

1 Barriers to fish passage and barriers to fish passage assessments: the
2 impact of assessment methods and assumptions on barrier identification and
3 quantification of watershed connectivity
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14

15 Abstract

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

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

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38 Introduction

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

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

64 1989). More recently, concepts from landscape ecology, such as fragmentation and patch dynamics, have
65 been applied to aquatic systems to investigate the impacts of barriers on entire stream networks and
66 catchments (Dunham et al. 1997; Jones et al. 2000; Park et al. 2008; Cote et al. 2009; Fullerton et al.
67 2010). This broad view is crucial to understanding and mitigating the ecological consequences of stream
68 fragmentation, as the effects of even a single barrier may have large impacts on entire stream networks,
69 and multiple barriers may lead to cumulative impacts (Kemp and O'Hanley 2010; Rolls 2011; however,
70 see Padgham and Webb 2010 for a model which suggests that multiple impacts are simply equal to the
71 sum of the parts).

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

80 Cote et al. (2009) suggested passability could be quantified in several different ways and noted
81 that decisions on how to define and measure passability would be important to interpret and evaluate
82 watershed connectivity. Interpretations that capture the variability in fish physiology within and among
83 species (e.g., assigning a passability of 0.5 to a barrier that is passable to 50% of the target population)
84 may be insensitive to temporal environmental variation, while definitions that account for temporal
85 variation of physical characteristics (e.g., the barrier is passable 50% of the time to fish with a defined
86 physiological capacity) may not account for variation amongst individual fish. Furthermore, once defined,
87 subsequent passability values will reflect decisions regarding the time period of the assessment (i.e.,
88 stream discharge), the species being modelled and the accuracy of the swim speeds estimates.
89 Unfortunately, the sensitivity of barrier passability estimates, and subsequent watershed connectivity

90 estimates, to these decisions is unknown. If these measures are highly sensitive to variation in fish
91 physiology or environmental conditions at barriers, then the utility and general applicability of watershed
92 connectivity estimates will be reduced, and managers wishing to use them will have to very careful about
93 how data are collected.

94 We used river/stream systems (hereafter “watersheds”) of Terra Nova National Park (TNNP),
95 Newfoundland and Labrador, Canada, (which ranged in area from 0.5 km² to 36 km²) as a case study to
96 examine the sensitivity of passability estimates and resulting river connectivity (watershed and park-
97 wide)to four aspects of barrier passability: i) the fish species of interest, ii) barrier assessment
98 methodology, iii) inter- and intra-annual variability in stream flow, and iv) assumptions about fish
99 swimming capacity. The results of these simulation scenarios are also evaluated in terms of their effects
100 on restoration priorities in the tested watershed. The simulations are interpreted with respect to the effect
101 on individual barrier assessments, and on the watershed connectivity using the DCI. Finally, we
102 demonstrate a means to include variation of fish physiological capacity and environmental conditions to
103 calculate an integrated DCI score.

104

105 Methods

106 Calculating the DCI

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

115 (2009) and requires dividing the watershed into segments, where segments are separated by barriers. The
116 formula is:

$$117 \quad DCI_P = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i}{L} \frac{l_j}{L}, \quad (1)$$

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

$$121 \quad DCI_D = \sum_{i=1}^n \frac{l_i}{L} \left(\prod_{m=1}^M p_m^u p_m^d \right) * 100, \quad (2)$$

122 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}
123 barrier ($m=1 \dots M$) between the river mouth and section i , and L is the total stream length. Maximum
124 DCI value is 100, which indicates a fully connected watershed, with connectivity decreasing as DCI
125 values decrease from 100.

126

127 Fish species of interest

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

135

136 Barrier assessment methodology – rapid assessment vs. modelling

137 We used two methods to evaluate passability of all culverts in TNNP ($n = 43$); rapid field assessments
138 (which examine culvert passabilities during a single visit), and more detailed field data coupled with

139 modelling software (that integrates variation in stream flow in the evaluation of culvert passabilities).
140 Field assessments consisted of a screening process for barriers, based on a set of criteria (Fig. 1) adapted
141 from previous culvert inventories (Clarkin et al. 2005). These criteria included culvert slope, outflow drop
142 height and presence of an outflow pool. FishXing, a widely used freeware, creates hydrological models of
143 culverts based on data collected in the field (culvert shape, length (m), material, slope, installation type)
144 together with flow equations and fish movement parameters. While FishXing can model culverts using
145 minimal field data, more detailed data can be included such as the cross-section topography of the
146 tailwater control area and discharge rates for the study stream. FishXing also identifies which of three
147 mechanisms impede the passage of fish: insufficient water depth in the culvert (depth barrier), excessive
148 height for fish to jump into the culvert (height barrier), and excessive water flow for fish passage (velocity
149 barrier).

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

159 We encountered some challenges when assessing culverts using FishXing. Specifically, the
160 default values provided by the software for the culvert entrance loss coefficient (K_e) and the culvert and
161 tailwater control roughness coefficients (n) – parameters used to model water flow in open channels
162 (Brater and King 1976) – did not provide accurate approximations of field conditions. Thus, at a given
163 discharge rate, modelled values of culvert water depth and velocity were often very different from the
164 actual values measured in the field at that discharge rate – leading us to suspect that the modelled values

165 provided by FishXing at other discharge rates were also inaccurate. This issue has been observed in other
166 evaluations using FishXing (Blank et al. 2005; Poplar-Jeffers et al. 2008) and likely occurs because the
167 software uses K_e values which are derived from culverts under full water and roughness coefficients
168 which are often derived from large streams and generalized to all streams without considering details such
169 as the presence of debris, inconsistencies in substrate across a small area or rapid changes in slope or
170 wetted width (R. Gubernick, FishXing design team, pers. comm.; see also Mangin et al. 2010). To more
171 accurately model the study sites, we obtained new K_e values for partially full culverts from Straub and
172 Morris (1950ab) and back-calculated new roughness coefficient values (n) using field data from original
173 culvert surveys and from the three culverts which were revisited for ground-truthing. Though the culvert
174 parameters provided by FishXing did not always match field values exactly, our modifications to the n
175 and K_e values did improve the precision of all culvert models. Passability estimates obtained from rapid
176 assessments (using first visit data only) and more detailed field surveys plus FishXing modelling were
177 used to calculate DCI_P and DCI_D for all catchments in Terra Nova National Park.

178

179 Temporal variability in stream flow

180 We investigated the effect of intra-annual stream flow variability for all park watersheds ($n = 15$). We
181 calculated the DCI_P and DCI_D for two time periods: when fish are migrating, and the whole year (Table
182 1), using daily discharge data averaged over a twenty year period from the Southwest Brook gauging
183 ($48^{\circ}36'27''$ N, $53^{\circ}58'44''$ W station 02YS003) station located in the national park. We investigated the
184 effect of inter-annual variability in water flow on the DCI_P and DCI_D within a test watershed, Big Brook
185 (Fig. 2). To investigate inter-annual variability, we calculated the DCI_P and DCI_D for twenty different
186 years using daily discharge data (Table 1).

187 For each analysis, we scaled gauging-station hydrographs for each barrier by calculating the ratio
188 of the area draining into the stream gauge location to that of the area draining into the barrier. This
189 assumes that discharge rate is proportional to catchment size. FishXing determines whether a barrier is

190 passable at a range of flow values between the minimum and maximum provided. Using these results, we
191 determined passability as the proportion of days the flow would allow a fish of the given size to pass.

192

193 Variable fish swim speed

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

204

205 Calculating a population-integrated watershed connectivity score.

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

208
$$\text{Weighted mean DCI} = \sum_l \text{DCI}_l \frac{n_l}{N} \quad (3)$$

209 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.

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

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

224

225 Identifying priority culverts for restoration of watershed connectivity

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

233

234 Results

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

238 Barrier passability

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

241 culverts (ak, an, u, y, and z) impervious to any change in methodology and definition and consistently
242 being completely impassable, and 4 culverts (22%) varying between a passability of 0 and 1 (ao, ag, aj,
243 and w). For these barriers, the range of passabilities was much more likely to include a full barrier (0)
244 than complete passability (1). We performed a simple analysis of variance to decompose the total
245 variance in passability, as represented by sums of squares, into contributions from each factor. Fish length
246 explained the majority of the variance, once the barrier effect was removed (sum of squares (SS) =
247 236.5), followed by variation in swimming speed (SS = 8.6), hydrological year (SS = 7.7), species
248 (SS=3.1) and finally period with the year used for the analysis (SS = 1.1).

249 Single watershed scale

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

263

264 National Park scale

265 Across all watersheds within Terra Nova National Park, DCI values varied depending on whether the
266 rapid field-based assessment or field assessment plus modelling in FishXing was used to estimate barrier

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

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

281

282 Barrier prioritization

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

290

291

292 Discussion

293 The preservation and restoration of aquatic connectivity has been recognized as a major conservation goal
294 in stream systems (Pringle 2003); and new methods have been developed to measure the alteration of
295 connectivity in dendritic systems. Common to all methods is the difficulty in assessing barrier passability
296 – the dynamic component of connectivity. Our results demonstrate how passability varies by species, size
297 and hydrological conditions (see also Poplar-Jeffers et al. 2008; Meizler et al. 2009; Kemp and O’Hanley
298 2010; Rolls 2011) and managers will often be forced to select a target demographic and/or target
299 conditions when evaluating barrier passability. In this study we showed the implications of making such
300 decisions (e.g., differences associated with picking a particular method, or a particular target species/size)
301 as well as the error that may be related to parameter estimates (e.g., swim speed) on passability and
302 connectivity at the watershed scale.

303 A useful result from this work is that watershed scale assessments of connectivity are less
304 sensitive to variations in passability definition or assessment method than estimates of passability for
305 individual barriers. For the DCI results, the choice of fish length had the largest impact on the
306 connectivity score. The effect of fish length on watershed connectivity yielded an unexpected hump-
307 shaped pattern, with smaller and larger fish experiencing lower values. However, this is readily explained
308 by the specific passage requirements of differing size classes. Smaller fish have lower swim speeds and
309 experience velocity barriers during high flow periods, whereas larger fish are limited by the depth of
310 water in the culvert during low flow periods. This is illustrated by the effect of swim speed assumptions
311 on the DCI for small fish, and the insensitivity of the DCI to swim speed assumptions for large fish (Fig.
312 4).

313 We found that watershed connectivity results can vary with barrier assessment methods – making
314 the choice of method a crucial and influential step in connectivity assessment. For most culverts, using a
315 simple set of criteria to do barrier field assessments produced passability values that were more
316 conservative than those calculated by computer modelling (FishXing) for fish of the same size and
317 species, which in turn led to reduced connectivity values (Figs. 3 and 4). It remains likely that the simple
318 field assessments were too conservative when compared to those provided by FishXing. Since the rapid

319 field-based assessments have been developed as general installation/assessment guidelines (Fig. 1; see
320 also Clarkin et al. 2005), they do not account for the variable nature of passability. Hence they are
321 necessarily precautionary and less accurate. Though the simplified field assessments did give very
322 different estimates of passability in this study, with modified criteria and further evaluations of partial
323 barriers using FishXing, they could be used more efficiently as tools to save time during culvert surveys
324 by ‘screening’ obvious barriers – a practice which has been implemented in other studies and surveys
325 (e.g., Clarkin et al. 2005). The modelling approach has an advantage in that it can account for variability
326 in passability through time and for different species. Unfortunately, specific biological data (i.e., fish
327 telemetry data) were not available to directly assess the accuracy of culvert passability estimates in this
328 study. Such information would enable researchers to assess key assumptions in fish passage but remains a
329 common data gap in passability assessments.

330 In this study, the assessment period (i.e., full year vs. migration period) did not have a substantial
331 impact on watershed connectivity due to the fact that stream hydrology during the migration period for
332 the two species assessed was representative of the entire year (i.e., both including floods and low water
333 events). Thus, in similar systems to TNNP, watershed connectivity estimates based on a shorter
334 hydrological time period might be reliable. These results are specific to the Terra Nova situation, but are
335 likely relevant to watersheds in elsewhere. For example, in an examination of fish community
336 assemblages above and below low-head dams in Kansas, Gillette et al. (2005) found seasonal effects.
337 Similarly, Rolls (2011) examined watersheds with and without barriers in Australia, and found a
338 significant effect of migratory period on barrier passage for some species. Both of these studies (Gillette
339 et al. 2005; Rolls 2011) did not consider overall watershed connectivity, but at the barrier scale the
340 patterns observed were similar to ours in Terra Nova, suggesting that some of our overall conclusions and
341 recommendations on assessment methods may be worth considering in other systems. The relatively
342 minimal impact of temporal scale observed here may not be the case in systems where species have more
343 restricted discharge-dependent migration periods (e.g., Pacific salmon and see Rolls 2011 for an example
344 of variation in connectivity depending on migration strategy), or in seasonally arid landscapes where

345 streambeds go dry for months at a time (Eby et al. 2003). Nonetheless, our assessment clearly
346 demonstrates that field assessments that evaluate barriers based on conditions for only a single day (the
347 rapid assessment method, Fig. 1) gives very different values for connectivity than those that use more
348 dynamic assessment methods to evaluate passability. Thus, barrier assessments need to be considered in
349 the context of ecological conditions at a particular study site, and researchers should choose appropriate
350 assessment methods based on the local species and hydrology.

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

364 We demonstrate a means to calculate an integrated stream connectivity value that accounts for
365 variation in hydrology, fish size, and species variation. As such, it presents a useful approach for
366 ecosystem based management of aquatic systems. Though the data required to do this are considerable,
367 our results illustrate the difference when using a single target length in TNNP versus an integrated
368 analysis (see position of star on Fig. 4 relative to other data points). Thus, picking “target” species or sizes
369 could cause difficulty in determining a generalized connectivity value, particularly in systems with higher
370 diversity and more varied species. Wiens (2002) suggested that it could be useful to group similar species

371 in order to obtain fewer connectivity values per system. However, recent research on fish passage has
372 shown that taxonomic and physical similarities may not be adequate predictors of barrier sensitivity
373 (McLaughlin et al. 2006). Nonetheless, in many cases, assessing watershed connectivity for a specific
374 target species of management interest may be very useful and appropriate.

375

376 Restoration prioritization

377 Prioritization was done using the approach of systematically simulating the restoration of one culvert at a
378 time and assessing the effect on the DCI results. Connectivity in this case is based on the extent of
379 watershed (in km) that becomes available when a barrier is removed, without any consideration of habitat
380 quality (although incorporation of habitat quality is possible with these methods). This approach has the
381 benefit of examining all possible scenarios of which culvert to restore to assess the net gain in
382 connectivity with each. This facilitates a cost-benefit analysis; if the next-to-optimal culvert is
383 significantly cheaper to restore than the most optimal, then this may be the most pragmatic solution.

384 Alternative approaches have been proposed and include using integer-based programming to optimize
385 decisions (O'Hanley and Tomberlin 2005; Kemp and O'Hanley 2010, also see Kibler et al. 2010 for a
386 description of an experimental approach to assessing restoration effects). If restoration decisions were
387 based on prioritizing for the culvert with the lowest passability, then the barrier-scale results would make
388 it difficult to choose the best culvert for restoration. In this case, 5 culverts are tied for “worst” passability
389 across all scenarios but all culverts can have zero passability under some scenarios (Fig. 3). However, in
390 TNNP, considering the spatial arrangement of barriers within the watershed resulted in a consistent
391 prioritization for restoration (barrier ‘al’, Table 3) in virtually all scenarios examined. If a barrier in a key
392 location is severe enough, any assessment will conclude the same thing: that the barrier is impassable
393 under all conditions and the watershed connectivity may be heavily influenced by it.

394

395 Further work/management advice

396 While a useful tool, FishXing, was not without issues and limitations. As others have noted (Blank et al.
397 2005; Poplar-Jeffers et al. 2008; Mangin et al. 2010; R. Gubernick pers. comm.), FishXing uses
398 conservative modelling which does not account for all variables and, as with any model, must be used
399 with caution. Though we were able to improve the results provided by the software with field calibration,
400 it was still difficult to simulate passage for some culverts. Furthermore, there is limited behavioural
401 information available on how fish swim through culverts (e.g., to what extent they swim in the reduced
402 flow of the boundary layers) and whether they exhibit avoidance of these structures; Kemp et al. 2005;
403 Kemp and Williams 2008; Kemp et al. 2008).

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

420 When considering modifications to culvert structure to enhance restoration, it should be noted
421 that the type of barrier (velocity, depth or jump) varies based on discharge rates. If fish

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

433

434 Conclusion

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

444

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451

452

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- 558

559 Figure Captions

560

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

564

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

568

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

572

573 Fig. 4 Mean and range of connectivity measured for the potadromous case; DCI_P (top panels) and the
574 diadromous case; DCI_D (bottom panels) for different scenarios of fish swim speed (indicated by groups of
575 3 points per length class) and stream flow (indicated by error bars). Left hand panels are for brook trout
576 and right hand panels for salmon. Star symbol indicates weighted mean DCI for each case based on
577 length-frequency data for fish sampled from the Big Brook population.

578

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

584

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

592

593

594