the number, passability and placement of barriers on simulated river networks. We then apply this approach to a real world dendritic system in Newfoundland, Canada.

Methods

Development of the Dendritic Connectivity Index (DCI)

Riverine ecosystems can be examined at a variety of spatial scales and here we adopt Poole's (2002) "river discontinuum concept," which recognizes stream connectivity as a hierarchical system within the scale of the network as a whole and views stream sections (patches) as elements of a river from headwaters to mouth. Here, we define stream sections as the sections of river channel created by the presence of a barrier (natural or anthropogenic). Barriers have an associated passability value, p , which depends on the physical (e.g., dam height), chemical and/or the hydrologic (flow rates, which vary temporally) attributes of the barrier as well as the biology of the organism in question (which can vary by species, age, etc.). Barriers are assumed to take no real space, and hence do not reduce the total river network length. We developed an index that measures the effect of barriers (e.g., culverts) on connectivity. We focused on fish movement in conceptualizing connectivity since fish play an important ecological role, are commercially important, and a great deal is known about the effects of waterway barriers on fish movement.

Theoretical framework

We assess connectivity in terms of coincidence probability (sensu Pascual-Hortal and Saura 2006), that is, the probability that fish can move between two randomly chosen points in a river network. Hence, connectivity depends on how many barriers are between the two points, and the passability of these barriers. Here, passability refers to the probability of fish being able to cross a barrier in both the upstream or downstream direction. An obvious distinction between riverine and terrestrial systems is the effect of the unidirectional water flow on movement. Concretely, this translates into barriers that are potentially more likely to impede upstream than downstream movement. This conceptual view of connectivity can be simplified by considering that pairs of sections in a river network share a connectivity

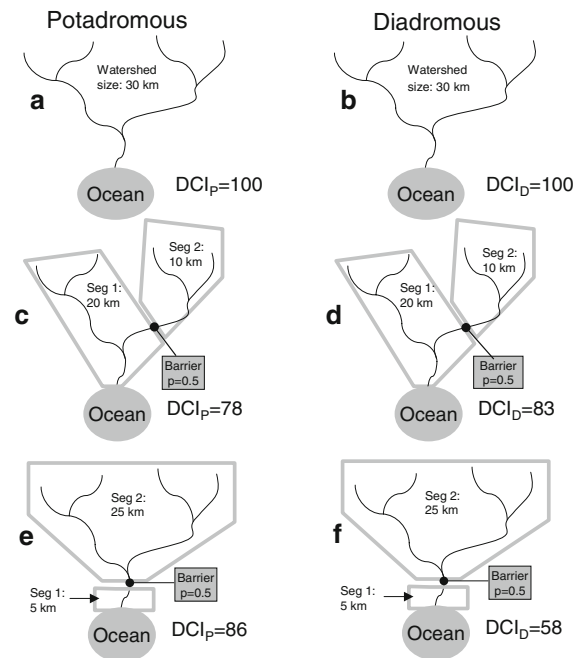


Fig. 1 Components of the Dendritic Connectivity Index (DCI). In systems with no barriers, the system is fully connected and the DCI has a maximum value of 100 for both life histories considered: potadromous (a) and diadromous (b). The introduction of a single barrier creates two stream sections, and the DCI is based on both the sizes (total channel lengths) of the resulting sections, the permeability of the barrier in both upstream and downstream directions (in this case, the product of the two permeabilities = 0.5) and in the diadromous case, the location relative to the downstream end (represented by the ocean) of the system (b, c). Changing the barrier location to create a greater inequality in stream section sizes results in a more connected system (higher DCI) for the potadromous life history (e), and moving the barrier closer to the ocean significantly reduces connectivity (lower DCI) for the diadromous life history (f)

value (Fig. 1). We can then think of connectivity having only as many potential values as there are pairs of stream sections. Since our interest is making a single integrated assessment for the river network, we use the expected (i.e., weighted average) connectivity value of stream section pairs. More formally, let C be a discrete random variable that denotes connectivity, and let c_{ij} be a realization of C for stream sections i and j , where $\{i, j\} = 1, \dots, n$, where n is the number of stream sections, and is equal to the number of barriers plus one. The Dendritic Connectivity Index (DCI) can be expressed as:

$$DCI = E[C] = \sum_{i=1}^n \sum_{j=1}^n c_{ij} P(C = c_{ij}). \quad (1)$$

The DCI can be calculated for any size stream network, or portion of a stream network. For example, the DCI could be calculated for the entire Mississippi river watershed, by choosing the estuary as the furthest downstream point, or for any tributary of the watershed (e.g., the Missouri River), by choosing the intersection of the tributary with the main stem as the furthest downstream point.

In the following sections, we illustrate how to apply this general framework to accommodate two different life history constraints (e.g., diadromy and potadromy). For simplicity, we first tested the index on a simulated dendritic network. We then compared the performance of the index on the simulated dendritic network to that on a real-world dendritic stream system in Newfoundland, Canada. We illustrate how this index could be used to prioritize barrier restoration or replacement in this real stream system. All simulations and tests of the indices were carried out using the R statistical software package (v. 2.7.0, R Development Core Team 2007; code to calculate the index is available on request from the authors).

Dendritic Connectivity Index: potadromous application (DCI_P)

Potadromous fish make migrations within freshwater, and we are principally concerned with the ability of fish to make regular migratory movements between patches (Harden Jones 1984; Dodson 1997). Thus patches are only connected if an individual can navigate between patches in both upstream and downstream directions. We assume that potadromous fish are equally likely to move upstream as downstream (Warren and Pardew 1998). For the potadromous context, the probability of observing a particular c_{ij} depends on the lengths of the sections i and j , identified by l_i and l_j , as a fraction of the total length of the drainage network, L .

$$DCI_P = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i l_j}{LL} * 100. \quad (2)$$

Note that we multiply the index by 100 simply to rescale the index between 0 and 100. The value of c_{ij} will depend on the number and passability of barriers

between sections i and j . We begin by assuming that the passability of multiple barriers is independent, i.e., that a fish passing one barrier does not in any way affect the probability of the same fish passing another barrier. If there are M barriers between sections i and j , then c_{ij} is defined as:

$$c_{ij} = \prod_{m=1}^M p_m^u p_m^d, \quad (3)$$

where p_m^u and p_m^d are the upstream and downstream passabilities of the m th barrier, respectively.

If passability is assessed as a binary outcome, i.e., a potential barrier meets designated fish passability criteria (p_m^d and $p_m^u = 1$) or it does not (p_m^d and $p_m^u = 0$) (e.g., Clarkin et al. 2005), then the index simplifies to:

$$DCI_P = \sum_{i=1}^n \frac{l_i^2}{L^2} * 100, \quad (4)$$

since neighbouring sections separated by fully passable barriers are merged, and hence only impassable barriers remain. Thus the binary case only sums connectivity contributions from movements within the same stream section.

Dendritic Connectivity Index: diadromous application (DCI_D)

Diadromous fish make migrations between marine and freshwater environments, and hence we are principally concerned with their ability to reach stream sections from a single point: the river mouth, and return. Therefore, we calculate connectivity in terms of the probability that a fish can move in both directions between the mouth of the river and another section of the river network (note that DCI_D can be applied from any section in the network). Assuming that the probabilities of crossing successive barriers are independent, the expected connectivity is the Dendritic Connectivity Index for diadromous species:

$$DCI_D = \sum_{i=1}^n \frac{l_i}{L} \left(\prod_{m=1}^M p_m^u p_m^d \right) * 100, \quad (5)$$

where L is the length of all stream sections in the drainage network, l_i the length of section i , ($i = 1, \dots, n$), p_m^u and p_m^d are the upstream and downstream passabilities of the m th barrier ($m = 1, \dots, M$)

between the river mouth and section i , respectively. If passability is measured as a binary outcome, i.e., a potential barrier meets designated fish passability criteria or it does not (e.g., Clarkin et al. 2005), the index simplifies to:

$$\text{DCI}_D = \frac{l_1}{L} * 100, \quad (6)$$

where l_1 is the length of the section closest to the mouth of the system and L is the summed length of all stream sections in the drainage network.

Applying the index to a simulated dendritic system

To test our connectivity metric, we developed a simple third order dendritic river network (Fig. 2) with 50 barriers spaced evenly (though no barriers were placed on stream intersections). We calculated index values for both life histories under two scenarios: (a) varying the barrier passability from 0 to 1 and (b) varying the number of barriers from



Fig. 2 A simulated three-order dendritic stream network, with 50 systematically placed barriers, used to test the Dendritic Connectivity Index

0 to 50. The latter was done by randomly omitting a specified number of barriers from the network 500 times and calculating the mean index value. We then investigated variations of the index, namely, the effect of treating barriers independently on overall river network connectivity.

Independent versus dependent barriers

The proposed index assumes that the probability of passing one barrier is independent of the probability of passing another barrier in the same river network. Such an assumption may not be biologically realistic in a system where connectivity is a function of water flow, and multiple barriers will experience the same water flow conditions simultaneously. To evaluate the impact of this assumption, we also calculated connectivity values when passability values of multiple barriers are completely dependent. In biological terms, this scenario models the case where, if an individual can navigate the worst barrier, all remaining barriers with equal or higher passability values between two given patches are considered fully passable.

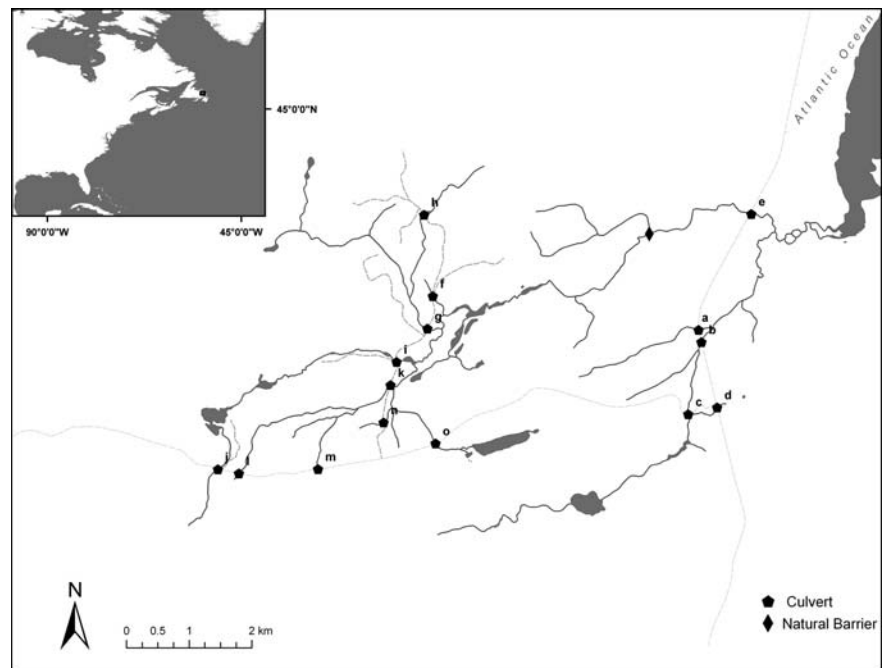
Discriminating between anthropogenic and natural fragmentation

In some situations (for example, when considering targets for ecological restoration) it will be desirable to consider existing levels of river network connectivity relative to a natural baseline. Such a natural baseline could include natural barriers (e.g., waterfalls) that restrict movement and hence affect connectivity. If we consider the natural barriers to represent an absolute state of “natural connectivity” (NC) we can evaluate the effect of adding anthropogenic barriers relative to this natural state, by expressing the connectivity index (DCI_P or DCI_D) as a percentage of the absolute “natural connectivity” value. To illustrate this, we discriminate the effects of anthropogenic barriers from a natural barrier on a real world dendritic river network.

Extending the DCI to a real world dendritic system

We apply the DCI to evaluate the connectivity of the Big Brook stream system (48°30' N, 54°01' W) in

Fig. 3 The Big Brook river drainage network of Terra Nova National Park, Newfoundland, Canada. Anthropogenic barriers are indexed by letters. The waterfall is a complete natural barrier



Terra Nova National Park, Newfoundland, Canada (Fig. 3), to assess how the index performs in a real world stream system. Stream and road networks from the Big Brook watershed, as well as the locations of barriers were analyzed using ArcGIS (ESRI v. 8.2). Barriers consisted of culverts ($n = 15$) and one naturally occurring waterfall. Length of stream sections (extent defined by adjacent barriers) was measured; their combined length (L) totalled 55.9 km. Since barrier passability is currently unknown for this watershed, we applied a uniform passability of 0.5 to all anthropogenic barriers and a passability of 0 to the natural barrier. We calculated DCI for both potadromous and diadromous applications. We also examined how the number of barriers, together with their spatial arrangement, affected the DCI_P and DCI_D . To do this for each set of potential barriers i , $i = 1, \dots, 15$, we calculated the DCI_P and DCI_D for all $\binom{15}{i}$ possible permutations of culvert locations, using only the existing culvert locations. This gives the range of possible DCI_P and DCI_D values for a given number of barriers and barrier locations on this drainage network.

Results

As expected, connectivity of the simulated river network with independent barriers declined as the number of barriers increased. However, the relationship was curvilinear, with the biggest losses to connectivity occurring with the addition of the first few barriers (Fig. 4b, d). Subsequent barrier additions had increasingly smaller impacts, with an eventual asymptote as the number of barriers $\rightarrow \infty$. These relationships were maintained across all passability standards and are qualitatively similar for both diadromous and potadromous life histories, though the impact of barriers is more severe for diadromous than for the potadromous scenario. One less intuitive property of the index proposed is that, particularly for systems composed of many independent barriers, a greater increase in connectivity is achieved by small improvements to barriers with moderate to good passability than with the same improvement to barriers with poor to moderate passability (Fig. 4a, c).

For scenarios with dependence among barriers, DCI_P and passability showed a positive linear relationship (Fig. 5). However, adding additional barriers

Fig. 4 The effect of passability (**a, c**) and number of barriers (**b, d**) on the potadromous (**a, b**) and diadromous (**c, d**) DCI when barriers are considered independently in a simulated dendritic river system. Lines in the left hand panels (**a, c**) represent different numbers of barriers ($b = 0, 1, 2, 4,$ and 50). Lines in the right hand panels (**b, d**) represent different passability values for the barriers ($p = 1, 0.9, 0.8, 0.6,$ and 0)

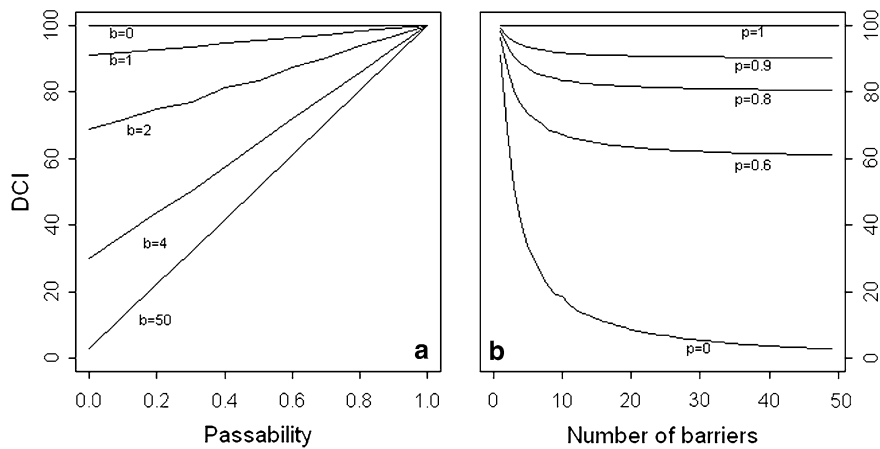
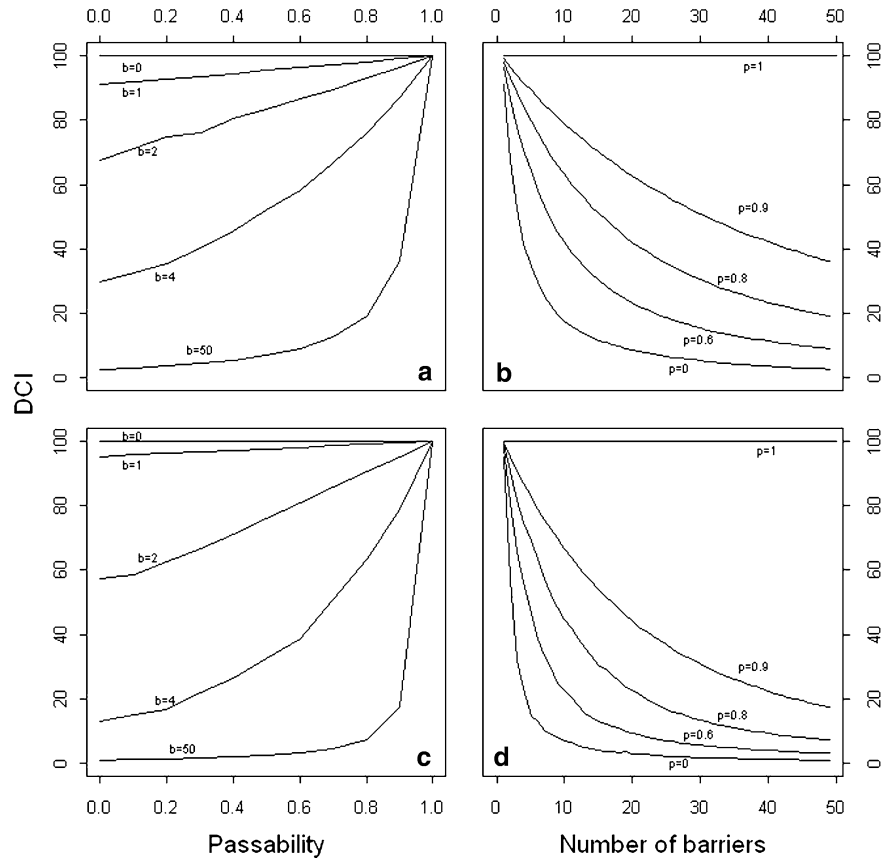


Fig. 5 The effect of passability (**a**) and number of barriers (**b**) on the potadromous DCI when passability of barriers is dependent (i.e., an individual that passes through the worst barrier is assumed to be able to pass through all barriers with

higher passability values) in a simulated dendritic river system. Lines in panel a represent different numbers of barriers ($b = 0, 1, 2, 4,$ and 50). Lines in the panel b represent different passability values for the barriers ($p = 1, 0.9, 0.8, 0.6,$ and 0)

beyond a certain point (~ 5 – 20 , depending on the passability) had very little effect on the connectivity of the system (Fig. 5, right-hand panel).

Extending the DCI to a real world dendritic system

The DCI for the Big Brook river network was 29.7 and 22.5 for potadromous and diadromous life histories, respectively. However, when scaled relative to the natural condition (DCI calculated with only the natural (and assumed to be complete) barrier present) the drainage network scored 57.1% and 56.4% of the absolute (natural) DCI for the respective potadromous and diadromous life histories. Random removal of existing barriers in the Big Brook watershed produced a slight curvilinear response between average %-of-natural DCI and number of barriers for the potadromous life history, but a linear relationship for the diadromous life history (Fig. 6). The lack of a strong curvilinear response (as observed in Fig. 4) is an expected by-product of accounting for the effect of the natural barrier (i.e., scaling the DCI relative to the natural condition). Since the natural barrier alone is responsible for a considerable portion of the fragmentation in the system, subsequent barriers have weaker effects than they would in the absence of the natural barrier.

Table 1 provides an illustration of how the index can be used for prioritization of barrier removal. For

Table 1 An example of barrier prioritization for restoration efforts in the Big Brook river drainage network in Newfoundland, Canada (Fig. 3) using the DCI

Culvert restored	Percentage of natural DCI _P	Percentage of natural DCI _D
None	57.1	56.4
a	58.8	61.0
b	60.1	69.0
c	60.2	63.1
d	57.1	56.5
e	62.4	69.0
f	57.4	56.4
g	66.2	56.4
h	58.4	56.4
i	63.4	56.4
j	58.0	56.4
k	64.1	56.4
l	57.1	56.4
m	57.0	56.4
n	57.6	56.4
o	59.9	56.4

Prioritization is based on the elimination of one of the 15 culverts and recalculating the DCI values. Culvert letters correspond to culvert identifiers on the map in Fig. 3. Since the watershed contains a full natural barrier, the results are presented as %-of-natural DCI_P and DCI_D values. Higher values of the connectivity index indicate higher priorities for culvert restoration. The highest priorities for restoration are indicated in bold. Culverts had an assumed net passability (product of upstream and downstream passability) of 0.5, and all barriers (culverts and the natural barrier) were assumed to be independent

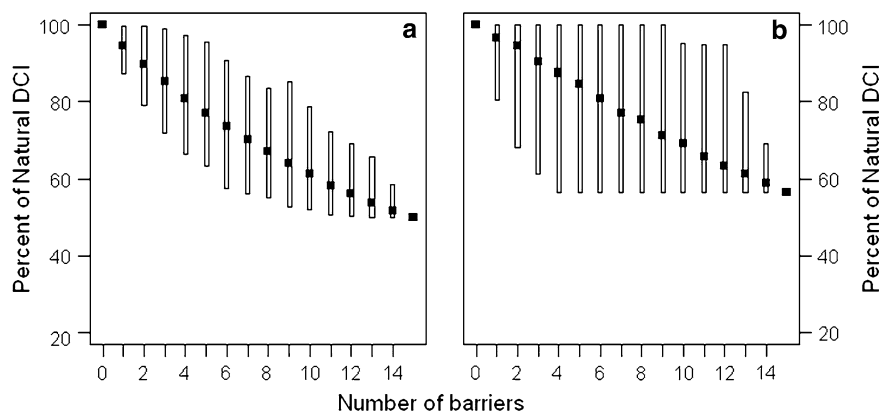


Fig. 6 The relationship between the number of barriers and the DCI for the Big Brook river network, for both the potadromous (a) and diadromous (b) life histories. The relationship is based on removing differing numbers of barriers from the existing set of barriers on the drainage network, and calculating the DCI for all permutations of that number of

barriers. Only the 15 barrier locations were used in determining the permutations (see text for additional detail). The dark square represents the mean value from all possible permutations, and bars give the range of potential values from all possible permutations

the potadromous case, it is possible to increase the %-of-natural DCI from 57.1 to 66.2, by choosing the most important barrier to remove, whereas most barrier removals would lead to little improvement (1–3%). In the diadromous case, the results are more intuitive, as removing barriers upstream of the full natural barrier had no effect on the index. Removal of either of the two barriers downstream of the natural barrier would increase the %-of-natural DCI from 56.4 to 69.0.

Spatial effects of barriers

Barriers impose differential effects on the DCI based on their location in the river network, and these effects are manifested differently for each life history (Table 1; Fig. 6). This is evident from the range of variability in DCI for various restoration scenarios (Fig. 6) and by comparing the results from single barrier restorations (Table 1) with the barrier locations (Fig. 3). Restoring centrally located barriers had the largest effect on the DCI_P (Table 1), whereas restoring barriers near the ocean had the largest effect on the DCI_D (Table 1). Due to these strong spatial effects, if restoration is done wisely on Big Brook, the removal of the barrier with the greatest impact on the DCI could achieve the same connectivity gains as the removal of 11 poorly chosen barriers for the diadromous life history. Spatial effects are not as strong for potadromous life histories, where the removal of one carefully selected barrier would have equal effects to the removal of only eight poorly chosen barriers for the potadromous life history.

Discussion

Fluvial landscape ecology has yet to develop as an integrated field, however, the need for concepts and landscape analysis tools tailored to lotic ecosystem dynamics is recognized (Poole 2002; Wiens 2002). The dramatic rate of alteration to natural connectivity further underscores the urgency for these tools (Pringle 2003). Our index suggests that longitudinal connectivity in river networks suffers the most in the early stages of fragmentation, because there are fewer alternative paths available (Jones et al. 2000). This is in contrast to 2-D systems (e.g., most terrestrial environments), where overall landscape connectivity

is generally maintained until later periods of fragmentation, since there are usually alternative paths available after the first few patches/nodes are lost (Gardner et al. 1987; Plotnick and Gardner 1993; Fortuna et al. 2006). Particular care should be taken in relatively well-connected areas to maintain a high level of barrier passability. In some cases, such impacts can be mitigated somewhat by prudent barrier placement (i.e., near a natural barrier or at the extremities of a stream network). In river networks with natural barriers, where connectivity is expressed relative to a natural level of fragmentation, the effect of additional anthropogenic barriers is predictably diminished, but still of considerable importance. Results from the Big Brook watershed indicate that the current 15 barriers, assuming a barrier passability of 0.5, reduce the connectivity index to almost one half its natural value for both potadromous and diadromous life histories.

Not unexpectedly, connectivity from the perspective of a potadromous species is less impacted from reduced habitat connectivity than for diadromous life histories (DCI_D had a median difference of 9 units when compared to DCI_P over the range of values in our simulations). By definition, diadromous species must access freshwater environments from the ocean, thus barriers make all habitat upstream unusable. In contrast, potadromous species can make use of habitats above and below the same barriers (assuming that sufficient habitat exists on each side of the barrier to sustain a separate population). The increased sensitivity of diadromous species is exemplified by widespread declines of diadromous species (Pacific Rivers Council 1993; Beechie et al. 1994; Moyle 1995; Berkamp et al. 2000), for which loss of connectivity has been at least in part to blame. Nonetheless, the impacts on potadromous fish (e.g., Moyle 1995; Muhar 1996; Dunham et al. 1997; Fagan et al. 2002; Morita and Yamamoto 2002) and aquatic invertebrates (Master 1990) are also widespread.

Location of barriers within the watersheds was also very important in influencing the DCI for both life histories. As evidenced in the Big Brook river network, barriers located at the headwaters minimized loss of diadromous connectivity, while barriers placed at the extremities of river networks minimized loss of potadromous connectivity. The diadromous results are intuitive given that a greater proportion of

diadromous individuals will need to pass through barriers that are closer to the ocean. In the potadromous case, the response can be attributed to the fact that the contribution to the DCI_P of a stream section increases proportionally to the squared section size. For example, in a simple network of two patches, the DCI_P increases as the barrier moves to the extremity of the network and the disparity in patch size increases. Such results are consistent with persistence estimates of populations, which scale exponentially to the number of individuals within a population (Lande 1993).

River network configuration

Though the results of our simulated river networks were qualitatively similar to those of a real world dendritic river network, the unique spatial arrangement of stream networks will have implications for connectivity impacts. In networks with fewer branches, the random placement of a single barrier results in less variability in patch size compared to highly branched arrangements (i.e., the disparity between resulting patches in highly branched networks would be greater; Fagan 2002). Furthermore, in networks with similar stream length and numbers of barriers, the number of barriers an individual (potadromous or diadromous) would have to pass to reach another randomly selected section would, on average, be lower in highly branched configurations. Therefore, we would expect that, on average, highly branched networks with a barrier would have higher potadromous DCI values than a comparable network with fewer branches. From an ecological perspective, highly branched networks should be more resilient since at low levels of fragmentation, the resulting fragments could leave at least one functioning component for diadromous species (outflow to headwater).

Applications

The approach presented here has utility in both practical and theoretical applications. From a theoretical perspective, connectivity has been identified as a central biological process for terrestrial fauna (e.g., Bennett et al. 1994; Moilanen and Nieminen 2002; Broquet et al. 2006; With et al. 2006) and more recently in aquatic systems (Stanford et al. 1996;

Wiens 2002; Pringle 2003). As far as we are aware, we are the first to propose a general purpose methodology, with minimal biological inputs, to quantify network-scale habitat connectivity in aquatic systems. The ability to quantify structural connectivity will provide researchers with a means to better understand how this process affects evolutionary trajectories, population persistence, and community dynamics. Furthermore, though we applied the DCI_D specifically to migrations from the marine environment, such a methodology can be applied to any particular point within a river network. Thus, the DCI can be included as an attribute of habitat studies being conducted at much smaller scales (e.g., a single reach).

From a practical perspective, the DCI can facilitate consideration of longitudinal connectivity in river networks. Considerable effort in aquatic systems has been focused on improving or restoring patch quality (e.g., in-stream restoration projects), but this has often been done without recognition of connectivity between patches (Pringle 2003; Kondolf et al. 2006). This can be a crucial oversight in aquatic ecosystem management (Muhar 1996; Stanford et al. 1996; Cooper and Mangel 1999), given that aquatic organisms may require several habitat types as they grow and may exhibit life histories and behaviours that are manifested at several spatial scales. The proposed approach will allow resource managers to characterize watersheds, determine priorities for restoration, optimize resource allocation (i.e., barrier passability standards) and infrastructure plans (placement of roads, dams, etc.) and report on connectivity as a component of ecosystem integrity. For example, for the watershed shown in Fig. 3, potadromous connectivity could be improved between 0 and 9% of natural connectivity, depending on which single barrier is restored (Table 1). An advantage of the approach presented here is that it allows the evaluation of impacts on individual projects at the scale of the entire river network that includes cumulative impacts of many small developments (e.g., Beechie et al. 1994; Pringle 2003). As relationships with structural connectivity and biological communities develop through further research in fluvial landscape ecology, a standardized method such as we propose here will allow comparison of multiple watersheds and will aid in identifying extirpation hotspots or areas in need of enhanced protective measures.

Future refinements: applications to biota

For the sake of simplicity, universal passability standards were applied to the simulated river drainage networks. In practice, passability will vary for each barrier, which the index can readily accommodate. Estimating passability is more problematic as it needs to be considered from an organism's perspective. The ability of organisms to pass through barriers will be a function of physiology, which differs among and within species (e.g., Berry and Pimentel 1985; Myrick and Cech 2000), and physical conditions (e.g., Belford and Gould 1989; Spens et al. 2007; Jones et al., 2008) that would vary spatially and temporally within a watershed. As an example of a method to estimate passability of hydrological barriers (e.g., culverts), the proposed connectivity index could be merged with hydrological models that estimate variation in stream flow (discharge) over time and relate these parameters to variation in passability as a function of flow for species with different swimming abilities.

A second challenge is identifying whether the probability of passing a barrier is independent among nearby barriers. Independence may not be appropriate in situations where passability is dependent on discharge (which varies at large spatial scales) or the size of the individual (if an individual is enough large to pass one barrier, it can then pass all more permeable barriers). Where on this spectrum true connectivity lies will depend on the organism, its behaviour and spatial arrangement of the barriers.

The DCI can be further developed to incorporate aspects of lotic ecological theory. As presented in this paper, stream sections are treated with equal weight regardless of where they occur within the drainage network. As discussed by Poole (2002), the physical characteristics and ecology of sections would be expected to vary along longitudinal gradients (Vannote et al. 1980; Poole 2002; Thorp et al. 2006) as well as within sections (Ward and Stanford 1983; Stanford and Ward 2001; Thorp et al. 2006). Improved biological inference will also require improved quantification of what constitutes habitat versus movement corridors (Fagan 2002). In the simulations described in this paper, stream length was considered the metric of available habitat. Habitats in river networks, however, are patchy and differ in

quality (Poole 2002). With enhanced knowledge of habitat suitability, stream length can be replaced by any measure of habitat extent. In cases where more biological insight is available, this additional information could be incorporated to refine the model, analogous to the detail provided by Schick and Lindley (2007) for a model to estimate independence (a measure of connectivity) of riverine populations of salmon.

Conclusions

The proposed index provides a means to quantify (longitudinal) connectivity within dendritic ecological networks (Grant et al. 2007). It is conceptually simple and sufficiently flexible to deal with variations in river structure (linear through highly branched dendritic networks) and biological communities (e.g., diadromous versus potadromous life histories). Quantifying and addressing issues of habitat connectivity continue to be an important research focus in terrestrial landscape ecology. The importance of aquatic connectivity and the need to develop fluvial landscape ecology research have begun to be recognized. It is our hope that the metric proposed here will stimulate further discussion and collaboration between landscape and aquatic ecologists and lead to a greater understanding of the landscape-scale effects of human disturbance on riverine patterns and processes.

Acknowledgments This work was supported by Parks Canada and a CFI grant to YFW. Thanks to B. Adams, L. Johnson, N. Schumaker, and five anonymous reviewers for helpful feedback on earlier drafts of the manuscript.

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