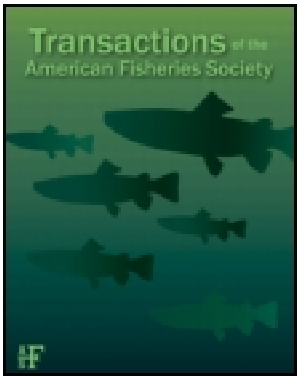

Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Evaluating the Barrier Assessment Technique Derived from FishXing Software and the Upstream Movement of Brook Trout through Road Culverts

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Published online: 09 Jan 2014.

Transactions of the American Fisheries Society 143:39–48, 2014

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2013.825641

ARTICLE

Evaluating the Barrier Assessment Technique Derived from FishXing Software and the Upstream Movement of Brook Trout through Road Culverts

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Abstract
Anthropogenic barriers to fish passage, such as culverts and dams, are major factors impeding the persistence and recovery of aquatic species. Considerable work has focused on mitigating these impacts; however, activities associated with measuring and restoring connectivity of aquatic ecosystems often face challenges in determining the passability of barriers by aquatic species. Hydrological modeling software that incorporates biological aspects of a focal species is often used as a relatively inexpensive method for assessing barrier passability for restoration decisions. However, the biological relevance of these approaches remains to be rigorously tested. We assessed passage rates of PIT-tagged Brook Trout *Salvelinus fontinalis* through four road culverts and adjacent reference sites (unaltered areas of the streams) on the island of Newfoundland to determine whether upstream passage through road culverts was more restrictive than unaltered reference areas of the stream. Next, we examined the usefulness of barrier passability predictions derived from FishXing software by comparing them with in situ movement data for this species. Brook Trout passage for three of the four reference sites had a significantly higher range of passable stream flows compared with that for culverts, indicating the presence of velocity barriers in culverts. However, FishXing predictions of suitable fish passage discharges were conservative, and tagged fish successfully navigated partial barriers that were at least 2–3 times the upper limits of stream flow predicted to allow successful passage. The results of our study show a clear need for an improved understanding of fish movement through these structures so that barrier assessment techniques can be refined. The implications of not doing so may lead to restoration actions that result in limited biological benefit.

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Received February 6, 2013; accepted July 2, 2013

The reestablishment of natural processes is a critical step in restoring and maintaining diverse biological communities (Roni et al. 2002; Palmer et al. 2005). Aquatic connectivity is increasingly recognized as an important characteristic of aquatic ecosystems and has gained considerable attention in recent years (Fullerton et al. 2010; Olden et al. 2010). Unlike terrestrial landscapes that may have multiple pathways between habitat patches, riverscapes have a single movement corridor among habitat patches for obligate aquatic species. Consequently, the obstruction of these pathways by culverts, dams, and other barriers can alter community assemblages, impede the completion of life history stages, and limit the dispersal of aquatic species within metacommunities (Fagan 2002; Fahrig 2003; Schick and Lindley 2007; Fullerton et al. 2010; Perkin and Gido 2012). Recent advancements in connectivity models have developed riverscape approaches to measure the fragmentation of dendritic ecosystems (Cote et al. 2009; Padgham and Webb 2010; O'Hanley 2011) since terrestrial metrics of fragmentation (e.g., Kindlmann and Burel 2008) are of limited utility in riverine systems.

Barrier location and passability are two components routinely used in assessing the degree of fragmentation in watersheds. The first component helps determine the maximum amount of total habitat that could be gained by restoring or removing a single barrier (Cote et al. 2009; O'Hanley 2011). For the second component, determining how a focal species navigates past a barrier can indicate the degree to which an obstacle impedes stream movement for an aquatic species. This is often difficult to resolve because of the complex and dynamic nature of passability (Cote et al. 2009; Padgham and Webb 2010; Bourne et al. 2011). Furthermore, accurate measures of connectivity are sensitive to barrier assessment methods (Bourne et al. 2011), and thus it is critical to know whether barrier assessment methods are representative of fish movements.

Various methods exist to analyze the passability of barriers (Kemp and O'Hanley 2010). Common methods used to calculate culvert passability include flow charts (Taylor and Love 2003; Clarkin et al. 2005; Coffman 2005) and computer simulations (Hotchkiss et al. 2008). These barrier assessment methods are particularly appealing because of their simplicity and affordability in gathering and processing the required information. However, hydrological data needed to assess barriers are often missing or the data can be difficult to obtain (Kemp and O'Hanley 2010), and only a few studies have examined the accuracy of barrier assessment methods using in situ field experiments (Coffman 2005; Burford et al. 2009).

The software program FishXing is one commonly used method that was originally designed to assist in the evaluation and design of culverts to promote upstream fish passage (Furniss et al. 2006). By incorporating species-specific metrics (e.g., species length and swimming capabilities) and hydrologic properties of the culvert (e.g., culvert slope, length, and roughness), FishXing is able to estimate the stream flow that a particular individual fish is able to pass. In theory, this should lead to a more accurate passability estimates than simpler, rule-of-thumb type assessments. FishXing has been used extensively to model culverts for fish passage (Flanders and Cariello 2000; Taylor and Love 2003; Standage and Gagen 2007; Davis and Davis 2008; Hendrickson et al. 2008). However, remarkably few studies have analyzed the effectiveness of FishXing as a barrier assessment tool (Burford et al. 2009), despite the widespread perception that FishXing produces conservative outputs (Poplar-Jeffers et al. 2009; Bourne et al. 2011).

Poplar-Jeffers et al. (2009) found that outputs from FishXing appear to categorize most barriers as completely impassible, when in reality some form of intermediate passability may be more appropriate (Anderson et al. 2012). Potentially, default swim speeds in FishXing are underestimated since they are calculated in laboratory settings through forced swim performance methods (Castro-Santos 2006; Peake and Farrell 2006). Furthermore, culvert hydrological properties, used for FishXing, are modeled after maximum stream flow characteristics within the culvert (Burford et al. 2009; Bourne et al. 2011), which have been shown to overestimate the severity of a barrier (Lang et al. 2004). In reality, culverts rarely exhibit the flows that are predicted by FishXing default parameters. Several studies have focused on the accurate calculation of hydrological properties in hopes of improving predictions of fish movement. For instance, Burford et al. (2009), following the approach of Karl (2005), adjusted the roughness coefficient but found only modest changes in their error rate between observed and actual flow depths. Moreover, Bourne et al. (2011) did extensive culvert modeling using methods from Straub and Morris (1950a, 1950b) to adjust the roughness coefficients of barriers. Although they could not always predict water flow through culverts, the use of the more precise entrance loss and roughness coefficients improved the accuracy of the stream flow predictions (Bourne et al. 2011). However, even with the increased precision of the hydrological modeling by Bourne et al. (2011) it is still unknown whether the stream flows predicted by FishXing to be passable are representative of what fish can navigate under natural conditions.

We monitored the upstream passage of Brook Trout *Salvelinus fontinalis* across four culverts over 3 years in the Terra Nova National Park area of the island of Newfoundland using PIT tags. The use of PIT tags to study fish movement allows an opportunity to analyze, under natural flow conditions, whether culverts alter fish movement and, if so, test whether the predictions of a commonly used barrier assessment technique are accurate. We first evaluated whether there were differences between upstream fish passage in culverts compared with reference sites (unaltered areas of the streams). If culverts influence the movement of Brook Trout we expected to see a wider range of stream flows that Brook Trout are able to pass in reference sites when compared with culverts. We also determined the accuracy of FishXing estimates with the use of in situ fish movements. Verifying the accuracy of FishXing with in situ Brook Trout movements will provide direct empirical support for the efficacy of FishXing for use in barrier assessments.

METHODS

Study area.—The study was conducted in the boreal stream systems of the Terra Nova National Park area (TNNP) of Newfoundland. This is a low productivity system with low species richness and is dominated by salmonids (Cote 2007). Native Brook Trout exhibit both anadromous and diadromous life histories in the study area.

Field data collection.—We used a portable Smith-Root model 12-B electrofisher to capture fish for tagging at the four study sites (∼150 m upstream and downstream from the culverts of interest). Sampling intervals occurred yearly in May and June from 2009 to 2011 after the installation of fish tracking arrays. We attempted to tag sea-run Brook Trout in some systems but these were not well represented in our study area. As a result we focused on juveniles. All fish were measured (FL, mm) and weighed (wet mass, g). Fish greater than 95 mm FL were implanted with PIT tags (model RI-TRP-WRHP, Texas Instruments; 23.1 mm in length and 3.9 mm in diameter; mass in air, 0.6 g; tag-to-fish mass ratio, 0.9–5.7%) through a small ventral incision made anterior to the pelvic girdle. One suture (4-0 SoftSild^{TM}) was used to close the incision and the fish were then placed within the capture area in holding pens having flow-through water to recover for 24 h before release.

Fish passage was monitored using detection arrays (Oregon RFID, www.oregonrfid.biz) placed near culverts and reference sites from May to November during the sampling years. At culvert locations, arrays were established across the stream, and two antennae were deployed upstream from the culvert (one at the culvert entrance and one 2–3 m upstream) and two were deployed downstream (one at the culvert outlet and one 2–3 m downstream; see Figure 1). The order of detection on the antennae allowed the direction of movement to be determined and the success or failure of an upstream passage attempt. We considered a pass attempt successful if a fish registered at one of the downstream antennae followed by a detection at either upstream antennae. Conversely, it was considered a failed attempt if the individual moved upstream past the two downstream antennae, did not register at either of the upstream antennae before being recorded a second time at the farthest downstream antennae. Reference sites were established with detection arrays in unaltered adjacent areas of the stream approximately 50 m from the culvert and in a manner that mimicked culvert orientation. The reference sites for culverts A, B, and C were located downstream from the culvert while the reference site for culvert D was located upstream because culvert D was located close to the ocean.

Discharge was derived from water-level loggers (Solinst Levellogger Gold) deployed in each study stream to record hourly water temperature and depth during the study period. Each site was visited across a broad range of discharges to establish a rating curve with which discharge could be modeled on an hourly basis based on water depth (Riggs 1985:131–143). To determine the temporal availability of suitable stream flow we calculated the cumulative frequency of stream discharge for each culvert.

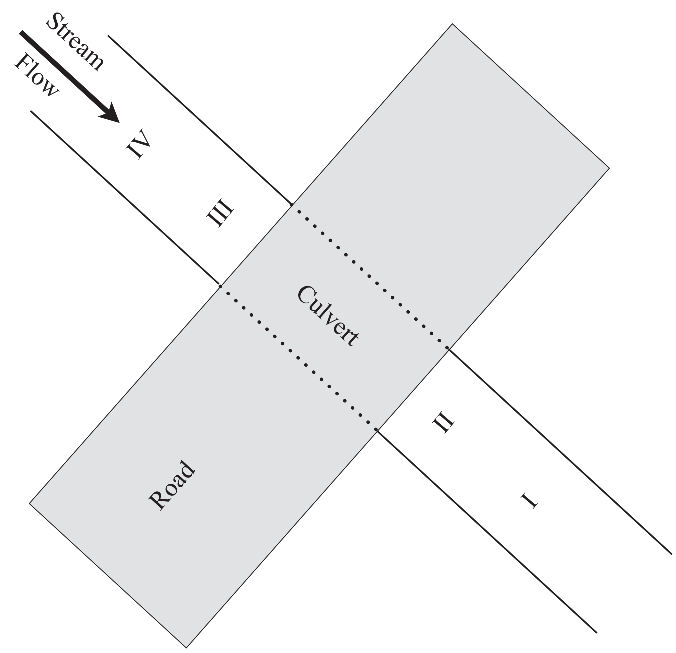

FIGURE 1. Antennae setup for all culvert sites. Antennae II and III are on the inlet and outlet of the culvert respectively. Antennae I and IV are located at the outlet and inlet pools approximately 2–3 m from the culvert, respectively.

We chose three partial barriers (culverts A, B, and C) based on a previous assessment in conjunction with a cost–benefit analysis of all barriers in TNNP that indicated improving passage at these locations would provide the most ecological benefit. Culvert D was an opportunistic addition to the study after Hurricane Igor washed it out in 2010. We used culvert measurements collected from various sources (Table 1). Detailed characteristics of culverts A, B, and C were acquired in Bourne (2013) and culvert D was resurveyed after it was replaced.

Analysis.—We used FishXing to predict the stream flows for each culvert that 50–250-mm Brook Trout were able to pass. We used sustained and burst speeds for Brook Trout that had been defined by Peake et al. (1997; Table 2). Minimum depths were based on two-fifths of the body length. This is less than earlier studies that used minimum depths between 9 and 24 cm (Bates et al. 2003; Burford et al. 2009; Bourne 2013). Previous work in TNNP used a value of three-quarters of a body length (Bourne et al. 2011), which was considered conservative given prior field observations of fish movements within the study area. We therefore selected a lower value of two-fifths of the body length. Lastly, jumping height was based on two times the length of the Brook Trout (Bourne 2013). Using methods outlined by Bourne et al. (2011), we calculated K_e values from Straub and Morris (1950a, 1950b) and back-calculated the Manning's roughness coefficient (n) using data from the culvert surveys. Finally, we

TABLE 1. FishXing hydrologic input parameters used for each culvert in TNNP (see Figure 1). Culvert roughness was back-calculated using the entrance loss coefficients of Straub and Morris (1950a, 1950b). Elevations are above sea level. CMP = corrugated metal pipe.

Measurement	Culvert A	Culvert B[a]	Culvert C	Culvert D[a]
Shape	Circular	Circular	Circular	Circular
Diameter (cm)	87	75	78	240
Material	CMP	CMP	Concrete	CMP
Entrance type	Projecting	Projecting	Projecting	Projecting
Entrance loss (K_e)	0.7	0.9	0.9	0.9
Culvert roughness (n)	0.01	0.024	0.16	0.015
Length (m)	14	12	6.2	36
Inlet bottom elevation (m)	147.32	67.18	98.6	10.10
Slope (%)	2.29	1.50	1.77	1.83
Outlet bottom elevation (m)	147	67	98.6	9.44
Outlet pool surface elevation (m)	147.07	67.22	99.05	9.64
Velocity reduction factors inlet/barrel/outlet (unitless)	0.8/0.6/0.8	0.8/0.6/0.8	0.8/0.6/0.8	0.8/0.6/0.8
Channel bottom slope (%)	3.4	4.6	3.1	2.1
Outlet pool bottom elevation (m)	146.75	67.146	98.66	9.3
Tailwater roughness (unitless)	0.2	0.05	0.46	0.04
Tailwater cross section station (m) (elevation, m)	0.00 (146.95)	0.00 (67.57)	1.0 (98.96)	1.50 (10.33)
	1.70 (146.82)	0.45 (67.53)	2.0 (98.73)	1.95 (9.83)
	1.90 (146.78)	1.05 (67.15)	3.0 (98.77)	3.80 (9.82)
	1.95 (146.82)	1.40 (67.22)	4.0 (98.80)	5.25 (9.69)
	2.10 (146.75)	1.80 (67.20)	5.0 (98.86)	6.00 (9.45)
	2.40 (146.75)	2.15 (67.20)	6.0 (98.73)	6.30 (9.40)
	2.70 (146.80)	2.45 (67.23)	7.0 (98.78)	6.60 (9.30)
	2.80 (146.77)	2.70 (67.29)	8.0 (98.77)	6.90 (9.30)
	3.05 (146.79)	3.66 (67.75)	9.0 (98.83)	7.20 (9.30)
	3.50 (146.77)	4.45 (67.69)	10.0 (99.0)	7.50 (9.36)
	4.20 (147.02)			7.80 (9.43)
				8.30 (9.64)
				9.10 (9.75)
				9.90 (9.98)
				10.70 (9.92)
				12.00 (10.33)

[a]Culverts A and D had secondary overflow culverts that were not modeled in FishXing.

TABLE 2. The biological parameters for Brook Trout used for FishXing. Burst swim speed (BS, maintaining swim speeds for 20 s) and sustained swim speed (SS, maintaining speeds for 600 s) based on swim speed models by Peake et al. (1997). Minimum depth was calculated as two-fifths of the fish length, while jump height was calculated as two times the fish length.

Fish length (FL; mm)	BS (m/s)	SS (m/s)	Minimum depth (m)	Jump height (m)
50	0.374	0.266	0.02	0.1
100	0.599	0.491	0.04	0.2
150	0.824	0.716	0.06	0.3
200	1.049	0.941	0.08	0.4
250	1.274	1.166	0.1	0.5

modeled tailwater depth using the channel cross-section method outlined by the FishXing user manual (Furniss et al. 2006). For a given range of water flow values, FishXing predicts the range at which a fish will experience (1) passable flows, (2) a depth barrier (insufficient water depth for fish to navigate), (3) a leap barrier (perched culvert elevation too high), or (4) a velocity barrier (water velocity is too great for an individual to pass).

Fish movements in unaltered systems are temporally variable. For example, it may be expected that fish movement rates would be affected by discharge or seasonal life history demands, or both (Gowan and Fausch 1996; Klemetsen et al. 2003). To isolate the effects of culverts on fish movement, reference sites were monitored to compare fish movement in relation to stream discharge in the absence of anthropogenic barriers. We compared the range of discharges associated with successful passage across culverts and reference sites. To limit the influence of outliers, passage range was defined as the 25th percentile minus 1.5 times the interquartile range (IQR) and the 75th percentile plus 1.5 times the IQR. A permutation test was used to determine significance. Specifically, we randomly reassigned the stream discharges associated with passage events to either reference or culvert locations and recalculated the range for the permuted reference and culverts sites (10,000 permutations). The distribution of permuted values was compared with the observed value to evaluate whether there were significant differences in the discharge range where Brook Trout passability occurred ($\alpha = 0.05$).

We also tested to see whether observed fish movement was consistent with predicted movement as calculated with FishXing, by using a generalized linear mixed effects model (GLMM) with a binomial distribution (Bates et al. 2011; R Development Core Team 2012) as follows:

$$\text{Event}_{ijk} = \text{intercept} + \text{individual}_i + \text{site}_k + \text{predicted}_{ijk},$$

where Event_{ijk} was binary (successful passage–failed passage) for individual i at site k. We included individual_i and site_k as random effects to account for variation associated with repeated observations at the same levels of these variables. The final term, predicted_{ijk} variable, was also a binary event (successful passage–failed passage) that represented the FishXing prediction, given the associated culvert and flow parameters. To test the significance of the fixed effect, we used a likelihood ratio test ($\alpha = 0.05$). All statistical analyses were carried out with the program R (version 2.15.2; R Development Core Team 2012).

RESULTS

We captured and tagged 462 Brook Trout across the four culverts in the study. Seventy of these trout were later observed in the culvert and reference arrays, which generated a total of 415 upstream passage attempts in culverts (69% success rate) and 1,123 passage attempts at reference sites (56% success rate). Furthermore, 26 individuals of those 70 individuals were observed in both reference and culvert sites. Brook Trout that successfully moved through the culvert and reference sites did not differ significantly in size compared with the population of Brook Trout caught and tagged ($\chi^2 = 0.9576$, df $= 1$, $P = 0.33$). Moreover, lengths of successful Brook Trout migrants did not significantly differ ($\chi^2 = 0.1312$, df $= 1$, $P = 0.72$) between culvert and reference sites. Timing of the passage events occurred throughout the day with peaks in the early morning and afternoon. Three of the four culverts were predicted by FishXing to have passable stream flows (Figure 2, grey zones). Only culvert D was predicted to be an impassable barrier by FishXing. Predicted passable stream flows increased with increases in Brook Trout size (Figure 2, grey zones). Stream flows that were considered barriers were classified by FishXing as either depth or velocity barriers, and depth barriers were observed during low flows and velocity barriers were observed during high flow periods. No jump barriers were observed across the four culverts in this study, regardless of stream flows.

By comparing the range of passable flows between reference sites and stream culverts we determined there was a decreased range of passable flows through culverts. Permutation tests showed that culverts A, B, and C had a significantly smaller range of passable flows compared with their respective reference stream sections (Figure 3). However, culvert D had a significantly higher range of passable flows compared with its reference stream site (Figure 3). The decreased range of passable flows in culverts A, B, and C support the presence of a velocity barrier. Failed attempts were more frequent at lower flows but often corresponded to at least one successful passage at similar flows (Figure 2).

The prediction from FishXing regarding whether the fish would pass was not a significant explanatory variable in observed passage events. We were unable to accurately predict fish passage with FishXing across the four culverts ($\chi^2 = 0.9192$, df $= 415$, $P = 0.338$; Figure 2). In each culvert, with the exception of culvert A, fish were able to pass stream discharges that exceeded two or three times the upper discharge threshold predicted using FishXing. We also observed fish passage at flows that were considered depth barriers to Brook Trout movement (Figure 2A). To identify the minimum water depth and maximum water velocity that Brook Trout successfully passed, we used FishXing to calculate hydraulic characteristics at observed flows. Brook Trout were recorded successfully passing estimated water depths as low as 3 cm (135-mm Brook Trout in culvert A at discharge of 0.009 m^3/s) and a maximum water velocity of 1.56 m/s (135-mm Brook Trout in culvert D at 0.628 m^3/s), which were respectively predicted as depth and velocity barriers to Brook Trout movement.

DISCUSSION

The frequency of fish movement is temporally variable and fluctuates according to season, environmental factors, and life history stages (Riley et al. 1992; Gowan and Fausch 1996; Klemetsen et al. 2003). It is therefore important to assess fish passage through barriers within the context of when fish are moving under natural conditions. The use of reference sites allowed us to isolate the effects of culverts from other confounding influences. Comparison of movements of PIT-tagged Brook Trout in reference sites and culverts indicated that culverts impair fish passage. Because stream discharge was the same in paired reference and culvert sites, disparities in fish movement indicated that barriers existed in culverts due to low water depth or increased velocities (Cote et al. 2005). This supports previous studies that found barriers impaired the movement of Brook Trout through culverts when fish movement was compared with reference sites (Belford and Gould 1989; Thompson and Rahel

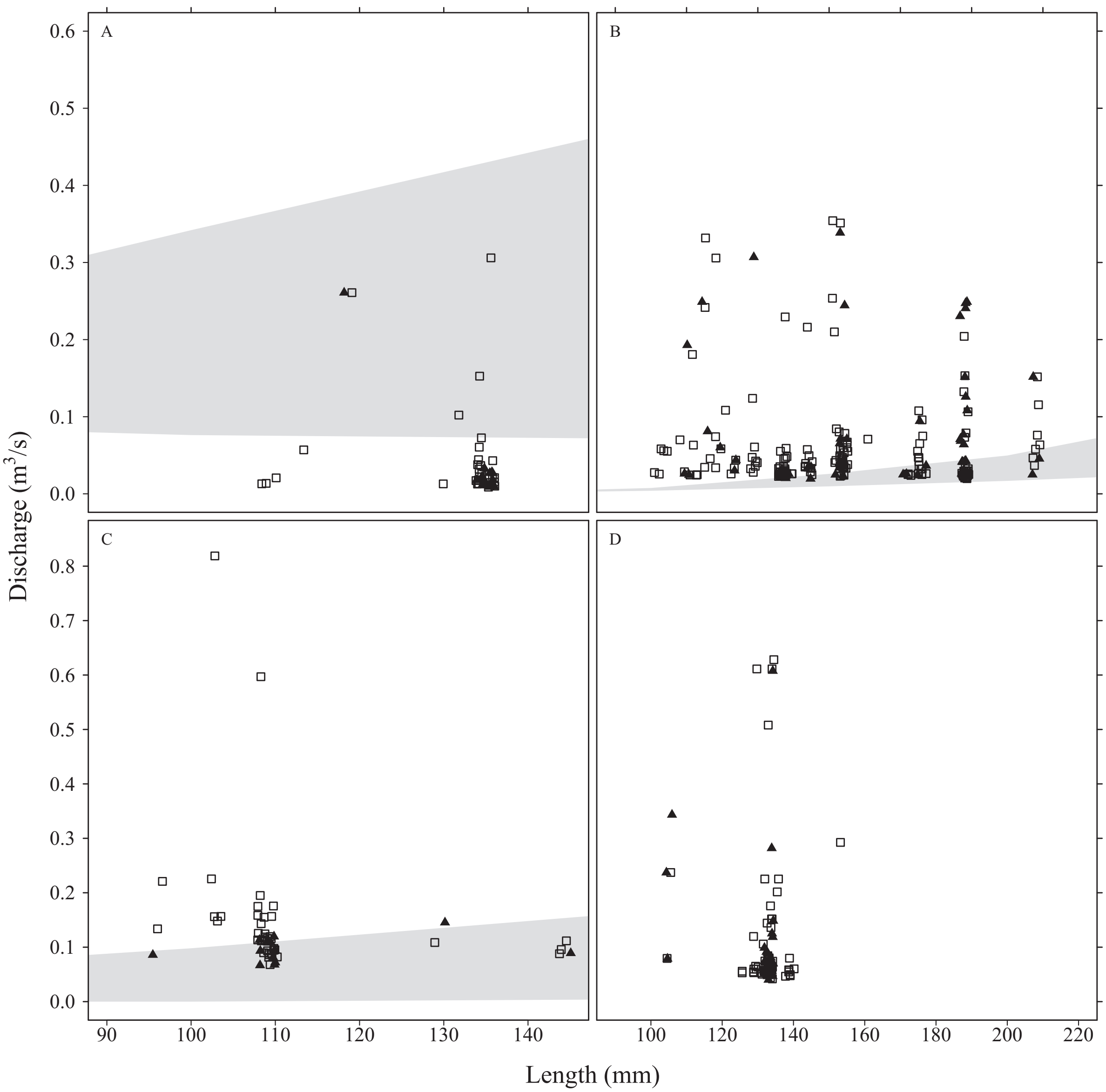

FIGURE 2. Successful and failed passage of Brook Trout based on fish length and stream discharge at the time of the pass attempt. Grey zones indicated the conditions under which Brook Trout are predicted to be able to pass at each culvert based on FishXing. Open squares respresent successful pass attempts and black triangles represent unsuccessful pass attempts. Panels A–D correspond to data from the four culverts, and culvert parameters (A–D) are given in Table 1.

1998; Burford et al. 2009). It is therefore important to recognize that nonperched culverts can also be problematic and create conditions that limit the upstream movement of fish (see also MacPherson et al. 2012). This underscores the complexity of connectivity in many systems as barriers may not always be easily characterized as fully passable or impassable (e.g., Park et al. 2008; Burford et al. 2009; O'Hanley 2011).

We were unable to accurately predict the movement of fish passage through culverts using FishXing. As efforts increase to improve hydrological modeling of culverts, it was expected that FishXing predictions would be useful in determining fish passage. Unfortunately, FishXing is a complex model that incorporates physiological information of the species and hydrological information associated with the culvert. While qualitative assessments of barriers from FishXing remain useful (they were accurate for three of the four barriers), the severity of a barrier is an important element for quantifying connectivity or prioritizing restoration.

Beyond refining hydrologic parameters, the predictive shortcomings of FishXing may be associated with an incomplete knowledge of fish physiology, behavior, or both. The underestimation of fish swimming abilities can account for the conservative estimates by FishXing. Past studies that have derived swim speeds from forced-swimming methodologies have been

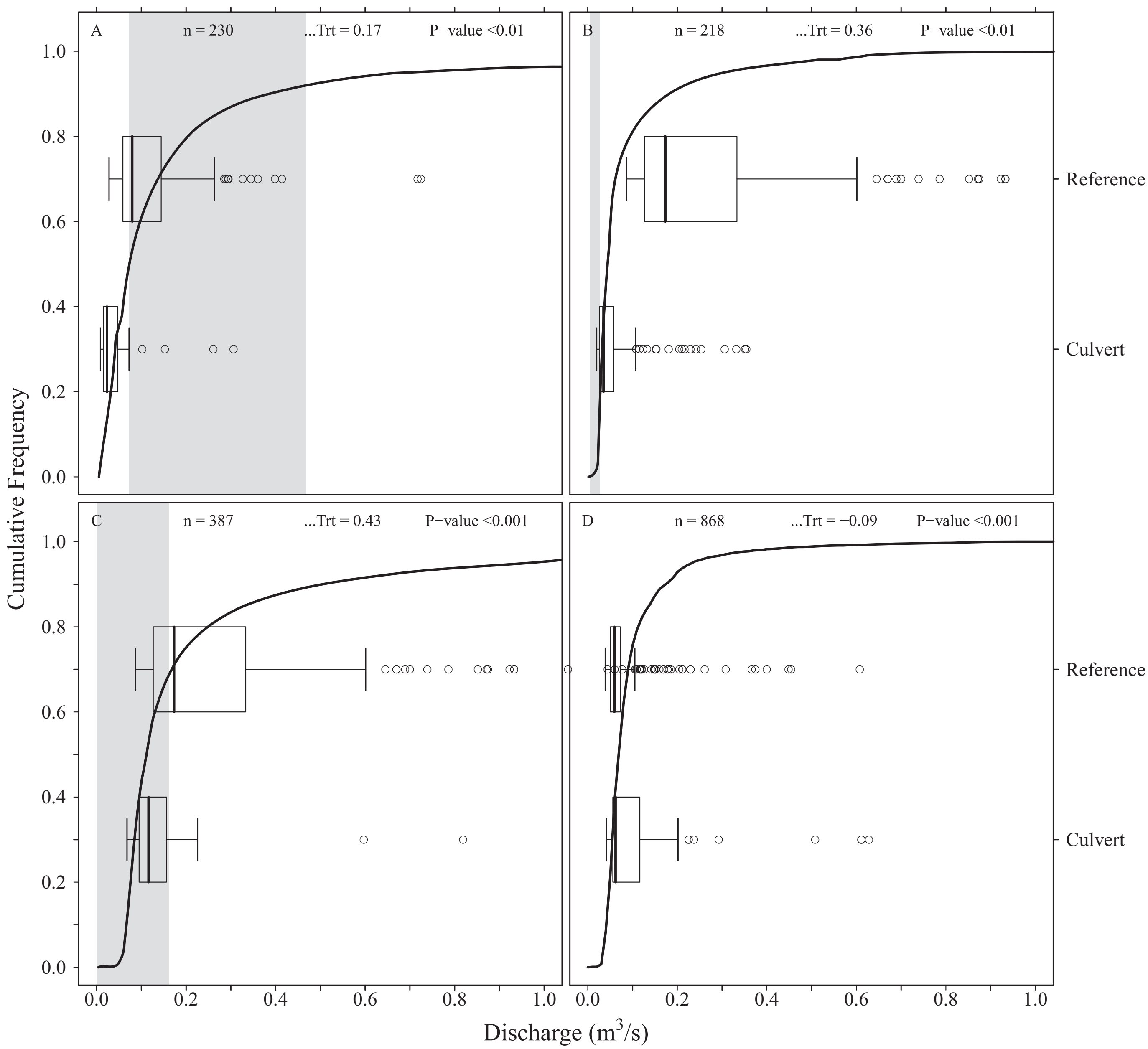

FIGURE 3. Timing of Brook Trout passage relative to the cumulative distribution of stream discharge (black line), observed culvert and reference site passage (box plots), and predicted passage as determine by FishXing (grey zone). Predicted passage was based on FishXing passable flows outputs for 100–150-mm Brook Trout. The boxes represent the interquartile range (IQR), solid dark line is the median, whiskers are 1.5 times the IQR. Outliers are represented by open circles. Sample size (*n*) is the total number of successful pass events for a given site, which consists of a reference and culvert telemetry array. ΔTrt is the difference of the range (represented by the whiskers) of passable flows between the reference site and culvert site. Positive numbers indicate that culverts had a smaller range of passable discharges compared with reference sites.

criticized because they do not reflect conditions in natural systems (Castro-Santos 2006; Peake and Farrell 2006). Haro et al. (2004) analyzed swim speeds of several species of fish exhibiting anadromous, amphidromous, and potamodromous life histories using an open-channel flume. In that study, fish were allowed to transverse the flume under their own volition, which is different from past studies that used forced swim speeds. They found that by allowing fish to mimic their natural tendencies (multiple pass attempts, movement under own volition) to navigate the flume, they were able to record speeds that were well above those previously observed. However, Haro et al. (2004) used a smooth-channeled flume with relatively constant flow regimes and recommended that these swim speeds should be used in situations that mimic these flow profiles (e.g., box culverts). Such improvements in understanding species' swim performance would enhance the performance of fish passage assessment methods like FishXing that rely on swimming performances.

Many obstacles to fish movement, both natural and anthropogenic, incorporate nonuniform flow characteristics with areas of velocity refugia consisting of lower velocity flow patterns (e.g., culvert boundary layers). For instance, in this study, fish were observed idly resting in the boundary layers of culverts (low velocity zones near the edge of the culvert) using little or no effort to maintain their position. Clearly, laboratory settings that replicate the turbulent conditions found in nature would be useful in understanding of how fish optimize passage (Haro et al. 2004; Castro-Santos 2006; Neary 2012) and would benefit future assessments and restoration practices by allowing us to focus on velocity zones that are critical to fish passage.

Behavior plays an important role in how fish move past barriers. Minimum depth is a biological parameter incorporated into FishXing that determines whether individuals are able to successfully navigate a culvert at low stream flows. Water depth remains an important aspect of culvert passage as predictions of depth barriers can be common in studies using FishXing (Gibson et al. 2005). However, Burford et al. (2009) indicated that this parameter had very little influence on determining the upstream movement of fish. Inconsistencies with FishXing predictions from previous work (Bourne 2013) and field observations of fish movements led us to reduce the model's minimum depth measurement. Our results indicate that this threshold remains conservative. We defined the minimum depth as two-fifths of the body length (minimum depth from 4 to 8 cm) of an individual, which was more liberal than the 9.1 cm used by Burford et al. (2009). Both the values in this study and in Burford et al. (2009) are considerably lower than the recommended minimum depth values (Bates et al. 2003). However, we found that using two-fifths of the body length was accurate in three of the culverts in this study (only culvert A was considered a depth barrier). Unfortunately, we were unable to capture in situ measurements of culvert hydrologic characteristics to calculate minimum depth, and thus we used FishXing outputs to derive minimum depth for culvert A. While it is useful to know at what depth fish are able to pass, it is unclear whether the precision of FishXing is accurate enough to back-calculate such parameters. Therefore, further work is needed to continue to refine how depth influences fish movements and how individuals interact with anthropogenic structures in low flow situations.

The installation and replacement of stream crossings is an expensive endeavor (Bernhardt et al. 2005), and using inaccurate barrier assessment methods to prioritize culvert restoration could unnecessarily burden limited financial resources when no action is needed to promote fish passage. However, the conservative outputs of FishXing, when predicting fish movement, may be advantageous as a precautionary tool. FishXing was created to help in the design of culverts to promote fish passage, and within this framework, a precautionary approach is beneficial. Designing culverts in excess of what is needed for fish passage will ensure fish movement throughout the range of flows encountered by fish. However, at what point does designing culverts for fish passage based on a conservative FishXing output become too costly when a less conservative design can have the same outcome on the aquatic community? Continued advancements in the understanding of fish passage should lead to a balance that will promote effective culvert designs without accruing unneeded expenditures.

An alternate approach to FishXing would be to focus on identifying specific physical thresholds that create a pass–no pass scenario and would continue to capitalize on the simplicity and affordability of commonly used barrier assessment methods. Past methods such as flow-chart methods, have calculated culvert passabilities, but few have been rigorously tested as to whether these predictions match actual fish movement (Kemp and O'Hanley 2010). Despite this, one flow chart model developed by Coffman (2005) uses several easy-to-calculate measurements based on culvert slope, length, and tailwater area to calculate the passability of a culvert. Although the methods used by Coffman (2005) (mark–recapture using fin clips) probably produce conservative results, it is still appealing in that model estimates were based on observations of fish movement to determine thresholds. The benefit of using a model like that of Coffman (2005) is that it allows the user to quickly and easily assess a culvert and assign a passability value to it with an associated degree of confidence. However, Anderson et al. (2012) postulated that binary responses probably oversimplify culvert passage of many fish species. Using Bayesian belief networks (BBNs), Anderson et al. (2012) concluded that the inclusion of two and three levels of criteria would distinguish partial barriers that were previously labeled as complete barriers with a pass–no pass analysis. But not unlike other barrier assessment methods, the use of BBNs to calculate probabilities of culvert passage is still dependent on accurately defining thresholds, a trait shared by other culvert assessment techniques (Haro et al. 2004; Coffman 2005; Furniss et al. 2006; Kondratieff and Myrick 2006; Kemp and O'Hanley 2010; Anderson et al. 2012).

Barrier assessments are an integral part of understanding and maintaining riverscape connectivity. Passability metrics are one measurement that can be difficult to assess but have been shown to influence connectivity models (Bourne et al. 2011). Our results isolate the effects of culvert impacts on fish movements and provide support to previous studies that speculated on the conservative nature of FishXing (Burford et al. 2009; Bourne et al. 2011); they also highlight the need to continue to validate the effectiveness of common barrier assessment models and how fish interact with barriers. The implications of using inaccurate barrier assessment techniques could lead to misidentifying barriers as impassable and result in costly management actions that have little or no ecological impact on the focal species.

ACKNOWLEDGMENTS

The authors are grateful to M. Langdon, T. Mulrooney, and R. Collier (Parks Canada) and C. Pennell and C. Kelly (Fisheries and Oceans Canada) for tagging fish and maintaining telemetry stations. Furthermore, the authors acknowledge the input and guidance from I. Gidge, R. Randall, M. Underwood, and the Landscape Ecology and Spatial Analysis Lab at Memorial University for valuable feedback throughout the study. Support for this research was provided by Parks Canada Action on the Ground Funding, Canadian Foundation for Innovation, and Natural Sciences and Engineering Research Council Discovery grants to Y.F.W. and by AMEC Environment and Infrastructure grant to D.C.

REFERENCES

Anderson, G. B., M. C. Freeman, B. J. Freeman, C. A. Straight, M. M. Hagler, and J. T. Peterson. 2012. Dealing with uncertainty when assessing fish passage through culvert road crossings. Environmental Management 50:462–477.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: linear mixed-effects models using s4 classes, R package version 0.999375-42. R Foundation for Statistical Computing, Vienna. Available: CRAN.R-project.org/package=lme4. (February 2013).

Bates, K., B. Barnard, B. Heiner, J. P. Klavas, and P. D. Powers. 2003. Design of road culverts for fish passage. Washington Department of Fish and Wildlife, Olympia.

Belford, D. A., and W. R. Gould. 1989. An evaluation of trout passage through six highway culverts in Montana. North American Journal of Fisheries Management 9:437–445.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308:636–637.

Bourne, C. M. 2013. How to quantify aquatic connectivity? verifying the effectivness of the dendritic connectivity index as a tool for assessing stream fragmentation. Master's thesis. Memorial University of Newfoundland, St. John's.

Bourne, C. M., D. G. Kehler, Y. F. Wiersma, and D. Cote. 2011. 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. Aquatic Ecology 45:389–403.

Burford, D. D., T. E. McMahon, J. E. Cahoon, and M. Blank. 2009. Assessment of trout passage through culverts in a large Montana drainage during summer low flow. North American Journal of Fisheries Management 29:739–752.

Castro-Santos, T. 2006. Modeling the effect of varying swim speeds on fish passage through velocity barriers. Transactions of the American Fisheries Society 135:1230–1237.

Clarkin, K., A. Connor, M. J. Furniss, B. Gubernick, M. Love, K. Moynan, and S. Wilson-Musser. 2005. National inventory and assessment procedure for identifying barriers to aquatic organism passage at road-stream crossings. U.S. Department of Agriculture, Forest Service, National Technology and Development Program, Report 7700, San Dimas, California.

Coffman, J. S. 2005. Evaluation of a predictive model for upstream fish passage through culverts. Master's thesis. James Madison University, Harrisonburg, Virginia.

Cote, D. 2007. Measurements of salmonid population performance in relation to habitat in eastern Newfoundland streams. Journal of Fish Biology 70:1134–1147.

Cote, D., P. C. B. Frampton, M. Langdon, and R. Collier. 2005. Fish passage and stream habitat restoration in Terra Nova National Park highway culverts. Parks Canada Technical Report in Ecosystem Science 41, Glovertown, Newfoundland and Labrador.

Cote, D., D. G. Kehler, C. Bourne, and Y. F. Wiersma. 2009. A new measure of longitudinal connectivity for stream networks. Landscape Ecology 24:101–113.

Davis, J. C., and G. A. Davis. 2008. Restoration evaluation—fish passage: final report. Aquatic Restoration and Research Institute, Talkeetna, Alaska.

Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243–3249.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Flanders, L. S., and J. Cariello. 2000. Tongass road condition survey report. Alaska Department of Fish and Game, Habitat and Restoration Division, Technical Report 00-7, Douglas.

Fullerton, A. H., K. M. Burnett, E. A. Steel, R. L. Flitcroft, G. R. Pess, B. E. Feist, C. E. Torgersen, D. J. Miller, and B. L. Sanderson. 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshwater Biology 55:2215–2237.

Furniss, M., M. Love, S. Firor, K. Moynan, A. Llanos, J. Guntle, and R. Gubernick. 2006. FishXing: software and learning systems for fish passage through culverts, version 3.0. U.S. Forest Sevice, San Dimas Technology and Development Center, San Dimas, California.

Gibson, R. J., R. L. Haedrich, and C. M. Wernerheim. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. Fisheries 30(1):10–17.

Gowan, C., and K. D. Fausch. 1996. Mobile Brook Trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Haro, A., T. Castro-Santos, J. Noreika, and M. Odeh. 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences 61:1590–1601.

Hendrickson, S., K. Walker, S. Jacobson, and F. Bower. 2008. Assessment of aquatic organism passage at road/stream crossings for the northern region of the USDA Forest Service. U.S. Department of Agriculture, Forest Service, Northern Region, Missoula, Montana. Available: www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5117508.pdf. (February 2013).

Hotchkiss, R. H., E. A. Thiele, E. J. Nelson, and P. L. Thompson. 2008. Culvert hydraulics comparison of current computer models and recommended improvements. Transportation Research Record 2060:141–149.

Karle, K. F. 2005. Analysis of an efficient fish barrier assessment protocol for highway culverts. Alaska Department of Transportation, Report FHWA-AK-RD-05-02, Fairbanks.

Kemp, P. S., and J. R. O'Hanley. 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fisheries Management and Ecology 17:297–322.

Kindlmann, P., and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23:879–890.

Klemetsen, A., P. A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic Salmon *Salmo salar* L., Brown Trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12: 1–59.

Kondratieff, M. C., and C. A. Myrick. 2006. How high can Brook Trout jump? a laboratory evaluation of Brook Trout jumping performance. Transactions of the American Fisheries Society 135:361–370.

Lang, M., M. Love, and W. Trush. 2004. Improving stream crossings for fish passage: final report. National Marine Fisheries Service, Humboldt State University, Arcata, California.

MacPherson, L. M., M. G. Sullivan, A. L. Foote, and C. E. Stevens. 2012. Effects of culverts on stream fish assemblages in the Alberta foothills. North American Journal of Fisheries Management 32:480–490.

Neary, V. S. 2012. Binary fish passage models for uniform and nonuniform flows. River Research and Applications 28:418–428.

O'Hanley, J. R. 2011. Open rivers: barrier removal planning and the restoration of free-flowing rivers. Journal of Environmental Management 92:3112–3120.

Olden, J. D., M. J. Kennard, F. Leprieur, P. A. Tedesco, K. O. Winemiller, and E. García-Berthou. 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. Diversity and Distributions 16:496–513.

Padgham, M., and J. A. Webb. 2010. Multiple structural modifications to dendritic ecological networks produce simple responses. Ecological Modelling 221:2537–2545.

Palmer, M. A., E. S. Bernhardt, J. D. Allan, P. S. Lake, G. Alexander, S. Brooks, J. Carr, S. Clayton, C. N. Dahm, J. Follstad Shah, D. L. Galat, S. G. Loss, P. Goodwin, D. D. Hart, B. Hassett, R. Jenkinson, G. M. Kondolf, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, and E. Sudduth. 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology 42:208–217.

Park, D., M. Sullivan, E. Bayne, and G. Scrimgeour. 2008. Landscape-level stream fragmentation caused by hanging culverts along roads in Alberta's boreal forest. Canadian Journal of Forest Research 38:566–575.

Peake, S. J., and A. P. Farrell. 2006. Fatigue is a behavioural response in respirometer-confined Smallmouth Bass. Journal of Fish Biology 68:1742–1755.

Peake, S. J., R. S. McKinley, and D. A. Scruton. 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. Journal of Fish Biology 51:710–723.

Perkin, J. S., and K. B. Gido. 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. Ecological Applications 22:2176–2187.

Poplar-Jeffers, I. O., J. T. Petty, J. T. Anderson, S. J. Kite, M. P. Strager, and R. H. Fortney. 2009. Culvert replacement and stream habitat restoration: implications from Brook Trout management in an Appalachian watershed, U.S.A. Restoration Ecology 17:404–413.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org./ (February 2013).

Riggs, H. C., editor 1985. Developments in water science, volume 22: streamflow characteristics. Elsevier, New York.

Riley, S. C., K. D. Fausch, and C. Gowan. 1992. Movement of Brook Trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1:112–122.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1–20.

Schick, R. S., and S. T. Lindley. 2007. Directed connectivity among fish populations in a riverine network. Journal of Applied Ecology 44:1116–1126.

Standage, R. W., and C. J. Gagen. 2007. A review of the influences of road crossings on warmwater fishes in Ouachita mountain streams, Ouachita national forest. Pages 180–186 *in* C. L. Irwin, D. Nelson, and K. P. McDermott, editors. Proceedings of the 2007 international conference on ecology and transportation. North Carolina State University, Center for Transportation and the Environment, Raleigh.

Straub, L. G., and H. M. Morris. 1950a. Hydraulic tests on concrete culvert pipes. St. Anthony Falls Hydraulic Laboratory, University of Minnesota, Technical Paper 4, Series B, Minneapolis.

Straub, L. G., and H. M. Morris. 1950b. Hydraulic tests on corrugated metal culvert pipes. St. Anthony Falls Hydraulic Laboratory, University of Minnesota, Technical Paper 5, Series B, Minneapolis.

Taylor, R. N., and M. Love. 2003. California salmonid stream habitat restoration manual: part IX—fish passage evaluation at stream crossings. California Department of Fish and Wildlife, Sacramento.

Thompson, P. D., and F. J. Rahel. 1998. Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of Brook Trout. North American Journal of Fisheries Management 18:206–210.