Barriers to fish passage and barriers to fish passage assessments: the impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity

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Abstract

Barriers (culverts and dams) can impede fish passage and affect the overall habitat connectivity of rivers. However, a challenge lies in how to conceptualize and adequately measure passability at barriers. We hypothesize that estimates of barrier and watershed connectivity are dependent on assumptions about the nature of passability, and how it is measured. Specifically, we compare passability estimates in Terra Nova National Park, Canada for individual barriers for two barrier assessment methods (a rapid assessment, and one based on FishXing software), two salmonid species, different fish sizes and swimming speeds, and varying hydrological conditions. Watershed connectivity was calculated using the Dendritic Connectivity Index (DCI). Lastly, we test to see what the impact of the various factors is on the practical goal: prioritizing barriers for restoration. Our results show that barrier passability estimates can vary drastically for some barriers (0-100%). In general, the rapid field-based assessment tended to give more conservative estimates of passability than those based on FishXing. Estimates of watershed connectivity were not as sensitive to the assumptions and methods used (DCI: 40-83). Fish size had the greatest effect on DCI. Importantly, variation in DCI had little impact on the restoration priorities. The same barrier was retained as the top priority >96% of the time. Thus, managers wishing to assess barriers for restoration need to carefully consider how passability is to be measured, but can reduce the impact of these decision by considering barriers in their watershed context by using a connectivity index such as the DCI.

Keywords: barrier assessment; connectivity; dendritic connectivity index; passability; salmonids

Introduction

Fragmentation of many of the world's stream networks has been recognized as a serious threat to the population diversity, abundance, and persistence of a variety of aquatic species (e.g., Sheldon 1988; Dunham et al. 1997; Khan and Colbo 2008). Human activities are largely to blame for these connectivity losses, often through the installation of physical barriers (such as dams and culverts) to movement (e.g., Morita and Yamamoto 2002; Park et al. 2008; Doehrign et al. 2011; Hall et al. 2011; Rolls 2011). While many of these barriers can be eliminated or mitigated by modification, such as by the construction of fishways, the process is typically expensive and budgetary constraints restrict the amount of restoration that can occur (Gibson et al. 2005; Poplar-Jeffers et al. 2008). Thus, a solid understanding of the ecological impacts of potential barriers is essential to prioritize restoration efforts and maximize returns on limited funding. Although in simplest terms we know that barriers impact the passage of fish, quantifying this impact is challenging because barrier passability is difficult to define and measure. Many definitions and methods for estimating passability exist (see Kemp and O'Hanley 2010 for a recent summary). Common methods include measuring or modelling the physical characteristics of a barrier and comparing it to known fish physiological parameters (e.g., FishXing; USFS 2003 for culverts), through mark-recapture (e.g., Helfrich et al. 1999; Porto et al. 1999 for dams; Blank et al. 2005 for culverts), analysis of genetic structure of the population (Neraas and Spruell 2001; Kemp and O'Hanley 2010) or by tracking individual fish attempting to navigate the barrier (Bjornn and Peery 1992; Steig et al. 2005; Cahoon et al. 2007). Passability is also challenging to quantify because it is dynamic. Fish physiological capacity varies by species, size, amongst individuals and across environmental conditions, while the physical characteristics of barriers also vary temporally due to variations in stream flow (see Bjornn and Peery 1992; Rolls 2011). Such physiological and environmental variability makes the task of defining passability at a population or landscape scale challenging.

A second factor important to understanding barrier impacts is the need to consider the context in which a barrier is found (Cote et al. 2009; Rolls 2011). Previous studies of aquatic barriers were based largely on the effects that the barriers had on nearby portions of stream systems (e.g., Belford and Gould

1989). More recently, concepts from landscape ecology, such as fragmentation and patch dynamics, have been applied to aquatic systems to investigate the impacts of barriers on entire stream networks and catchments (Dunham et al. 1997; Jones et al. 2000; Park et al. 2008; Cote et al. 2009; Fullerton et al. 2010). This broad view is crucial to understanding and mitigating the ecological consequences of stream fragmentation, as the effects of even a single barrier may have large impacts on entire stream networks, and multiple barriers may lead to cumulative impacts (Kemp and O'Hanley 2010; Rolls 2011; however, see Padgham and Webb 2010 for a model which suggests that multiple impacts are simply equal to the sum of the parts).

One method for quantitatively evaluating the cumulative impacts of barriers on entire stream networks is the Dendritic Connectivity Index (DCI; Cote et al. 2009), which could be a valuable tool for assessing fragmentation in stream systems and for prioritizing barrier restoration. The DCI requires two key data inputs; spatial location of barriers (both artificial and natural) within a stream or river network, and a passability value for each individual barrier. While spatial data for the barriers are relatively simple to acquire, useful barrier passability estimates not. In this paper, we examine how different barrier assessment methods and definitions of passability affect i) estimates of connectivity at both the barrier and the landscape scale, as measured by the DCI, as well as ii) the prioritization of restoration efforts.

Cote et al. (2009) suggested passability could be quantified in several different ways and noted that decisions on how to define and measure passability would be important to interpret and evaluate watershed connectivity. Interpretations that capture the variability in fish physiology within and among species (e.g., assigning a passability of 0.5 to a barrier that is passable to 50% of the target population) may be insensitive to temporal environmental variation, while definitions that account for temporal variation of physical characteristics (e.g., the barrier is passable 50% of the time to fish with a defined physiological capacity) may not account for variation amongst individual fish. Furthermore, once defined, subsequent passability values will reflect decisions regarding the time period of the assessment (i.e., stream discharge), the species being modelled and the accuracy of the swim speeds estimates. Unfortunately, the sensitivity of barrier passability estimates, and subsequent watershed connectivity estimates, to these decisions is unknown. If these measures are highly sensitive to variation in fish physiology or environmental conditions at barriers, then the utility and general applicability of watershed connectivity estimates will be reduced, and managers wishing to use them will have to very careful about how data are collected.

We used river/stream systems (hereafter "watersheds") of Terra Nova National Park (TNNP), Newfoundland and Labrador, Canada, (which ranged in area from 0.5 km^2 to 36 km^2) as a case study to examine the sensitivity of passability estimates and resulting river connectivity (watershed and park-wide)to four aspects of barrier passability: i) the fish species of interest, ii) barrier assessment methodology, iii) inter- and intra-annual variability in stream flow, and iv) assumptions about fish swimming capacity. The results of these simulation scenarios are also evaluated in terms of their effects on restoration priorities in the tested watershed. The simulations are interpreted with respect to the effect on individual barrier assessments, and on the watershed connectivity using the DCI. Finally, we demonstrate a means to include variation of fish physiological capacity and environmental conditions to calculate an integrated DCI score.

Methods

Calculating the DCI

The barrier passability values used in DCI calculations range from 0 to 1, with 0 being impassable (a complete barrier), 1 fully passable and values in between considered partially passable. We obtained connectivity values for potamodromous (DCI_P,) and diadromous (DCI_D,) fish life histories for all park catchments using fish size/swim speed and stream flow parameters. Diadromous life history refers to fish that move between ocean and freshwater (in either direction) during their life cycle. The species examined in this study exhibit anadromy; a form of diadromy where spawning occurs in freshwater and adults spend part of their life at sea, but the form of diadromy is irrelevant for this analysis. The formula for calculating potamodromous connectivity (in both upsteam and downstream directions) is taken from Cote et al.

(2009) and requires dividing the watershed into segments, where segments are separated by barriers. The formula is:

$$DCI_P = \sum_{i=1}^{n} \sum_{j=1}^{n} c_{ij} \frac{l_i}{L} \frac{l_j}{L}, \tag{1}$$

where l is the length of segment i and j, c_{ij} is the connectivity between segments i and j, and L is the total stream length. Diadromous connectivity applies to both anadromous and catadromous (migrating from ocean to freshwater) cases and is calculated as follows from Cote et al. (2009):

$$DCI_D = \sum_{i=1}^{n} \tfrac{l_i}{L} \left(\prod_{m=1}^{M} p_m^u p_m^d\right) * 100, \tag{2}$$

where l_i is the length of segment i, p_m^u and p_m^d are upstream and downstream passabilities of the m^{th} barrier (m=1….M) between the river mouth and section i, and L is the total stream length. Maximum DCI value is 100, which indicates a fully connected watershed, with connectivity decreasing as DCI values decrease from 100.

Fish species of interest

Barrier assessments were conducted for two different salmonid species (brook trout, *Salvelinus fontinalis* and Atlantic salmon, *Salmo salar*). These species have well-studied physiology, are widely distributed in the study area and are culturally and recreationally important (Scott and Crossman 1973). Though brook trout and Atlantic salmon are of the same family, Atlantic salmon have superior swimming capabilities (Peake et al. 1997) and diadromous individuals can attain larger sizes than those of brook trout. We based our Atlantic salmon assessments on the physiology of a 50 cm (fork length; FL) individual and the physiology of a 15 cm (FL) individual for brook trout assessments.

Barrier assessment methodology – rapid assessment vs. modelling

We used two methods to evaluate passability of all culverts in TNNP (n = 43); rapid field assessments (which examine culvert passabilities during a single visit), and more detailed field data coupled with modelling software (that integrates variation in stream flow in the evaluation of culvert passabilities). Field assessments consisted of a screening process for barriers, based on a set of criteria (Fig. 1) adapted from previous culvert inventories (Clarkin et al. 2005). These criteria included culvert slope, outflow drop height and presence of an outflow pool. FishXing, a widely used freeware, creates hydrological models of culverts based on data collected in the field (culvert shape, length (m), material, slope, installation type) together with flow equations and fish movement parameters. While FishXing can model culverts using minimal field data, more detailed data can be included such as the cross-section topography of the tailwater control area and discharge rates for the study stream. FishXing also identifies which of three mechanisms impede the passage of fish: insufficient water depth in the culvert (depth barrier), excessive height for fish to jump into the culvert (height barrier), and excessive water flow for fish passage (velocity barrier).

The data collection for the rapid assessment surveys took from 5 to 15 minutes per culvert, whereas for the FishXing assessments, surveys in the field took from 20 to 40 minutes per culvert with an additional time of 5-10 minutes per culvert for computer simulations (and more when default values proved problematic - see below for details). We collected additional parameters (e.g., water depth and water velocity in culvert) to ground-truth FishXing results, and three culverts were revisited to improve congruence between field and FishXing outputs. Rapid assessment surveys were carried out in May and June of 2007. Using the FishXing software also requires additional inputs of fish limitations for burst and sustained swimming speed, minimum water depth and maximum outflow drop. These values were obtained for our species from Peake et al. (1997) and from Peake (unpublished data).

We encountered some challenges when assessing culverts using FishXing. Specifically, the default values provided by the software for the culvert entrance loss coefficient (K_e) and the culvert and tailwater control roughness coefficients (n) – parameters used to model water flow in open channels (Brater and King 1976) – did not provide accurate approximations of field conditions. Thus, at a given discharge rate, modelled values of culvert water depth and velocity were often very different from the actual values measured in the field at that discharge rate – leading us to suspect that the modelled values provided by FishXing at other discharge rates were also inaccurate. This issue has been observed in other evaluations using FishXing (Blank et al. 2005; Poplar-Jeffers et al. 2008) and likely occurs because the software uses K_e values which are derived from culverts under full water and roughness coefficients which are often derived from large streams and generalized to all streams without considering details such as the presence of debris, inconsistencies in substrate across a small area or rapid changes in slope or wetted width (R. Gubernick, FishXing design team, pers. comm.; see also Mangin et al. 2010). To more accurately model the study sites, we obtained new K_e values for partially full culverts from Straub and Morris (1950ab) and back-calculated new roughness coefficient values (n) using field data from original culvert surveys and from the three culverts which were revisited for ground-truthing. Though the culvert parameters provided by FishXing did not always match field values exactly, our modifications to the n and K_e values did improve the precision of all culvert models. Passability estimates obtained from rapid assessments (using first visit data only) and more detailed field surveys plus FishXing modelling were used to calculate DCI_P and DCI_D for all catchments in Terra Nova National Park.

Temporal variability in stream flow

We investigated the effect of intra-annual stream flow variability for all park watersheds (n = 15). We calculated the DCI_P and DCI_D for two time periods: when fish are migrating, and the whole year (Table 1), using daily discharge data averaged over a twenty year period from the Southwest Brook gauging (48°36’27” N, 53°58’44”W station 02YS003) station located in the national park. We investigated the effect of inter-annual variability in water flow on the DCI_P and DCI_D within a test watershed, Big Brook (Fig. 2). To investigate inter-annual variability, we calculated the DCI_P and DCI_D for twenty different years using daily discharge data (Table 1).

For each analysis, we scaled gauging-station hydrographs for each barrier by calculating the ratio of the area draining into the stream gauge location to that of the area draining into the barrier. This assumes that discharge rate is proportional to catchment size. FishXing determines whether a barrier is passable at a range of flow values between the minimum and maximum provided. Using these results, we determined passability as the proportion of days the flow would allow a fish of the given size to pass.

Variable fish swim speed

We modelled fish passage for a range of swimming speed scenarios in each culvert in the test watershed, Big Brook (n = 18 culverts). We set a range of ‘user-defined’ burst and sustained swim speeds in FishXing for our study species to model the effect of fish size and swimming ability on passability. These speeds are summarized in Table 2, and are based on models for brook trout and Atlantic salmon by Peake et al. (1997), who conducted swim speed tests using fish from a watershed in north central Newfoundland. Though Peake’s study used forced performance models, which recent research has shown to produce conservative measures (Peake and Farrell 2006), it likely represents the best available data as fish were collected from an area close to the TNNP study site. We used this speed ±25% to account for individual variability and uncertainty due to the fact that speeds were based on forced performance models (Peake and Farrell 2006) (Table 1).

Calculating a population-integrated watershed connectivity score.

Using the barrier passability results for fish of different lengths, and a length-frequency distribution for a population of interest, we can calculate a population-integrated DCI score using a weighted mean:

$$\text{Weighted mean DCI} = \sum_{l} DCI_l \frac{n_l}{N} \tag{3}$$

where l is the length class, n_l is the number of fish of that length class, and N is the total number of fish.

Length-frequency data and species composition were obtained from past field sampling programs from ponds and streams throughout TNNP. These data were obtained from samples collected over many seasons and thus represent a general characterization of fish communities in the study area. Fish communities vary by habitat and life history types. Therefore we determined species composition and fish lengths according to each habitat (stream vs. lake) and life history subset (potamodromous vs.

diadromous). The diadromous length-frequency distribution and relative species abundance were derived from two fish counting fences of similar size to Big Brook (Minchins Brook, Cote et al. (2005); Wings Brook, Potter (1989)) during the migration period. Potamodromous fish communities were characterized based on electrofishing in streams (Cote 2007) and fyke netting in lakes (Cote et al. 2005; Cote et al. in press) throughout TNNP. Population abundance for brook trout and Atlantic salmon was calculated using available habitat in the Big Brook system and existing habitat models (Cote 2007; Cote et al. in press). Finally, the integrated abundance-weighted watershed connectivity value for Big Brook was calculated using equation 3. Since barrier passability values were not available for all fish lengths, we used length categories defined by the midpoints between length values in Table 2 for each of the two species.

Identifying priority culverts for restoration of watershed connectivity

To prioritize culvert replacement based on the greatest potential gains to connectivity, we simulated restoration of each culvert, individually, to full passability (i.e., barrier passability was set to 1) and then re-calculated DCI values for the Big Brook watershed using all possible scenarios of inter-annual stream flow variability between 1998-2008, and fish length/swim speed and for both Atlantic salmon and brook trout. For each scenario, we ranked the culverts from 1 (most improvement in connectivity) to 18 (least improvement in connectivity) and calculated the average rank, as well as the proportion of scenarios in which each culvert was ranked first for restoration.

Results

We calculated passability, DCI_P, and DCI_D with variations in fish species, barrier assessment method, stream flow period, fish length and in fish swimming ability, as described above. Here we report how estimated passability varied at the barrier, and DCI at the watershed, and park scales.

Barrier passability

The definition and method of measuring passability affected the passability estimate for individual barriers (Fig. 3). Furthermore, the results differed considerably among culverts, with 5 of 18 (28%)

culverts (ak, an, u, y, and z) impervious to any change in methodology and definition and consistently being completely impassable, and 4 culverts (22%) varying between a passability of 0 and 1 (ao, ag, aj, and w). For these barriers, the range of passabilities was much more likely to include a full barrier (0) than complete passability (1). We performed a simple analysis of variance to decompose the total variance in passability, as represented by sums of squares, into contributions from each factor. Fish length explained the majority of the variance, once the barrier effect was removed (sum of squares (SS) = 236.5), followed by variation in swimming speed (SS = 8.6), hydrological year (SS = 7.7), species (SS=3.1) and finally period with the year used for the analysis (SS = 1.1).

Single watershed scale

Connectivity values at the watershed scale varied less than the passability values of individual barriers (Fig. 3 vs. Fig. 4). For the DCI_P, the range of values encountered was 40-70, and for the DCI_D the range of values encountered was 62-83. There was a distinct hump-shaped pattern in DCI values when plotted against fish length for both species in both the potadromous and diadromous cases (Fig. 4). The DCI was lowest for very small fish, and highest for small to mid-sized fish. The DCI was also low for large fish, in some cases as low as that for the smallest size classes. Variation in the DCI due to swim speed was less than the variation due to different stream flows for large fish, but not for small fish (Fig. 4). The effect of interannual variability was fairly constant across both species and all length classes, but tended to be larger for the DCI_P than the DCI_D results. As with the barrier scale, we performed a simple analysis of variance to decompose the total variance in DCI_D as represented by sums of squares, into contributions from each factor. Again, fish length explained the majority of the variance, (~73% , followed by variation in swimming speed (~4%), hydrological year (~1.6%), species (~ 0.4%) and finally period with the year used for the analysis (SS = 1.1). Results for the DCI_D, are very similar.

National Park scale

Across all watersheds within Terra Nova National Park, DCI values varied depending on whether the rapid field-based assessment or field assessment plus modelling in FishXing was used to estimate barrier passability (Fig. 5). DCI values were lower for most catchments when the field assessment alone was used, although the difference was not as dramatic for the diadromous case as the potadromous one. In the potadromous case, 6 watersheds (40%) had DCI values between 0-40 when the field assessments were used, while all watersheds had DCI of 41 or higher when passability estimates from FishXing were used. Overall 12 watersheds (80%) dropped to a lower DCI category (based on categorizing DCI into intervals of 20) (Fig. 5). In the diadromous case, only 5 watersheds (33%) dropped to a lower DCI category (with the field assessment (Fig. 5). DCI values across park watersheds were also quite variable depending on whether passability was calculated based on an annual flow period, or restricted to flow during fish migration period. For example, more watersheds were in a lower category of DCI (<50) when passability was calculated during trout migration period than for the whole year (Fig. 6).

The integrated watershed connectivity score for the fish community in Big Brook was 58.3 for brook trout and 67.5 for Atlantic salmon (DCI_P); and 77.7 for brook trout and 78.1 for salmon (DCI_D). Lower values indicate lower watershed connectivity. These values are plotted against the median length values in Figure 4.

Barrier prioritization

Finally, the results of the prioritization exercise are shown in Table 3. Since the results for salmon vs. brook trout are very similar, only those from brook trout are presented (the results for salmon are available from the corresponding author on request). For both the DCI_D and DCI_P, culvert “al” is the culvert identified as the highest priority for restoration. Culvert “al” was ranked as the priority for brook trout under all combinations of stream flow/swim speed 98% of the time and for salmon under all scenarios 99% of the time (Table 3 shows average data across the two species; data by species are available from corresponding author by request).

Discussion

The preservation and restoration of aquatic connectivity has been recognized as a major conservation goal in stream systems (Pringle 2003); and new methods have been developed to measure the alteration of connectivity in dendritic systems. Common to all methods is the difficulty in assessing barrier passability – the dynamic component of connectivity. Our results demonstrate how passability varies by species, size and hydrological conditions (see also Poplar-Jeffers et al. 2008; Meizler et al. 2009; Kemp and O'Hanley 2010; Rolls 2011) and managers will often be forced to select a target demographic and/or target conditions when evaluating barrier passability. In this study we showed the implications of making such decisions (e.g., differences associated with picking a particular method, or a particular target species/size) as well as the error that may be related to parameter estimates (e.g., swim speed) on passability and connectivity at the watershed scale.

A useful result from this work is that watershed scale assessments of connectivity are less sensitive to variations in passability definition or assessment method than estimates of passability for individual barriers. For the DCI results, the choice of fish length had the largest impact on the connectivity score. The effect of fish length on watershed connectivity yielded an unexpected hump-shaped pattern, with smaller and larger fish experiencing lower values. However, this is readily explained by the specific passage requirements of differing size classes. Smaller fish have lower swim speeds and experience velocity barriers during high flow periods, whereas larger fish are limited by the depth of water in the culvert during low flow periods. This is illustrated by the effect of swim speed assumptions on the DCI for small fish, and the insensitivity of the DCI to swim speed assumptions for large fish (Fig. 4).

We found that watershed connectivity results can vary with barrier assessment methods – making the choice of method a crucial and influential step in connectivity assessment. For most culverts, using a simple set of criteria to do barrier field assessments produced passability values that were more conservative than those calculated by computer modelling (FishXing) for fish of the same size and species, which in turn led to reduced connectivity values (Figs. 3 and 4). It remains likely that the simple field assessments were too conservative when compared to those provided by FishXing. Since the rapid field-based assessments have been developed as general installation/assessment guidelines (Fig. 1; see also Clarkin et al. 2005), they do not account for the variable nature of passability. Hence they are necessarily precautionary and less accurate. Though the simplified field assessments did give very different estimates of passability in this study, with modified criteria and further evaluations of partial barriers using FishXing, they could be used more efficiently as tools to save time during culvert surveys by ‘screening’ obvious barriers – a practice which has been implemented in other studies and surveys (e.g., Clarkin et al. 2005). The modelling approach has an advantage in that it can account for variability in passabilty through time and for different species. Unfortunately, specific biological data (i.e., fish telemetry data) were not available to directly assess the accuracy of culvert passability estimates in this study. Such information would enable researchers to assess key assumptions in fish passage but remains a common data gap in passability assessments.

In this study, the assessment period (i.e., full year vs. migration period) did not have a substantial impact on watershed connectivity due to the fact that stream hydrology during the migration period for the two species assessed was representative of the entire year (i.e., both including floods and low water events). Thus, in similar systems to TNNP, watershed connectivity estimates based on a shorter hydrological time period might be reliable. These results are specific to the Terra Nova situation, but are likely relevant to watersheds in elsewhere. For example, in an examination of fish community assemblages above and below low-head dams in Kansas, Gillette et al. (2005) found seasonal effects. Similarly, Rolls (2011) examined watersheds with and without barriers in Australia, and found a significant effect of migratory period on barrier passage for some species. Both of these studies (Gillette et al. 2005; Rolls 2011) did not consider overall watershed connectivity, but at the barrier scale the patterns observed were similar to ours in Terra Nova, suggesting that some of our overall conclusions and recommendations on assessment methods may be worth considering in other systems. The relatively minimal impact of temporal scale observed here may not be the case in systems where species have more restricted discharge-dependent migration periods (e.g., Pacific salmon and see Rolls 2011 for an example of variation in connectivity depending on migration strategy), or in seasonally arid landscapes where streambeds go dry for months at a time (Eby et al. 2003).Nonetheless, our assessment clearly demonstrates that field assessments that evaluate barriers based on conditions for only a single day (the rapid assessment method, Fig. 1) gives very different values for connectivity than those that use more dynamic assessment methods to evaluate passability. Thus, barrier assessments need to be considered in the context of ecological conditions at a particular study site, and researchers should choose appropriate assessment methods based on the local species and hydrology.

Barrier assessments done for two different salmonid species demonstrated the variation in passability values that can be associated with both species and size class. Though brook trout and Atlantic salmon are physically similar species, their swimming capabilities differ – with Atlantic salmon being able to attain higher swimming speeds (Peake et al. 1997) and larger sizes than brook trout. The highest DCI scores were observed for salmon, but the relatively low DCI values obtained for large salmon represents the numerous depth barriers in this system. We set the minimum culvert water depth for both species at 75% of their body length, giving depth values of 11.25cm for brook trout and 37.5cm for salmon. Many of the culverts in our study areas do not have water exceeding 30cm deep. These evaluations were likely conservative, as large Atlantic salmon have been observed moving upstream in water less than 30cm deep in TNNP (D. Cote, pers. obs.). This example demonstrates the importance in choosing parameters for barrier evaluations that are accurate for the study species, and if applicable, the sub-set of the population being targeted. There is a general requirement for better information on fish swimming capacity and behaviour, particularly for non-salmonids (Kemp and O'Hanley 2010).

We demonstrate a means to calculate an integrated stream connectivity value that accounts for variation in hydrology, fish size, and species variation. As such, it presents a useful approach for ecosystem based management of aquatic systems. Though the data required to do this are considerable, our results illustrate the difference when using a single target length in TNNP versus an integrated analysis (see position of star on Fig. 4 relative to other data points). Thus, picking "target" species or sizes could cause difficulty in determining a generalized connectivity value, particularly in systems with higher diversity and more varied species. Wiens (2002) suggested that it could be useful to group similar species in order to obtain fewer connectivity values per system. However, recent research on fish passage has shown that taxonomic and physical similarities may not be adequate predictors of barrier sensitivity (McLaughlin et al. 2006). Nonetheless, in many cases, assessing watershed connectivity for a specific target species of management interest may be very useful and appropriate.

Restoration prioritization

Prioritization was done using the approach of systematically simulating the restoration of one culvert at a time and assessing the effect on the DCI results. Connectivity in this case is based on the extent of watershed (in km) that becomes available when a barrier is removed, without any consideration of habitat quality (although incorporation of habitat quality is possible with these methods). This approach has the benefit of examining all possible scenarios of which culvert to restore to assess the net gain in connectivity with each. This facilitates a cost-benefit analysis; if the next-to-optimal culvert is significantly cheaper to restore than the most optimal, then this may be the most pragmatic solution. Alternative approaches have been proposed and include using integer-based programming to optimize decisions (O'Hanley and Tomberlin 2005; Kemp and O'Hanley 2010, also see Kibler et al. 2010 for a description of an experimental approach to assessing restoration effects). If restoration decisions were based on prioritizing for the culvert with the lowest passability, then the barrier-scale results would make it difficult to choose the best culvert for restoration. In this case, 5 culverts are tied for "worst" passability across all scenarios but all culverts can have zero passability under some scenarios (Fig. 3). However, in TNNP, considering the spatial arrangement of barriers within the watershed resulted in a consistent prioritization for restoration (barrier 'al', Table 3) in virtually all scenarios examined. If a barrier in a key location is severe enough, any assessment will conclude the same thing: that the barrier is impassable under all conditions and the watershed connectivity may be heavily influenced by it.

Further work/management advice

While a useful tool, FishXing, was not without issues and limitations. As others have noted (Blank et al. 2005; Poplar-Jeffers et al. 2008; Mangin et al. 2010; R. Gubernick pers. comm.), FishXing uses conservative modelling which does not account for all variables and, as with any model, must be used with caution. Though we were able to improve the results provided by the software with field calibration, it was still difficult to simulate passage for some culverts. Furthermore, there is limited behavioural information available on how fish swim through culverts (e.g., to what extent they swim in the reduced flow of the boundary layers) and whether they exhibit avoidance of these structures; Kemp et al. 2005; Kemp and Williams 2008; Kemp et al. 2008).

An examination of barrier properties across TNNP suggests some modifications to the preliminary screening process, based on physical characteristics of the culverts and the degree to which passability was compromised based on our assessments with FishXing. For the field screening method used for brook trout and salmon in our study area, we recommend altering both the maximum outflow drop height and slope in the evaluation flowchart (Fig. 1). Based on both simulations using FishXing and confirmed with the field data collected on multiple dates at the same site, we observed that outflow drops for partial and non-barriers were significantly lower than for full barriers. Therefore, the maximum outflow drop height could be changed from 30cm to 40cm (for 15cm salmonids) to compensate for the potential fluctuation in drops with discharge. For field assessments, we also recommend that the slope used to automatically designate a barrier as impassable be increased from 1.5 to 4.0%, based on the FishXing results discussed above. Though this is steeper than most culvert assessment guides recommend, the further evaluation of culverts using FishXing would be expected to identify barriers that were missed by the initial field assessment. Finally, we recommend caution when determining if culverts are backwatered as some culverts appeared to be passable at low flows, but were actually barriers at higher discharges. Drop height and slope have been shown to be the limiting factors for juvenile fish in a field experiment (Doehring et al. 2011), so we believe these parameters should be the primary focus.

When considering modifications to culvert structure to enhance restoration, it should be noted that the type of barrier (velocity, depth or jump) varies based on discharge rates. If fish migration/dispersal periods coincide with periods of high or low flow, than culvert modifications should be prioritized to address the main barrier type. For example, at low flow rates, most culverts in TNNP were depth barriers for adult/50cm salmon. Since periods of low stream flow coincide with salmon migration, then modifications should aim to increase water depth within the culvert. Conversely, for brook trout, most barriers at high flow rates (and some barriers for salmon) are velocity barriers, thus modifications should be carried out to reduce water velocity in culverts (for example though the use of flow baffles). These modifications are applicable to the system in Terra Nova National Park; similar modifications to a flowchart based assessment for systems in other parts of the world would have to be based on *in situ* assessments of local condition and species. However, our findings illustrate that coupling field-based assessments with modelling can help to customize the field-based assessments to better assess culvert passability.

Conclusion

Passability has long been acknowledged to be dynamic and specific to species physiology and morphometry and environmental conditions. Our results here illustrate the importance of making decisions on ecological and hydrological criteria when determining barrier passability, including the errors associated with selecting target species and sizes. In our system, static models, while simpler to implement, do not provide as clear a picture as dynamic models. We have shown that inter- and intra-species variation affects passabilities for individual culverts, and hence for estimates of watershed connectivity. Thus, future assessments of stream connectivity should attempt to be as comprehensive as possible and integrate data that captures the inherent variability in both the fish community and the stream properties.

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Figure Captions

Fig. 1 Flowchart for preliminary culvert evaluation based on criteria for 15 cm salmonid, (adapted from Clarkin et al. 2005). The flowchart has been used as a rapid assessment strategy in one-time field visits to culverts to assess whether they are passable, impassable or partially passable barriers.

Fig. 2 The Big Brook watershed of Terra Nova National Park, Newfoundland, Canada. Streams are and waterbodies are shown in dark grey and roads are dashed light grey lines. Anthropogenic barriers are indexed by letters and hexagons. The waterfall (diamond) is a complete natural barrier.

Fig. 3 The mean (solid bar) and range (empty rectangle) of passability values across all simulations of fish length/swim speed and stream flow for barriers in Big Brook. Barrier labels are shown on the x-axis and match those on Figure 2. Passability ranges from 0 (full barrier) to 1 (fully passable) on the y-axis.

Fig. 4 Mean and range of connectivity measured for the potadromous case; DCI_P (top panels) and the diadromous case; DCI_D (bottom panels) for different scenarios of fish swim speed (indicated by groups of 3 points per length class) and stream flow (indicated by error bars). Left hand panels are for brook trout and right hand panels for salmon. Star symbol indicates weighted mean DCI for each case based on length-frequency data for fish sampled from the Big Brook population.

Fig. 5 Comparison of connectivity measured using the DCI for potamodromous (top panels) and diadromous (bottom panels) in catchments in Terra Nova National Park, Newfoundland and Labrador, Canada. DCI values are calculated when passability estimates are obtained via computer modelling with FishXing (left hand panels) versus field evaluations (right hand panels) of culverts based on 15cm brook trout during the migration period.

Fig. 6 Comparison of variability in DCI as a result of using different seasons, species and methods to estimate passability. Figure shows the number of catchments containing culverts (n = 15) in Terra Nova National Park, Newfoundland and Labrador, Canada with very low (0-25), low (26-50), moderate (51-75) and high (76-100) connectivity measured using the DCI in the **a.** potamodromous case and **b.** diadromous case. DCI values are based on calculating passability with FishXing during fish migration period for brook trout and salmon, and with FishXing across the entire year (salmon only) as well as based on a rapid assessment of passability using only the simplified field-based method.