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Dams, Culverts, and Cumulative Effects: Quantifying Cumulative Effects of Barriers to Longitudinal Connectivity on Three Rivers in Nova Scotia, Canada

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Keywords:	aquatic landscape ecology, geographic information systems, network analysis, cumulative effects, watershed connectivity, aquatic organism passage, dam removal, culvert repair

Dams, Culverts, and Cumulative Effects: Quantifying Cumulative Effects of Barriers to Longitudinal Connectivity on Three Rivers in Nova Scotia, Canada[1]

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ABSTRACT

Anthropogenic fragmentation of rivers is now widely understood to be impacting freshwater biodiversity at the global scale. The cumulative impacts of dams on longitudinal connectivity are immense, though focus is shifting towards identifying the cumulative impacts of smaller barriers such as road culverts. However, the enormous numbers of these barriers coupled with a paucity of data and a lack of adequate analytical tools currently limit our ability to understand and address the problem. In this study, we present a suite of approaches that can be used to quantify and characterize the cumulative effects of different types of riverine barriers. We demonstrate these methods on three river systems in Nova Scotia, Canada, each heavily fragmented by road culverts and dams associated with hydroelectric and other development. We conduct a 'first-pass' investigation of the cumulative effects of barriers on these rivers by making use of widely available geospatial data, a geographic information system (GIS), a GIS network analysis toolset, connectivity metrics, and optimization. Our results indicate that the unit of measure (e.g., length, surface area) can affect connectivity assessments and that culverts appear to contribute less to longitudinal connectivity impairment here than dams. Cases of non-additive effects (i.e., antagonisms and synergies) were also apparent in results.

Keywords: aquatic landscape ecology, geographic information systems, network analysis, cumulative effects, watershed connectivity, fish passage, aquatic organism passage, dam removal, culvert repair

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INTRODUCTION

Human activity has led to a severe decline in global freshwater biodiversity (Dudgeon *et al.,* 2006; Vörösmarty *et al.,* 2010), even more so than in other biomes (Strayer & Dudgeon, 2010). Worldwide, rates of species extinctions for freshwater vertebrates in the past century were estimated to be 200 times higher than the background rate of extinction - for North American freshwater fish species that rate was found to be closer to 900 (Burkhead, 2012). Indeed, approximately 46% of known freshwater and diadromous fish species in North America are imperiled (Jelks et al., 2008). This has led to an urgent need to better understand anthropogenic effects on freshwater systems includng the impairment of longitudinal connectivity of rivers (Ward, 1989; Kondolf *et al.,* 2006), believed to be a major contributor to the rapid and widespread decline of resident migratory (i.e., potamodromous) and freshwater-marine migratory (i.e. diadromous) fish (Dudgeon *et al.,* 2006; Greathouse *et al.,* 2006; Limburg & Waldman, 2009; Humphries & Winemiller, 2009; Vörösmarty *et al.,* 2010; Moyle *et al.,* 2011; Horreo *et al.,* 2011; Liermann *et al*., 2012).

Dammin is in a large part responsible for the fragmentation of rivers on the global scale (Nilsson *et al.,* 2005; Lehner *et al.,* 2011, Grill *et al.* 2015). Yet, culverts commonly found at road crossings are also known to act as ecological stressors (Park *et al*., 2008; Eberhardt *et al.,* 2011) and impair fish movement to the detriment of fish assemblages (Vander Pluym *et al.,* 2008; Alexandre & Almeida, 2010; Nislow *et al.,* 2011; MacPherson *et al*., 2012). They are also far more numerous than dams (Januchowski-Hartley *et al*., 2013). There are indications that despite the estimated individual effects of culverts being smaller than those of dams, the cumulative effects of these barriers are significant (Alexandre & Almeida, 2010; Diebel *et al*., 2014; Neeson *et al*., 2015). Past studies have examined effects of small obstacles versus larger dams on fish populations (e.g., Alexandre & Almeida, 2010), though there have been few studies which have explicitly examined the cumulative effects of these barriers on longitudinal connectivity (though see Januchowski-Hartley *et al*., 2013 and Diebel *et al*., 2014).

Two sub-types of longitudinal connectivity are important to consider from an ecological standpoint. The first type, herein referred to as *directed* connectivity, is the degree to which upper reaches of the system are connected to the outflow, or *sink*, and vice versa (O'Hanley & Tomberlin, 2005; Cote *et al*., 2009). Directed connectivity is crucial to diadromous fish (Peter, 1998; Katano *et al*., 2006; Morita *et al*., 2009; Smith & Hightower, 2012) and to the transport of nutrients, woody debris, and sediment (Kroeze *et al*., 2012). For potamodromous fish, movement within river networks is important and a distinct type of connectivity is a requirement. This second type of longitudinal connectivity, considered herein as *undirected connectivity,* is the degree to which any given point in the river system is accessible from all other points in the system, regardless of the direction of flow (Cote *et al*., 2009; O'Hanley, 2011). Loss of undirected connectivity restricts the movement and adversely affects populations of resident fish (Warren & Pardew, 1998; Nislow *et al*., 2011) and can lead to local extirpations (Winston *et al*., 1991; Tsuboi *et al*., 2010). Landscape scale metrics of longitudinal connectivity such as the Dendritic Connecitivty Index (DCI; Cote *et al.,* 2009) can be used to quantify directed and undirected connectivity.

The need to assess the cumulative effects of river barriers at the riverscape scale has long been recognized (e.g., Pringle, 2001). However, the unusually strong connectivity of riverscapes compared to other landscapes (Eros *et al.,* 2012), a paucity of data, and the high numbers of barriers can make teasing apart the relative effects of barriers a challenging task. In this study, we present a number of approaches to quantifying the cumulative effects of road culverts compared to those of dams on longitudinal connectivity. In a similar approach employed by Diefenderfer *et al*. (2012) to examine non-additive cumulative effects associated with restoration of lateral connectivity of rivers, we attempt to quantify synergies and antagonism between culverts and dams through barrier removal simulations. We present a novel application of optimization models for directed and undirected connectivity, wherein all project costs are considered equal, thus isolating non-additive ecological effects of barrier removal from those that arise due to budget thresholds (e.g., O'Hanley & Tomberlin, 2005). The methods presented rely heavily on network analysis and Geographic Information Systems (GIS) which have been identified as showing promise in this context (e.g., Kemp & O'Hanley, 2010; Mao & Yang, 2011).

MATERIALS AND METHODS

Study Area

Three river systems in Nova Scotia, Canada, were selected for this study: the Mersey, Sheet Harbour (East River), and St. Margaret's Bay river systems. These rivers are actively managed for hydroelectric power generation and are home to important diadromous and potamodromous species of fish, though many populations are severely depleted. The Mersey river is located approximately 120 km southwest of Halifax and is the largest system of the three selected, with an approximate drainage area of 1963 km^2 (**Figure 1**). The St. Margaret's Bay river system is located approximately 20 km northwest of Halifax and has a drainage area of approximately 271 km^2 (**Figure 2**). The Sheet Harbour river system is located on the Eastern Shore of Nova Scotia, approximately 85 km northeast of Halifax and has a drainage area of approximately 570.6 km^2 (**Figure 3**). All three systems were once home to migratory runs of diadromous Atlantic salmon (*Salmo salar*). Alewife (*Alosa pseudoharengus*), another diadromous fish, were once present on the St. Margaret's Bay system. The numbers of migrating individuals are drastically lower than historical records indicate – no salmon were reported on the Mersey system between 1999 and 2010, for example (NSPI, 2010). The brook trout (*Salvelinus fontinalis*), a potamodromous species, is also present in the Mersey and Sheet Harbour systems (NSPI, 2009; NSPI, 2010). The threatened American eel (*Anguilla rostrata*), a catadromous species, has also been observed throughout all three river systems (Davis & Browne, 1996).

Barrier and River Network Data

River network lines and polygons were downloaded for the three river systems in digital GIS format from the Nova Scotia Topographic Database (NSTDB; 1:10,000 scale) in the ESRI feature class file format (ESRI, 2012a). The lines and polygons both contained standard feature codes that identified categories of features key for this study including 'canal', 'river', 'river lake spine', 'lake', 'lake spine', 'reservoir', 'swamp', 'dam', and 'fish ladder.' Surface areas for streams under 27 m were not available for 6436 out of 10854 line segments (59.3% by count, 59.6% by length). To address this, a rudimentary stream width model was used to fill in the data gaps and estimate surface area (details of this approach can be found in Oldford, 2013, and in Supplemental Materials).

Records of dams as point features were extracted from the NSTDB hydrographic network point layer. Additional dam locations were sourced from NSPI and Parks Canada (D. Pouliot, personal communication, August 20, 2011; D. Thompson, personal communication, May 22, 2012). A total of 36 dams were found in the dataset for the three systems. A further review of the dams with NSPI staff (D. Thompson, personal communication, May 22, 2012) was done to determine that 13 of the 36 dams were structures adjacent to or associated with another dam or were not on a waterway, thus leaving 23 dams for use in the analysis. A total of 181 culverts in the Mersey system, 250 culverts in the Sheet Harbour system, and 125 culverts in St. Margaret's Bay system were located using the NSTB database for a total of 556. Where needed, culverts were snapped up to 50 metres so they precisely intersected the river network lines to ensure topological connectivity.

The permeabilities of dams owned and operated by NSPI were estimated based on the expert opinion of biologists and environmental specialists working for NSPI. Of the 22 structures related to NSPI operations that restricted longitudinal connectivity, nine had fish passage measures installed (**Table 1**). Permeability estimates of the three dams present inside Kejimkujik National Park were made by Parks Canada staff using the Fish Xing software and methods (Washington Department of Fish and Wildlife, 2006). Full mitigation of permeability at a dam was considered to be achieved through the construction of both upstream and downstream passage structures. Options were considered at dams for 'partial' repair wherein a portion of bi-directional permeability was restored through the construction of either upstream or downstream passage.

A review of relevant literature on local culverts was conducted and permeabilities were estimated based on the findings. One local study surveyed 60 culverts and found that 33 (55%) impaired fish passage (Hicks & Sullivan, 2008). With few additional data available, it was estimated that all culverts had a 50% bidirectional permeability. At each culvert, one repair option was considered that was assumed to restore 100% bidirectional connectivity.

The effect of habitat quality on connectivity assessment and prioritization was explored by using two treatments for summarizing habitat upstream of barriers. In the first treatment, all network features were included in the habitat quantity estimate. In the second, network features representing reservoirs, river-lakes, wetlands, and lakes were excluded from consideration. These treatments were chosen primarily for two reasons: important native anadromous species such as the Atlantic Salmon are known to prefer moving, oxygenated, shallow water as spawning and rearing habitat (Amiro, 2006) and hydroelectric dams by design create an upstream reservoir that is often large and relatively anoxic. Thus, the treatments were intended to test the hypothesis that relatively large, anoxic reservoirs upstream of dams may skew priorities in favor of dam removal despite relatively unsuitable upstream habitat for diadromous species.

Software and Models

Geometric network

Network topologies of the three river systems were created using ArcGIS Desktop (ESRI, 2012a). Within ESRI ArcGIS Desktop, the 'geometric network' model was used along with a related toolset for analyzing electrical and water distribution networks, called Utility Network Analyst (UNA; ESRI, 2012b). System sinks were manually identified in a points layer and a geometric network was then built using the UNA using 'simple edges', no 'weights', and no 'm-values'. Flow direction was then set using the 'set flow direction' function. Time was taken to inspect river lines and barriers for each network and a number of common topological errors such as duplicate or disconnected features were corrected.

Optimization Models

We used two mixed integer linear programs for maximizing longitudinal connectivity via barrier removal. The objective of the first model is to maximize permeability-weighted connectivity between the outflow and the river network given a limited budget, described first by O'Hanley and Tomberlin as the *Fish Passage Barrier Removal Problem* (FPBRP; O'Hanley & Tomberlin, 2005). Herein, we refer to this model as the *directed model* as it accounts for directionality of flow to and from the river outflow. The directed model maximizes the diadromous Dendritic Connectivity Index (DCI_d; Cote et al., 2009) with the proviso that barrier permeability is calculated as the product of the upstream and downstream connectivities at a barrier. The second model used here was designed to maximize the single largest permeability-weighted sub-network (i.e., subgraph) given a limited budget. We refer to this model as the *undirected model*, as it assesses connectivity to and from all river segments regardless of flow direction. The models are similar structurally though not identical to the linear reformulations presented by O'Hanley et al. (2013) and King and O'Hanley (2014): barrier permeabilities may be partially passable instead of binary and the problem is formulated to avoid non-linearity. The undirected model aims to maximize the single largest undirected sub-network (O'Hanley, 2011) except permeabilities may be non-binary. The undirected model does not necessarily maximize the potamodromous Dendritic Connectivity Index (DCI_p; Cote *et al.,* 2009). The models are described in greater detail in the **Supplemental Materials**.

FIPEX GIS Toolset

The Fish Passage Extension for ArcMap (FIPEX; DFO, 2010) was used in this study to calculate connectivity statistics and generate tabular inputs for optimisation analyses (https://github.com/goldford/FIPEX_v10_23_ArcGIS10.x_2). FIPEX extends the capabilities of ArcMap to incorporate polygonal data into the results of network analyses, summarize upstream and downstream network statistics for a set of network barriers in one analysis, include / exclude features based on attributes, calculate the DCI_d and DCI_p statistics, and generate reports. Several new subroutines for this study were developed to call upon the Gurobi (Gurobi, 2012) and GLPK (Makhorin, 2012) optimisation solvers directly from ArcMap and to read the results back into the SDSS.

Analyses

River Impounded by Culverts versus Dams

The total river network upstream from each barrier until the next barrier(s) was extracted using a total four quantification methods that combine the quality treatments described previously with length and area quantification methods: (1) length, (2) length omitting stillwater, (3) surface area, and (4) surface area omitting stillwater. Results were summarized for culverts and dams separately by first scaling results using the total network available. Then, average impounded river per barrier was compared between culverts and dams and displayed using boxplots. The total proportion of river network impounded by each barrier type for each of the three treatments was also calculated for each river system and quantification method.

Connectivity Assessments using DCI

Initial assessment of all river networks were carried out using the DCI_p and DCI_d (Cote *et al*., 2009). The equations for the DCI_p and DCI_d (Cote *et al*., 2009) are:

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

$$DCI_p = \sum_{i=1}^{n} \sum_{j=i}^{n} c_{ij} \frac{l_i}{L} \frac{l_j}{L} * 100$$

In the DCI_d metric, the length, *l,* of each segment of river *i*, for all segments *n*, is scaled to the total length of all segments in the system. The second half of the equation ($\prod_{m=1}^{M} p_m^u \, p_m^d$) takes the set of barriers *M* between each segment *i* and the river mouth, and calculates the product of their permeabilities *p*, calculated as the product of the upstream and downstream permeabilities. The DCI_p equation can be read as the sum of all segment pair connectivities (c_{ij}) multiplied by the probability "of observing a particular c_{ij}" (Cote *et al.,* 2009, p. 104). The probability that a given segment pair is selected randomly is thus the product of the individual selection probabilities, $(l_i * l_j)/L^2$.

Instead of solely using length as a unit of measure, here the DCI statistics were calculated using each of the four quantification methods described previously. The FIPEX toolset was used to summarize river network upstream of all barriers four each of the four quantification treatments and calculate the DCI metrics. In the 'no stillwater' treatments, network features representing reservoirs, river-lakes, lakes, and wetlands were excluded from results using the FIPEX 'exclusions' option. In the 'surface area' treatments, the surface area of river features was used instead of lengths with precision reported to the nearest 100 m^2. Network length was calculated and reported to ten-metre precision.

Simulated Removal of Culverts and Dams

The relative connectivity gains associated with repair of all culverts versus all dams were compared. Gains to systemic connectivity were estimated using the change in DCI statistics before and after culvert removal as a group and barrier removal as a group. Changes were scaled relative to the initial DCI of the river system for comparisons between rivers.

Interactive Effects between Barrier Types on Connectivity Gains

To estimate the degree to which the total benefit to connectivity achieved by removing groups of barriers (i.e., culverts or dams) were masked by the presence of the other type, a barrier category was selected, removal of the barriers as a group was simulated, and the DCI_d, DCI_p, of the network was re-calculated. Next, removal of both groups together was simulated and the results compared. The gains-that were antagonized (i.e., 'masked') were thus isolated using the following formula:

$$Ant\% = \Delta DCI_{cul+dam} - (\Delta DCI_{cul} + \Delta DCI_{dam})$$

where ΔDCI_{cul} are the gains achieved through removal of all culverts in the presence of dams, ΔDCI_{dam} are the gains achieved through the removal of all dams in the presence of culverts, and $\Delta DCI_{cul+dam}$ is the gain in DCI achieved through removal of both culverts and dams simultaneously. The analysis was conducted using the 'Area' and 'Area No Stillwater' network quantification methods for all river systems.

Cumulative Benefits of Optimal Barrier Removal

To identify synergies achieved through barrier removals taken in combination, we applied the optimization models to select the most efficient priorities for various amounts of effort. We adapted the application of the optimization models by setting costs equal for the full repair of all barriers (though 'partial' repair, or half-repair, of dams was considered) - the budget constraint in the models was used to limit the total number of barriers selected by the optimization model, rather than using specific economics costs as budget constraints. We then examined the results to see whether the cumulative benefits of optimal culvert removal could out-weigh the benefits of optimal dam removal for a series of incremental effort. Cases of non-nestedness (O'Hanley, 2011) indicative of synergies were identified. The 'Area no Stillwater' quantification method was selected for this analysis given that surface area was deemed preferable to length as a quantification method for stream-lake networks (Jones et al., 2011) and omitting stillwater was judged to more accurately reflect the habitat needs of diadromous fish.

The directed and undirected models were run for the three systems for a suite of levels of 'effort, as quantified by the number of barriers allowed in the output. Solve-time was limited to 500 seconds for each optimisation analysis after which the best solution was accepted. The same workstation was used for each analysis which had an Intel i5 2500k processor cooled to maximum temperature of 60 degrees Celcius (temperature was found to affect solutions found in the time given), 64-bit Windows 7 operating system, and 12 gigabytes of DDR3 Random Access Memory.

RESULTS

Results of assessment of the impounded river network immediately upstream of barriers show that a consistently greater proportion of river is impounded by dams than culverts despite the relatively high numbers of culverts **(Figure 4**Figure 4**).** The proportion of total river impounded by culverts was found to be higher in most cases where stillwater was omitted. The Sheet Harbour river system was an exception where the proportion of river impounded by culverts using the ‘Area’ quantification method was found to be less than the area impounded by culverts using ‘Area no Stillwater’. In all river systems and treatments, those that utilized length as the unit of measure estimated culverts to impound a greater proportion of the total river system (26-46%) than those treatments that uses area as the unit of measure (11-34%). When taken individually, culverts were found to impound a consistently lower proportion of the river network on average than dams, though there were a number of outliers (**Figure 5).**

The DCI_d metrics were lower than the DCI_p metrics in all three systems using all four quantification methods (**Figure 6)**. The Mersey system had the most impairment of directed connectivity, whereas the connectivity within the system was higher than the others. Connectivity assessments differed depending on the quantification method used. For example, directed and undirected connectivity assessments for the Mersey river system differed particularly between the ‘area’ (DCI_d = 0.52; DCI_p = 64.37) and ‘area no stillwater’ methods (DCI_d = 4.38; DCI_p = 27.28). Variation was also observed in the undirected connectivity assessment of the Mersey system between the ‘length’ (DCI_p = 45.87) and ‘length no stillwater’ (DCI_p = 64.37) quantification methods.

Separate simulations of the removal of dams and culverts as groups indicated that dams have a greater cumulative impact on longitudinal connectivity than culverts on these river systems (**Figure 7**). Directed connectivity gains upon simulated removal of all dams, as measured by the ‘Areas’ quantification method (DCI_d:71.07 – 92.92), were found to be greater than those of simulated removal of all culverts (DCI_d: 0.01 – 1.79). The result was similar when the ‘Areas No Stillwater’ quantification method was used (dam removal gains DCI_d: 63.92 – 86.25; culvert removal DCI_d: 0.01 – 1.82). Gains to DCI_p upon simulated removal of dams were also greater than gains of simulated culvert removal for both the ‘Areas’ treatments (dam removal gains DCI_p: 23.05 – 49.81; culvert removal gains DCI_p: 3.61-7) and the ‘Areas No Stillwater’ treatment (dam removal gains DCI_p: 32.64 – 55.26; culvert removal gains DCI_p: 6.75 – 9.89). However, culverts removal appeared to achieve more gains to DCI_p than DCI_d for all rivers and quantification methods.

The DCI_d achieved through removal of both culverts and dams was found to be 6-22% lower than when both barrier groups were removed simultaneously. This effect was highest for the St. Margaret’s Bay river system (ΔDCI_d =19-22%). Gains to DCI_p achieved through removal of culverts and dams as separate groups were found to be 6-29% reduced as compared to simultaneous removal of both groups. Antagonisms were again higher for the St. Margaret’s Bay river system (ΔDCI_p=28-29%) than for the Sheet Harbour river system (ΔDCI_p=7-12%) and the Mersey river system (ΔDCI_p=6-11%).

Culverts rarely appeared before dams in combinations of barriers selected by the directed optimization model (**Figure 8**). However, the results of the undirected model indicated that certain culverts would achieve more gains to undirected connectivity than dams. Removal of Culvert 217 on the Mersey river system, for example, was found to improve undirected connectivity more than any other single barrier. Non-nestedness of results was also observed. For example, when two barriers were permitted to be selected for removal, the Upper and Lower Lake Falls dams in the Mersey system appeared to perform synergistically, displacing Culvert 217.

DISCUSSION

There are indications that individual road crossings can exhibit effects on the ecology of rivers that are comparable to larger dams (Alexandra & Almeida, 2010) and are priority for restoration (e.g. Diebel *et al.,* 2014; Neeson *et al.,* 2015). When the cumulative effects of these barriers are taken into account, they can have a greater impact than dams on the ability for resident fish populations to move freely within the system and can affect subsequent prioritizations of restoration efforts (Diebel *et al.,* 2014). Yet, the relatively high number of these barriers and a paucity of associated data remains a substantial challenge (Januchowski-Hartley *et al*., 2013; Januchowski-Hartley *et al.,* 2014). In this study, we presented a variety of approaches to quantifying the individual and cumulative effects of road culverts relative to hydroelectric dams using widely available geospatial data, geospatial tools, simple connectivity metrics, and optimization.

Results revealed that a greater proportion of the rivers studied are impounded upstream of dams than upstream of culverts. We found similar results when we accounted for the preference of important migratory fish species for moving, well-oxygenated water by excluding reservoirs and other lentic waterbodies from analysis. This suggests that the positioning of dams on the rivers and relative to other barriers leads to greater upstream impoundments. The method implemented involved the creation of a network using river and barrier point, line, and polygon data and subsequent analyses within ESRI ArcMap (ESRI, 2012a) and the FIPEX Toolset (DFO, 2010). Although it required technical expertise in GIS to manipulate and edit river network features to ensure correct topological relationships and run analyses, this was a relatively straightforward and rapid assessment. However, as upstream impounded river is a localized metric, it is less desirable than metrics that assess connectivity at the riverscape scale (Melles *et al.,* 2012; Fuller *et al.,* 2015).

River segment length is prevalently used to quantify river network size (O'Hanley & Tomberlin, 2005; Hicks & Sullivan, 2008; Mader & Maier, 2008; Cote *et al.* 2009, Kocovsky *et al*., 2009; Anderson *et al.,* 2012; Nunn & Cowx, 2012; McKay *et al*. 2013, Segurado *et al*. 2013, Diebel *et al.* 2014; King and O'Hanley, 2014), despite surface area being a better representation of habitat size for some fish (Cote *et al*., 2011; Brevé *et al*., 2014) and more suited to the study of stream-lake networks (Jones, 2010). Presumably, the frequent choice of length as the unit of measure is due to the scarcity of surface area data at the broad scale lower order streams. Here, we demonstrated that the unit of quantification can substantially affect estimates of impounded river upstream of barriers. It was largely progress in GIS technology, the FIPEX toolset in particular, and the recent development of geospatial datasets that allowed us to conduct these analyses and make comparisons at the riverscape scale. A rudimentary stream width model similar to the one developed by Betz et al. (2010) enabled us to estimate surface area of unknown stream segments. Further work should be done to refine this model and test its applicability on other river systems.

By conducting scenario-based analysis using GIS and the DCI metrics to add and substract groups of barriers, we were able to determine that based on available data (1) culverts play a less important role on impairing connectivity than dams on these river systems and (2) that masking effects occur wherein the respective benefits of culvert and dam removal as groups is less than when removed together. The positioning of dams near river outlets, especially on the St. Margaret's Bay river system, apparently masked the potential directed (i.e., diadromous) connectivity gains associated with culvert removal. This effect is not captured by alternative approaches that attempt to quantify cumulative connectivity effects of river barriers solely using metrics of upstream impounded river (e.g., Kibler and Tulos, 2013). The results from the simulations of restoring undirected connectivity were especially intriguing. We had hypothesized that if the 'reservoir effect' was accounted for by removing large, non-moving bodies of water from analyses (i.e., the 'no stillwater' treatment), the numeric dominance of culverts coupled with their tendency to be positioned farther from the system outflow than dams would result in greater cumulative benefits associated with culvert removal (Diebel *et al*., 2014). It should be noted, however, that in contrast to Diebel et al. (2014) we did not include a distance decay function which could affect our results. We did find that removing culverts played a more important role in restoring undirected (i.e., potamodromous) connectivity than it did in restoring directed connectivity (ΔDCI_p = 4-10% versus ΔDCI_d = 0-2%), though restoration of dams yielded greater gains in both cases (ΔDCI_p = 23-55% versus ΔDCI_d = 63-93%). The increased importance culverts played in impairing undirected versus directed connectivity may be explained by their tendency to be positioned further from the system outflow to dams, as DCI_p gains can be attained by restoring connectivity between any two fragments of river, not just to and from the river mouth as in the DCI_d.

To date, studies that have employed optimization in this context have used economic costs as a budget constraint (e.g., O'Hanley & Tomberlin, 2005; Zheng *et al.,* 2009; O'Hanley, 2011; O'Hanley *et al.,* 2013; Wu *et al*., 2014). When variable project costs are incorporated into optimization, key budget thresholds may be reached where high-return barriers are affordable (see O'Hanley, 2011), obscuring synergies that may be occurring between projects. There is even currently some doubt that ecological synergies between river restoration projects exist (Pagdam & Webb, 2010). Thus, to further explore this we isolated synergistic effects by setting costs equal for all barrier removal projects and incrementally increasing the number of barriers selected by the optimization models. We were able to (1) identify individual and combinations of barriers that yield the greatest returns in terms of longitudinal connectivity, (2) isolate indications of synergies between barrier removal projects, and (3) identify cases where culverts or combinations of culverts out-ranked dams. When the objective was to maximize undirected connectivity in the Mersey river system, a single culvert out-ranked all other individual barriers for removal. However, when two barriers were permitted to be selected, the culvert was not included having been displaced by the Upper and Lower Lake falls dams. This type of non-additive synergy between individual projects has been reported when simulating restoration of riverine lateral connectivity (Diefenderfer *et al.,* 2012) but to our knowledge this is the first time it has been explicitly reported for barrier removal intended to improve the longitudinal connectivity of rivers.

It is important to emphasize a number of limitations and caveats associated with results reported in this study. First, a comprehensive barrier inventory has not been conducted for these three river systems studied – data was acquired opportunistically from local and governmental datasets. It is thus likely that the numbers of culverts incorporated in our analyses is an underestimate. The permeability of culverts was only crudely estimated and could be also be affecting our results (Bourne *et al.,* 2011). Data collected from site visits to culverts could be used to increase confidence in our estimates of permeability (e.g., Meixler *et al.,* 2009) and stochastic analyses could be conducted to test the sensitivity of results to permeability (e.g., Bourne *et al.,* 2011). Habitat suitability indices could be developed from field surveys or widely available geological data (e.g., Kocovsky *et al*., 2008). Important migratory paths could be pre-identified for species or guilds of species (e.g., Breve *et al.,* 2014) and incorporated using river segment weightings. Dispersal limitations and the spatial arrangement of source populations of key species can also influence the results and should be taken into account, if possible (Pépino *et al*., 2012; Radinger & Wolter, 2015). The timing of migration for key species (Rolls, 2011) could be tied to the temporal dimension of barrier permeability (Bourne *et al*., 2011). Furthermore, more research is needed to understand the limitations of structural connectivity metrics such as the DCI in accounting for population dynamics (Sarnia *et al*., 2015). We note that we did not assess the antagonism on the benefits of individual barrier removal, only groups of barriers, as the computation time required was prohibitive, especially for the DCI_p metric. To address the problem of computational burden, the DCI model formulation could be improved to utilize multiple processors (i.e., multithreading) or dynamic programming methods could be applied to reduce repetitive calculations. Examining the antagonism of the presence of other barriers on the benefits associated with individual barrier removal, rather than barriers removed as groups, would further strengthen our findings by enabling an investigation of the symmetry of antagonism (i.e., culverts masking benefits of dam removal and vice versa). Lastly, we note that the methods presented here not are intended to be used as for rigorous restoration prioritizations, rather we envision they can be used to provide decision makers with a suite of approaches to use as a first-pass assessment towards better understanding of the relative effects of different types of barriers.

It is well established that the unusually strong connectivity of rivers as dendritic ecological systems (Fagan 2002, Grant *et al.,* 2007; Pagdham & Webb, 2010; Eros *et al*., 2012; Seguardo *et al.,* 2013, Peterson *et al*., 2013) leads to spatial interdependence between connectivity restoration projects (O'Hanley & Tomberlin, 2005; Diefenderfer *et al*., 2012; Segurado *et al.,* 2013). Our effort to estimate the degree to which non-additive interactions are associate with barrier removal is an attempt to address one challenge associated the study of cumulative effects of river restoration (Diefenderfer *et al*., 2011). The presence of numerous culverts can result in doubt over whether the benefits of large passage projects at dams are being realized. We envision barrier removal simulations such as the ones presented here as a 'first pass' approach to gauge the interaction between culvert and dam removal. Barrier addition and subtraction simulations such as those presented here show potential to help tease apart the effects of proposed barriers from the effects of existing ones. This approach would help avoid a situation where a new barrier added on a relatively important position of the river would be assessed to have similar or equal connectivity impact as a barrier added to a position of lesser importance. For example, a barrier added in close proximity to a large, impassable barrier near the outflow of the river may be assessed as minimally impairing directed connectivity to and from the ocean due to the presence of the other barrier. However, a barrier at this location would hinder future restoration of directed connectivity more than if it were positioned next to an impassable barrier on a relatively minor tributary. Thus, the methods presented here provide a way to consider the antagonistic masking effects during cumulative effects assessment of proposed projects (Greig *et al.,* 2003; Appendix 2, CEAA, 2014).

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TABLES

Table 1: Dams included in analyses with existing fish passage structures, associated permeability estimates, and repair options.

#	Dam name	River System	Existing Fishway Type	Perm-eability	Option 1: Project Type	Option 1: Pass. After	Option 2: Project Type	Option 2: Pass. After	Option 3: Pro-ject Type	Option 3: Pass. After
1	Jordan Lake	Mersey	No Passage	0.0	US	0.5	DS	0.5	US & DS	1.0
2	Milton Roll	Mersey	Variable upstream passage	0.3	US	0.5				
3	Cowie Falls	Mersey	Pool & weir concrete upstream	0.5	DS	1.0				
4	Deep Brook	Mersey	Pool & weir concrete upstream	0.5	DS	1.0				
5	Lower Great Brook	Mersey	Pool & weir concrete upstream	0.5	DS	1.0				
6	Big Falls	Mersey	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
7	Upper Lake Falls	Mersey	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
8	Lower Lake Falls	Mersey	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
9	Jordan Lake	Mersey	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
10	Beaverskin Lake	Mersey	Downstream passage present	0.5	US	1.0				
11	Hilchemakaar Lake	Mersey	Downstream passage present	0.5	US	1.0				
12	Little Peskowesk Lake	Mersey	Downstream passage present	0.5	US	1.0				
13	Marshall	Sheet Harb.	Downstream bypass	0.5	US	1.0				
14	Ruth Falls	Sheet Harb.	Pool & weirupstream; louver & downstream bypass	1.0		0.0				
15	Malay	Sheet Harb.	Two downstream bypasses	0.5	US	1.0				
16	Governor Lake	Sheet Harb.	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
17	Seloam Lake	Sheet Harb.	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
18	Anti	Sheet Harb.	Downstream bypass	0.5	US	1.0				
19	Ten Mile Lake	Sheet Harb.	Downstream bypass	0.5	US	1.0				
20	Little Indian	St. Marg. Bay	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
20	Sandy Lake	St. Marg. Bay	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
21	Big Indian Lake	St. Marg. Bay	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
22	Five Mile Lake	St. Marg. Bay	No passage	0.0	US	0.5	DS	0.5	US & DS	1.0
23	Impass. Channel	St. Marg. Bay	No passage	0.0	US & DS	1.0				

FIGURES

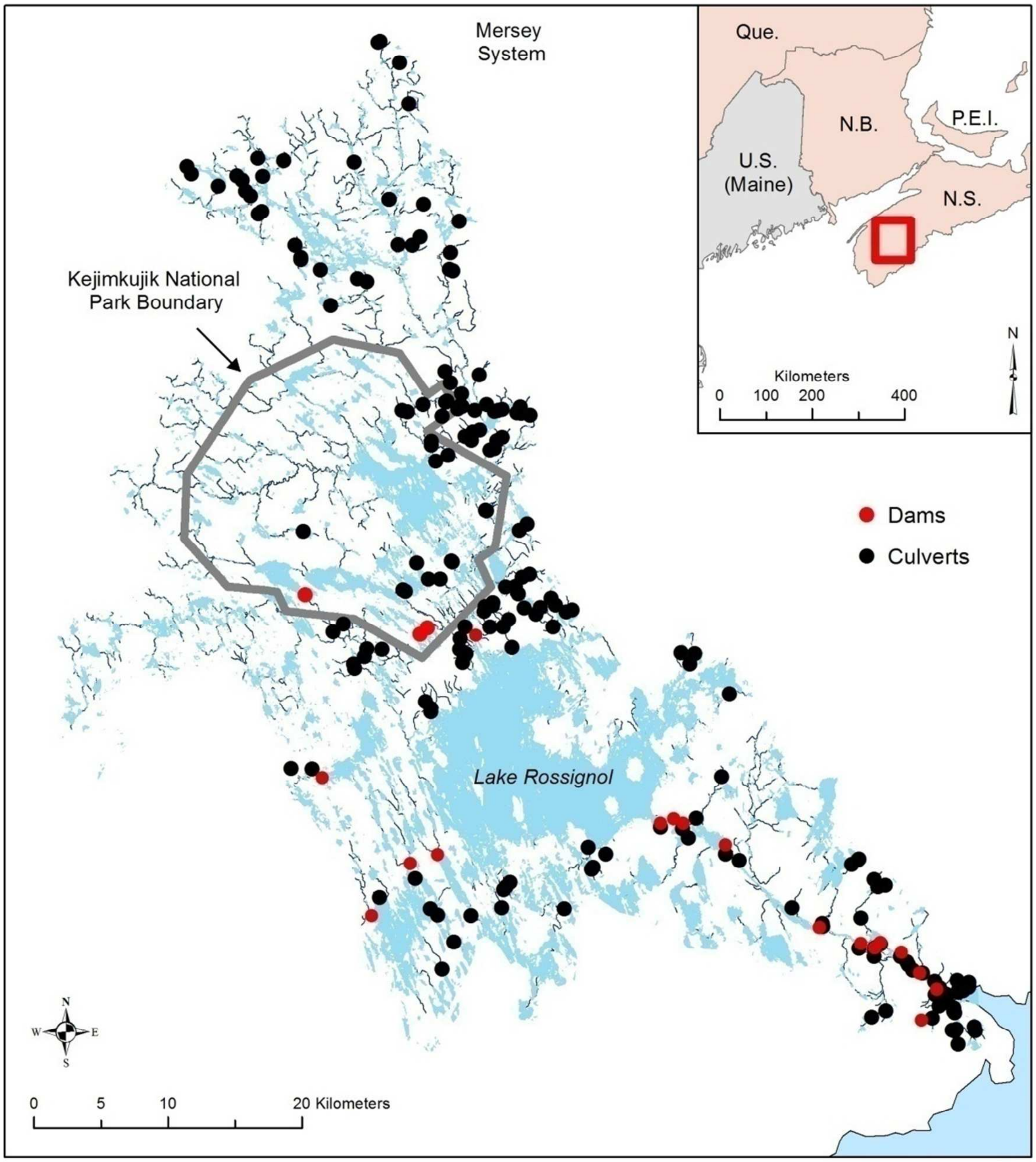

Figure 1: The Mersey River system contains Kejimkujik National Park at its centre. 177 culverts and 11 dams were included in analyses.

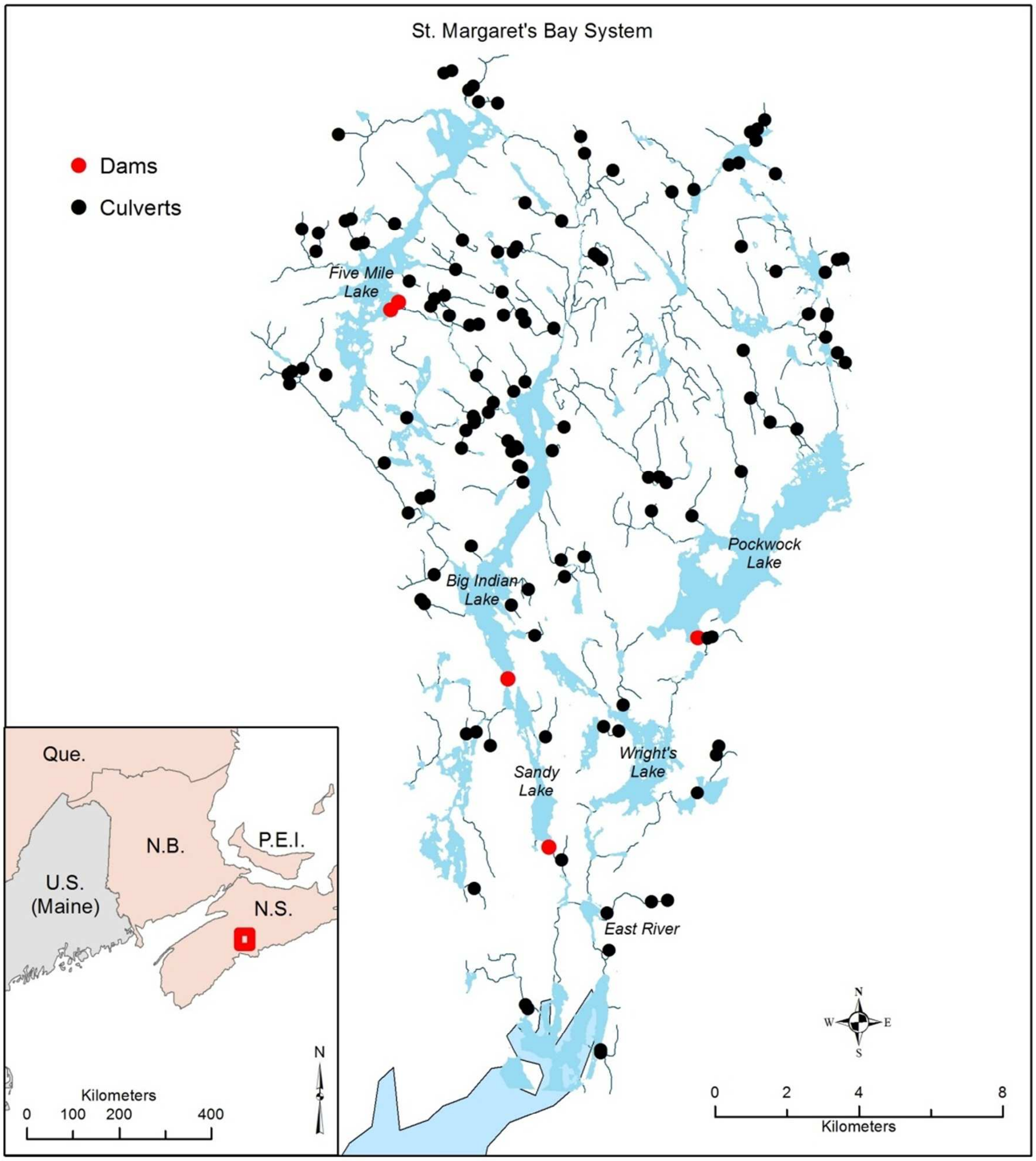

Figure 2: The St. Margaret's Bay system had 125 culverts and nine dams included in analyses.

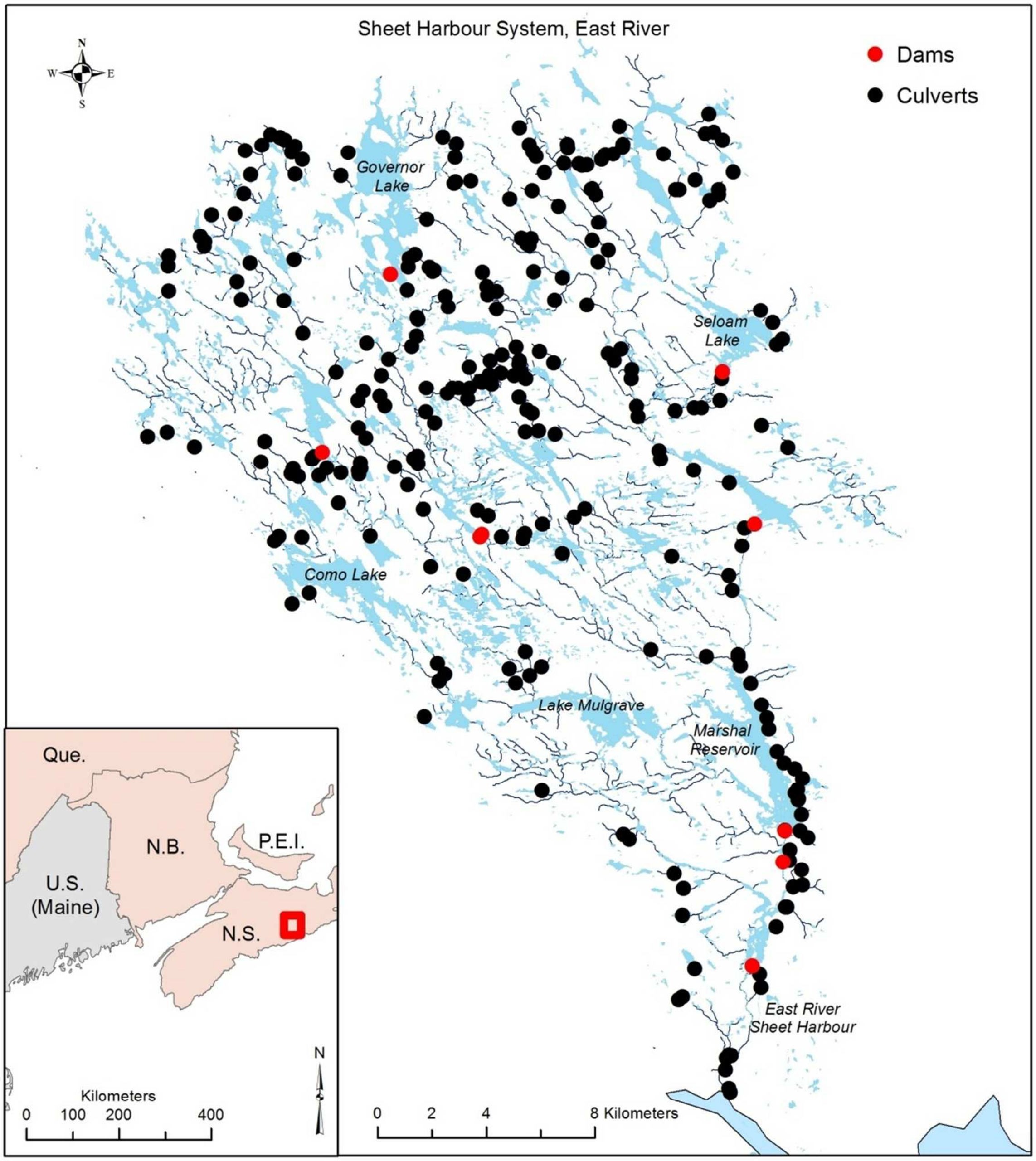

Figure 3: The Sheet Harbour (East River) system had 250 culverts and six dams included in analyses.

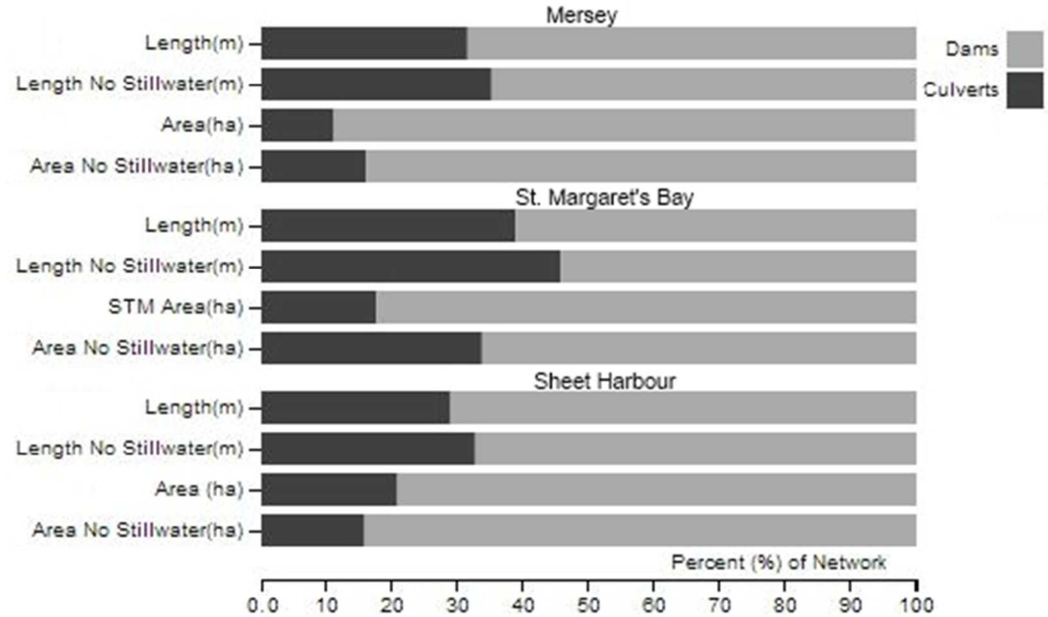

Figure 4: Impounded network by barrier type using four methods of quantification for each system. Results show consistently lower aggregate impounded river network by culverts than dams. Notable differences exist between aggregated impounded network by barrier type between quantification methods, with the amount of network impounded by culverts particularly reduced when area quantification measures were used versus length.

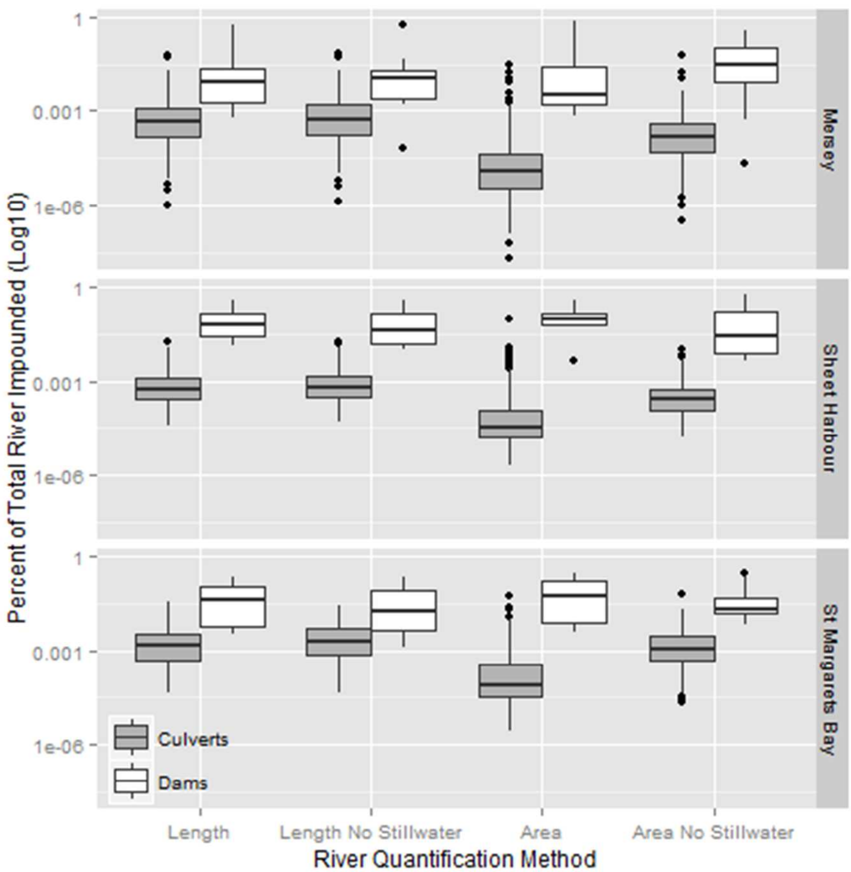

Figure 5: Average river impounded by barrier type was consistently lower for culverts compared to dams for all three systems and all river quantification methods.

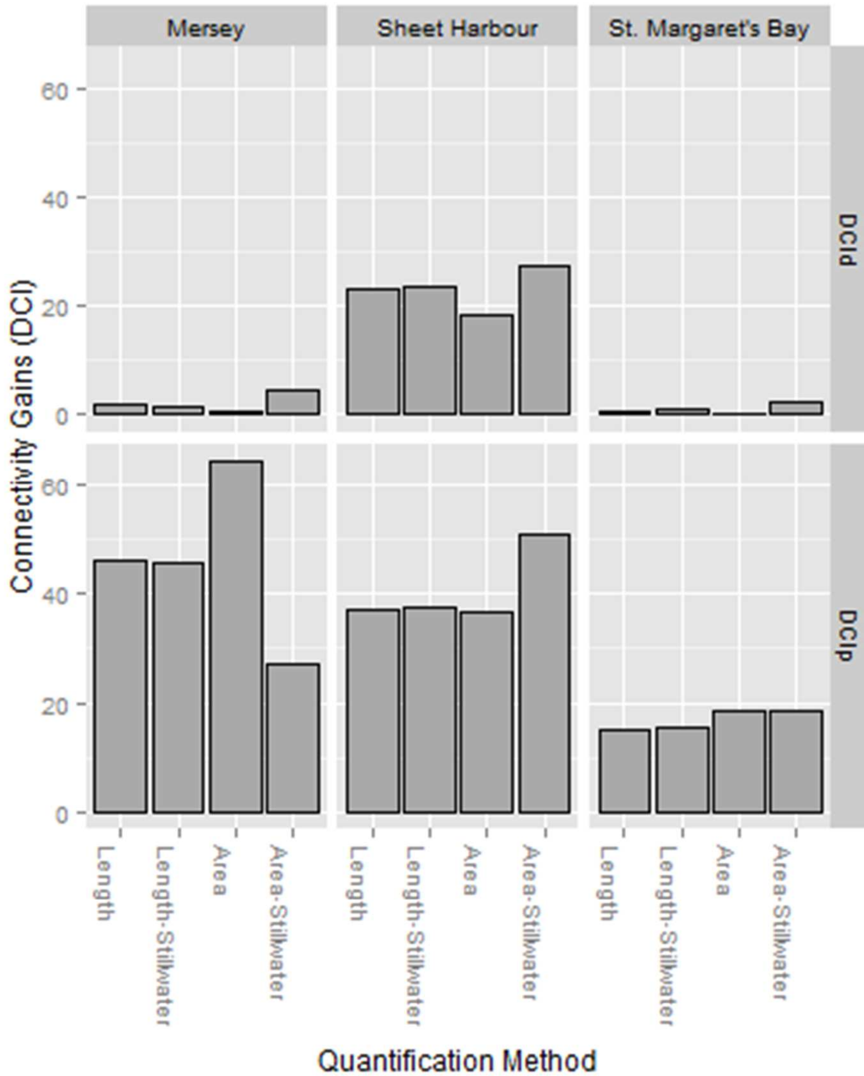

Figure 6: Initial connectivity assessments using the DCI metrics differed between quantification method.

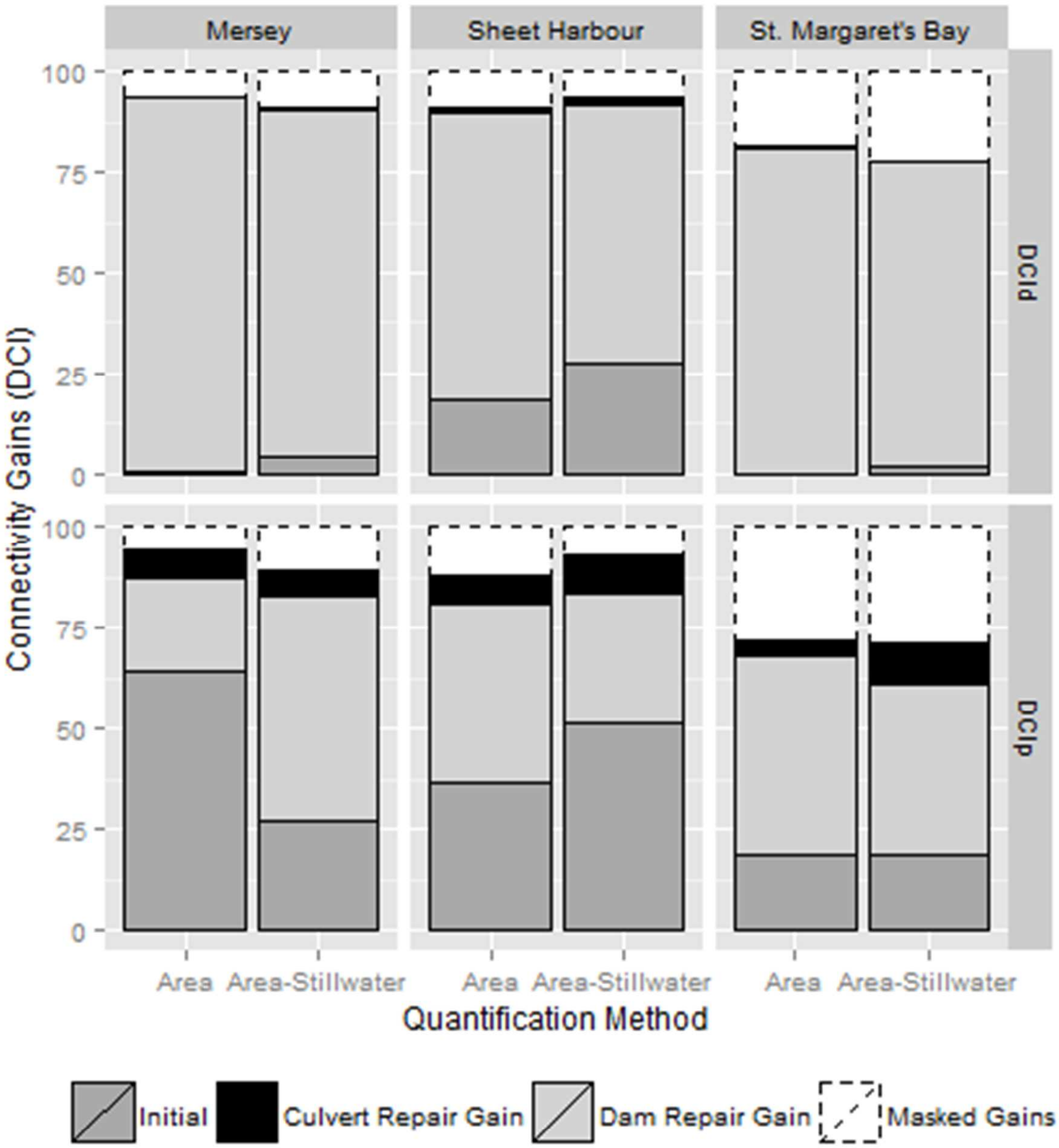

Figure 7: Separate simulations of removing all barriers of a selected type (i.e., culverts or dams) in the presence of the other type were conducted for both culverts and dams as groups. Dashed bars indicate the gains that would have been achieved had both types of barrier been removed at once, indicating a non-additive antagonistic or 'masking' effect of barrier removal.

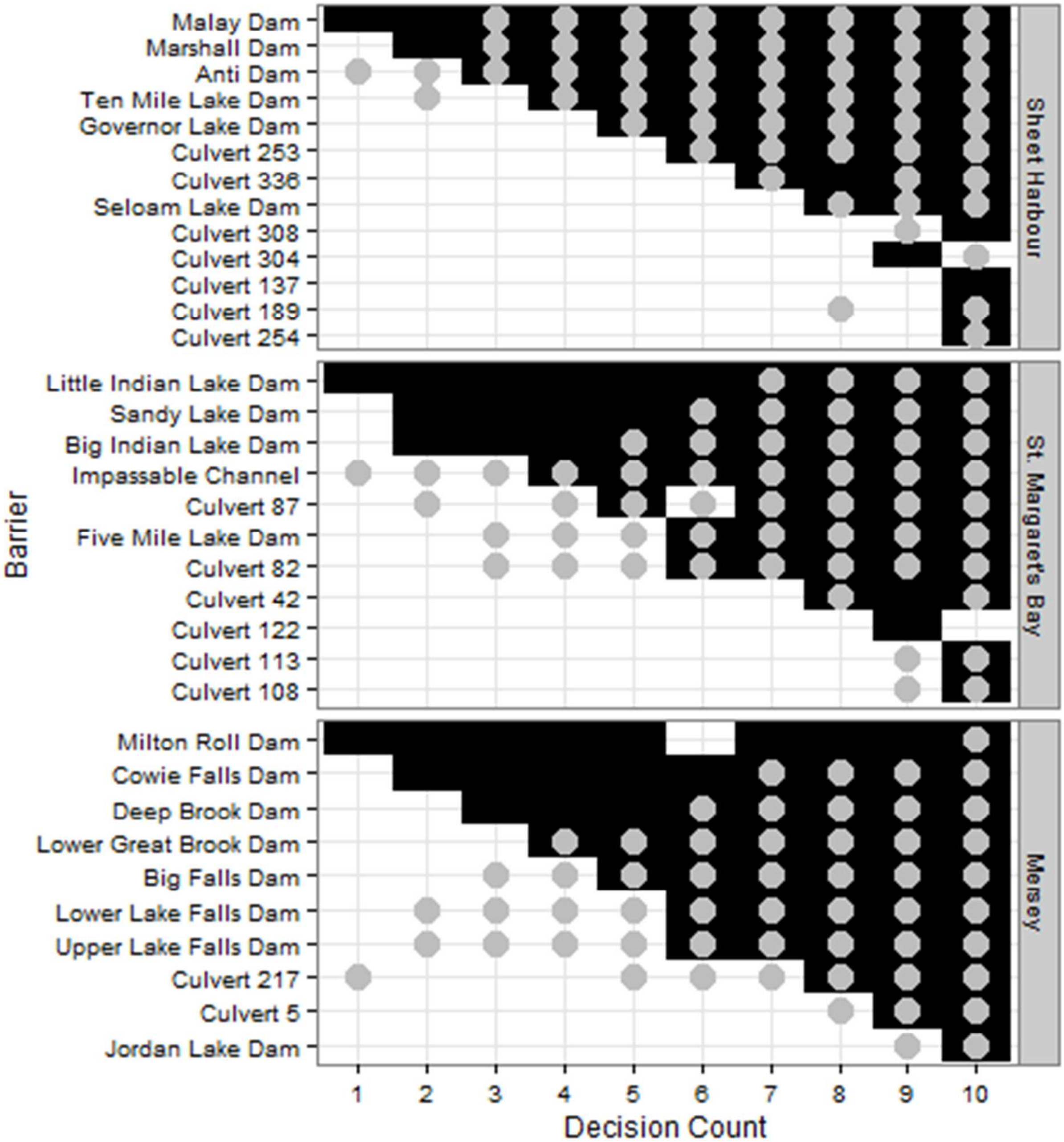

Figure 8: Presence of dams and culverts in optimization outputs for a series of optimization analyses using the directed (rectangles) and undirected (circles) models and the 'Area No Stillwater' river quantification method. X-axis represents number of barriers allowed in outputs. Cases of non-nestedness are apparent where barriers that appear at lower decision counts do not appear at higher ones, indicating synergisms occurring.

Supplemental Materials

Directed Model

We present a mixed integer linear program with the objective of maximizing the largest directed permeability-weighted subnetwork upstream of the network sink (i.e., outflow) given a limited budget. Consider the following notation for maximizing the permeability-weighted river network accessible to and from the ocean or network sink. The set of barriers I are indexed by i and it is assumed that all barriers impair longitudinal connectivity to some degree. The network upstream of any barrier, y_i , is denoted H_i. At each barrier there is a set of options O, indexed by k, each of which has a cost c_{ik}. The options at each barrier are assumed to include a 'do nothing' option which costs nothing and leaves the permeability of that barrier, p_i, unchanged. The permeability of each barrier is assumed to be the product of the upstream and downstream permeabilities. Assuming each barrier has potentially many upstream barriers and exactly one downstream barrier, the set of upstream barriers from a barrier, i, is denoted $U(i)$, indexed by j. The total budget is denoted by β. The following decision variable is used:

$$x_{ik} = \begin{cases} 1 \text{ if option } k \text{ at barrier } i \text{ is chosen} \\ 0 \text{ otherwise} \end{cases}$$

Objective:

$$\text{Maximize } y_0 \tag{1.1}$$

Subject to the following constraints:

$$y_i = \sum_{k \in O(i)} z_{ik} \qquad \forall\, i \in I \tag{1.2}$$

$$z_{ik} \le \sum_{j \in U(i)} p_{ik} y_j + p_{ik} H_i \quad \forall\, i \in I, k \in O(i) \tag{1.3}$$

$$z_{ik} \le z_{ik}^{max} x_{ik} \qquad \forall\, i \in I, k \in O(i) \tag{1.4}$$

$$\sum_{k \in O(i)} x_{ik} = 1 \qquad \forall\, i \in I \tag{1.5}$$

$$\sum_{i \in I} \sum_{k \in O(i)} c_{ik} x_{ik} \le \beta \tag{1.6}$$

where:

y_0 = accessible network upstream of the system sink
I = the set of all barriers
i = a single barrier in the set of all barriers
O_i = the set of optionsat barrier i
k = a single option in the set of options
U(i) = the barrier(s) immediately upstream of i
H = the network immediately upstream of a barrier
j = a single barrier in the set of upstream barriers
y = optimised network upstream
z = accessible network upstream if an option is chosen
x = a binary decision variable
c = the cost of a repair option
β = the total budget

Constraint (1.2) defines the accessible amount of network upstream of any given barrier, *i*, if an option, *k,* is chosen, or z_{ik}. Inequality (1.3) both constrains and defines the accessible network amount above *i* if option *k* is chosen as equal to or less than the sum of the permeability-weighted habitat for all barriers upstream ($p_{ik}y_{j\,j\in\boldsymbol{U}(\boldsymbol{i})}$) plus the accessible network immediately above barrier i (p_{ik} H_i). Combined, (1.3) and (1.4) yield all permeability-weighted network available upstream from barrier i. Inequality (1.5) is the basic connection between the choice of option k and the habitat z_{ik} due to choosing that option; if xi_k is 0 then so is z_{ik}. The maximum possible network upstream is constrained in eqn. (1.5) to *zmax*. Contraint (1.6) limits the number of decisions at each barrier to exactly one and prevents 'partial' projects. The selection of options are constrained by the total budget in (3.7). This model was created for the GLPK as a .mod file (SUPPLEMENT OF MOD FILE). Scaling y_0 to the total network available upstream would yield the DCI_d metric (i.e., $y_0/y_{total}*100$), assuming permeability is defined as the product of the upstream and downstream permeabilities and that successful passage past a barrier in one direction does not affect the probability of successful passage in the opposite direction or past additional barriers (Coté et al., 2009). Thus, applying this model to a single river system also maximizes the DCI_d of the system.

Directed MOD File (GLPK)

```
param nNodes;
param FirstNod;
param mOptions;
set I; /* barriers set - G */
set O, default {1 .. mOptions};
set Upstream, within I cross I; /* matrix of barriers for connectivity -
G*/
set Options, within I cross O;/* matrix of barriers vs. options - G */
param dummy{(i,j) in Upstream}, default 1;
table tab_upstream IN "CSV"
"C:\GunnsModel_REPLACE\FIPEX_GLPKConnectivity.csv":
  Upstream <- [BEID,UpEID], dummy ~ DUMMY;
param perm{ (i,k) in Options} , default 1;
param cost{ (i,k) in Options} , default 100;
table tab_options IN "CSV" "C:\GunnsModel_REPLACE\FIPEX_GLPKOptions.csv":
  Options <- [BARRIER,OPTION1], perm ~ PERM, cost ~ COST;
param Zmax{(i,k) in Options} , default 50000000;

param habitat{ i in I} , default 0;
table tabitat_heheh IN "CSV" "C:\GunnsModel_REPLACE\FIPEX_GLPKHabitat3.csv":
  I <- [BARRIER], habitat ~ HABITAT;

param Budget, default 1000;
```

```
var y{ i in I}, >=0;                  /* optimized acessible habit above i
*/
var z{ (i,k) in Options}, >=0;        /*  accessible habit above i  if op-
tion k is chosen*/
var x{ (i,k) in Options}, binary;    /* option choice variables at node i
*/

maximize obj:  y[FirstNod];

s.t. HabAbove{i in I}:  y[i] = sum{ k in O: (i,k) in Options} z[i,k];

s.t.  HabZ{ i in I,  k in O: (i,k) in Options}:  z[i,k] <=  sum{j in I:
(i,j) in Upstream}( perm[i,k] * y[j]) + perm[i,k]*habitat[i];

s.t.  UpZ{ i in I,  k in O: (i,k) in Options}:  z[i,k] <= Zmax[i,k]*x[i,k];

s.t.  SumX{ i in I}:  sum{ k in O: (i,k) in Options} x[i,k] = 1;

s.t.  BudgetCon:  sum { i in I,  k in O: (i,k) in Options} cost[i,k]* x[i,k]
<= Budget;

solve;

printf "         Barrier       Option     \n";
printf {i in I,  k in O: ((i,k) in Options) and (x[i,k] !=0) }:
"%13s   %11s     %12g  \n", i,  k,   x[i,k];

table res1{i in I,  k in O: ((i,k) in Options) and (x[i,k] !=0) } OUT "CSV"
"C:\GunnsModel_REPLACE\Res1.csv": i~Barrier,k~Option, x[i,k]~OptionChioce;

printf "              \n";
printf "          Budget        Habitat     \n";
printf "   %12g    %12g  \n", Budget, y[FirstNod];

printf "Habitat     \n" > "C:\GunnsModel_REPLACE\ZMaxOutput.txt";
printf y[FirstNod] >> "C:\GunnsModel_REPLACE\ZMaxOutput.txt";

printf {i in I: (y[i] !=0) }: "   Y[i]     %13s     %12g  \n", i,   y[i];
table res3{i in I: (y[i] !=0) } OUT "CSV" "C:\GunnsModel_REPLACE\Res3.csv":
i~Barrier, y[i]~Habitat;

printf {i in I,  k in O: ((i,k) in Options) and (z[i,k] !=0) }: "
z[i,k]    %13s   %11s     %12g  \n", i,  k,  z[i,k];
table res2{i in I,  k in O: ((i,k) in Options) and (z[i,k] !=0) } OUT "CSV"
"C:\GunnsModel_REPLACE\Res2.csv": i~Barrier,k~Option, z[i,k]~Habitat;

end;
```

Undirected Model

To maximise undirected longitudinal connectivity, a similar approach can be taken. The undirected model has a similar objected to the program presented in O'Hanley (2011) and O'Hanley et al. (2013) and aims to maximise the *single largest undirected sub-network*. The problem of optimising for directed connectivity is a sub-problem of solving for undirected connectivity. Each barrier in the network is conceptualized as an outflow of both its connected upstream and downstream sub-networks; the barrier is the centre of two tree-like (i.e., dendritic) networks upstream and downstream.

To formulate the undirected model, consider the following notation in addition to what was defined for the directed model. Let the central barrier i to a given undirected subnetwork be defined as the single barrier downstream of the corresponding central river segment H_i. Let us assume for the moment that there are *many* barriers encountered 'downstream' from barrier i, denoted as a set by $D(i)$ and indexed by m. The term 'downstream' is thus applied loosely; all barriers in the downstream set are not necessarily downstream as defined by the flow of the river. Rather, they are the first barriers encountered in the subnetwork found in the downstream direction from barrier i. Note dendricity is still assumed. The network segment immediately downstream from a central barrier i can be given by H_m (i.e., the network upstream of the single downstream barrier m, following the flow of the river). Let the permeability-weighted accessible network found in the downstream direction from the central subnetwork H_i be denoted by q_i. Finally, the following additional decision variable is included:

$$\alpha_i = \begin{cases} 1 \; if \; barrier \; i \; is \; the \; central \; barrier \; to \; the \; maximal \; subnetwork \\ 0 \; otherwise \end{cases}$$

The upstream network accessible thru a given barrier z_i is calculated as it was in (1.3) of the directed model, but here the downstream accessible habitat is also required. The permeability-weighted accessible network downstream of a given barrier i is thus:

$$q_i = p_i H_m + \sum_{m \in D(i)} p_i w_m \quad i \in I \tag{1.4}$$

As in the directed model, the total network quantity downstream of *i* is defined by one contraint and one inequality. The partner constraint to (1.4) is thus the equivalent to constraint (1.2) which defines the optimal habitat downstream w_i:

$$w_i = \sum_{k \in O} q_{ik} \quad i \in I \tag{1.5}$$

The total accessible network through barrier *i* in both directions is thus:

$$y_i + w_i \tag{1.6}$$

In the undirected model, however, the 'centre' of the maximal sub-network must be a river segment, denoted H_i, and should not be weighted by permeability. The permeability-weighted H_i is calculated in (3.8) but must then be adjusted later to 'un-weight' it. 'Un-weighting'the network immediately upstream of the barrier, given by H_i, from the permeability, the sub-network quantity connected to the segment above barrier *i* becomes:

$$y_i + w_i - p_{ik} H_i + H_i \tag{1.7}$$

To determine the set of barriers immediately downstream of a barrier *D(i)*, more than one method could be employed. The connectivity matrix generated by the GIS toolset that defines network connectivity upstream from the network sink could be transformed; a sub-network downstream of barrier *i* could be extracted using a matrix transformation or with a simple algorithm. This could be performed 'on-the-fly' in the optimisation model or pre-calculated by the GIS toolset for all barriers (all i in *I*). Another approach was used here to avoid matrix transformations: to calculate permeability-weighted network downstream, the total network upstream of the single immediately downstream barrier *m* following network flow is found.

Let us now assume that the number of barriers in the set downstream *D(i)* from the central barrier i is restricted to one, and thus follows the flow of water in the network. Again, let us assume the network is dendritic. Let us also denote the set of barriers upstream from *m* as *U(m)* and be indexed by *j*. The calculation of downstream accessible habitat is thus reformulated as:

$$q_{ik} = p_{ik}H_m + \sum_{j\in U(m)} p_{ik}y_j - z_{ik} + p_{ik}w_m \quad i \in I, k \in O(i), m \in D(i) \qquad (1.8)$$

In (1.8), the habitat downstream of the central barrier in a subnetwork *i* is weighted by the permeability at *i* and is thus $p_{ik}H_m$. The sum of all permeability-weighted habitat upstream of the immediate down-stream barrier *m* is then found ($\sum_{j\in U(m)} p_{ik}y_j$) but, to avoid double-counting the network upstream of the central barrier *i,* this is subtracted ($-z_{ik}$). The habitat downstream of *m* is then subsequently found as $p_{ik}w_m$.

The entire second linear optimisation model, for maximising *the largest single undirected sub-network* is thus:

objective:

maximize Y^{max} (1.9)

subject to the following contraints:

$$y_i = \sum_{k \in O(i)} z_{ik} \qquad \forall\, i \in I \tag{1.10}$$

$$z_{ik} \leq \sum_{j \in U(i)} p_{ik} y_j + p_{ik} H_i \qquad \forall\, i \in I, k \in O(i) \tag{1.11}$$

$$z_{ik} \leq z_{ik}^{max} x_{ik} \qquad \forall\, i \in I \tag{1.12}$$

$$w_i = \sum_{k \in O} q_{ik} \qquad \forall\, i \in I \tag{1.13}$$

$$q_{ik} \leq \sum_{j \in U(m)} p_{ik} y_j - z_{ik} + p_{ik} H_m + p_{ik} w_m \qquad \forall\, i \in I, k \in O(i), m \in D(i) \tag{1.14}$$

$$q_{ik} \leq q_{ik}^{max} x_{ik} \qquad \forall\, i \in I \tag{1.15}$$

$$\sum_{i \in I} \sum_{k \in O(i)} c_{ik} x_{ik} \leq \beta \tag{1.16}$$

$$\sum_{k \in O(i)} x_{ik} = 1 \qquad \forall\, i \in I \tag{1.17}$$

$$\sum_{i \in I} a_i = 1 \tag{1.18}$$

$$Y^{max} \leq y_i + w_i - p_{ik} H_i + H_i + M^P (1 - a_i) \tag{1.19}$$

where:

y_0 = *accessible network upstream of the system sink*

I = the set of all barriers

i = a single barrier in the set of all barriers

O = the set of options

k = a single option in the set of options

U(i) = the barrier(s) immediately upstream of i

H = the network immediately upstream of a barrier

j = a single barrier in the set of upstream barriers

y = optimised network upstream

z = accessible network upstream if an option is chosen

x = a binary decision variable

c = the cost of a repair option

β = the total budget

α_i = *a binary integer variable indicating whether a barrier is the parent node of the maximal subnetwork*

Y^{max} = *the network quantity associated with the maximal subnetwork*

M^P = *the largest network quantity possible (bounding variable)*

w_i = *the optimal subnetwork downstream of i*

q_{ik} = *accessible network downstream of i if option k is chosen*

D(i) = the barrier downstream of i

The objective (3.13) is to maximise Y^{max}, the network quantity available above and below a central, undirected subnetwork barrier i. Constraint (1.10) and inequalities (1.11) and (1.12) are the same as the directed model and collectively define upstream permeability-weighted network. Constraint (1.13) and inequalities (1.14) and (1.15) collectively define the permeability-weighted downstream network from the central barrier i. Inequality (1.15) is formulated differently from the equivalent inequality (1.12) to avoid a matrix transformation. The 'set' of downstream barriers *D(i)* includes only one barrier m, thus assuming a dendritic network. All permeability-weighted network upstream from m is calculated ($\sum_{j\in U(m)} p_{ik}y_j$), subtracting the network upstream of the central barrier ($-z_{ik}$), already counted in (1.11). The permeability-weighted network downstream from m is then added ($+p_{ik}w_m$). Constraint (1.13) and inequality (1.14) therefore act together to calculate the permeability-weighted downstream network from barrier i. Inequalities (1.16) and constraint (1.17) are the same as in the directed model. Constraint (1.18) limits the choice of subnetwork to one, as the objective is to choose a single subnetwork that is the largest possible given the budget. Inequality (1.19) defines and bounds the size of the maximal subnetwork. It is calculated as the sum of the maximal upstream y_i and downstream w_i permeability-weighted network with an adjustment to de-weight the central network segment H_i from any permeability $(-p_{ik}H_i + H_i)$. M^p is a bounding variable that is the maximum possible subnetwork, used to bound the model if no subnetwork has been selected. This model was formulated for input into the the GLPK, as a .mod file (see UNDIRECTED MOD SUPPLEMENT).

Undirected Mod File (GLPK)

```
param nNodes;
param FirstNod;
param mOptions;
set I; /* barriers set - G */
set O, default {1 .. mOptions};
set Upstream, within I cross I; /* matrix of barriers for connectivity -
G*/
set Downstream, within I cross I; /* matrix of downstream barriers - G
NEW */
set Options, within I cross O;  /* matrix of barriers vs. options - G */
param dummy{(i,j) in Upstream}, default 1;
param dummy_d{(i,m) in Downstream}, default 1;
/* NEW reversed i,m? */

table tab_upstream IN "CSV"
"C:\GunnsModel_REPLACE\FIPEX_GLPKConnectivity.csv":
  Upstream <- [BEID,UpEID], dummy ~ DUMMY;

table tab_downstream IN "CSV"
"C:\GunnsModel_REPLACE\FIPEX_GLPKConnectivity.csv":   /* NEW */
  Downstream <- [UpEID,BEID], dummy_d ~ DUMMY;

param perm{ (i,k) in Options} , default 1;
param cost{ (i,k) in Options} , default 100;
table tab_options IN "CSV" "C:\GunnsModel_REPLACE\FIPEX_GLPKOptions.csv":
  Options <- [BARRIER,OPTION1], perm ~ PERM, cost ~ COST;
param Zmax{(i,k) in Options} , default 50000000;
param Qmax{(i,k) in Options} , default 50000000;
/* NEW */

param habitat{ i in I} , default 0;
table tabitat_heheh IN "CSV" "C:\GunnsModel_REPLACE\FIPEX_GLPKHabitat3.csv":
  I <- [BARRIER], habitat ~ HABITAT;


param Budget, default 1000;
param MArea, default 1.E+08;

var y{ i in I}, >=0;                    /* optimized acessible habit above
i */
```

```
var z{ (i,k) in Options}, >=0;          /*  acessible habit above i  if op-
tion k is chosen*/
var x{ (i,k) in Options}, binary;      /* option choice variables at node i
*/
var w{ i in I}, >=0;
/* NEW */
var q{ (i,k) in Options}, >=0;
/* NEW */


var iamx{i in I}, binary;
var AMaxMax, >=0;

maximize obj:  AMaxMax;

s.t. HabAbove{i in I}:  y[i] = sum{ k in O: (i,k) in Options} z[i,k];
s.t.  HabZ{ i in I,  k in O: (i,k) in Options}:  z[i,k] <=  sum{j in I:
(i,j) in Upstream}( perm[i,k] * y[j]) + perm[i,k] * habitat[i]; /* end mod-
ified */
s.t.  UpZ{ i in I,  k in O: (i,k) in Options}:  z[i,k] <= Zmax[i,k]*x[i,k];
s.t.  SumX{ i in I}:  sum{ k in O: (i,k) in Options} x[i,k] = 1;
s.t.  BudgetCon:  sum { i in I,  k in O: (i,k) in Options}(cost[i,k]*
x[i,k]) <= Budget;

s.t. DownQ{ i in I,  k in O: (i,k) in Options}:  q[i,k] <= Qmax[i,k]*x[i,k];
/* NEW */
s.t. MaxAMax{i in I, k in O: (i,k) in Options}: AMaxMax >= y[i] + w[i]-
perm[i,k] * habitat[i] + habitat[i] - MArea*iamx[i];
/* NEW */
s.t. BoundAmax{i in I, k in O: (i,k) in Options}: AMaxMax <= y[i] + w[i] -
perm[i,k] * habitat[i] + habitat[i] + MArea*(1-iamx[i]);
/* NEW */

s.t. HabBelow{i in I}:  w[i] = sum{ k in O: (i,k) in Options} q[i,k];
s.t. HabQ{ i in I, k in O: (i,k) in Options}:  q[i,k] <=  sum{m in I: (i,m)
in Downstream}(sum{j in I: (m,j) in Upstream}( perm[i,k] * y[j])) - z[i,k]
+ sum{m in I: (i,m) in Downstream}(perm[i,k] * habitat[m]) +sum{m in I:
(i,m) in Downstream}(perm[i,k] * w[m]);  /* NEW */

s.t. ChooseMx:  sum{i in I} iamx[i]=1;

solve;
printf {i in I: (iamx[i] !=0) }: "   The central
node:  %13s   %11s     %12g  \n", i;
printf "          Barrier         Option      \n";
printf {i in I,  k in O: ((i,k) in Options) and (x[i,k] !=0) }:
"%13s   %11s     %12g  \n", i,  k,  x[i,k];

table res1{i in I,  k in O: ((i,k) in Options) and (x[i,k] !=0) } OUT "CSV"
"C:\GunnsModel_REPLACE\Res1_undirected.csv": i~Barrier,k~Option,
x[i,k]~OptionChioce;

printf "              \n";
printf "           Budget        Habitat     \n";
```

```
printf "   %12g    %12g  \n", Budget, y[FirstNod];

printf "Habitat     \n" > "C:\GunnsModel_REPLACE\UNDIROutput.txt";
/* NEW */
printf AMaxMax >> "C:\GunnsModel_REPLACE\UNDIROutput.txt";
/* NEW */
printf  "\n The central node:     \n" >>
"C:\GunnsModel_REPLACE\UNDIROutput.txt";   /* NEW */
printf {i in I: (iamx[i] !=0) }: i >>
"C:\GunnsModel_REPLACE\UNDIROutput.txt";  /* NEW */

printf {i in I: (y[i] !=0) }: "   Y[i]     %13s     %12g  \n", i,   y[i];
table res3{i in I: (y[i] !=0) } OUT "CSV"
"C:\GunnsModel_REPLACE\Res3_undirected.csv": i~Barrier, y[i]~Habitat;

printf {i in I,  k in O: ((i,k) in Options) and (z[i,k] !=0) }: "
z[i,k]    %13s   %11s     %12g  \n", i,  k,  z[i,k];
printf {i in I,  k in O: ((i,k) in Options) and (q[i,k] !=0) }: "
q[i,k]    %13s   %11s     %12g  \n", i,  k,  q[i,k];
printf {i in I: (iamx[i] !=0) }: "   The central
node:  %13s   %11s     %12g  \n", i;
printf "The budget used:  %13s   %11s     %12g  \n", sum { i in I,  k in O:
(i,k) in Options}(cost[i,k]* x[i,k]);
printf "The maximal subnetwork: %13s   %11s     %12g  \n", AMaxMax;

table res2{i in I,  k in O: ((i,k) in Options) and (z[i,k] !=0) } OUT "CSV"
"C:\GunnsModel_REPLACE\Res2_undirected.csv": i~Barrier,k~Option,
z[i,k]~Habitat;

end;
```

Stream Width Model

Streams were represented by lines rather than polygons for stream widths less than about 27 m in the Nova Scotia Hydrographic Network (NSHN; Service Nova Scotia and Municipal Relations, 2012). To address this, relationships between stream width and five available variables were explored: 'Distance to Headwaters', 'Distance to Mouth', 'Strahler' stream order, 'Shreve' stream order, and gradient. A weak relationship between total upstream river network length and wetted stream widths was identified and chosen to calibrate a rudimentary stream width model. However, this was deemed acceptable as only 472 of 6436 (7.3% by count, 5.2% by length) line segments requiring width estimates had an associated 'Distance to Headwaters' greater than 25 km. Furthermore, only 261 of 6436 line segments (4.05% by count, 2.83% by total length) had more than 50 km of total network length between their midpoint and the headwaters. We note here that the relationship was derived from a subset of known widths acquired by site surveys that had a 'distance to headwaters' <= 25 km and wetted width <= 27 m (Pearson's R = 0.423, n=49).