Connectivity, passability and heterogeneity interact to determine fish population persistence in river networks

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Abstract

The movement of fish in watersheds is frequently inhibited by human-made migration barriers such as dams or culverts. The resulting lack of connectivity of spatial subpopulations is often cited as a cause for observed population decline. We formulate a matrix model for a spatially distributed fish population in a watershed, and we investigate how location and other characteristics of a single movement barrier impact the asymptotic growth rate of the population. We find that while population growth rate often decreases with the introduction of a movement obstacle, it may also increase due to a "retention effect". Furthermore, obstacle mortality greatly affects population growth rate. In practice, different connectivity indices are used to predict population effects of migration barriers, but the relation of these indices to population growth rates in demographic models is often unclear. When comparing our results with the Dentritic Connectivity Index, we see that the index cannot capture the retention effect nor the influences of obstacle mortality. We argue that structural indices cannot entirely replace more detailed demographic models to understand questions of persistence and extinction. We advocate the development of novel functional indices and characteristics.

Keywords

fish population, watershed, migration barrier, connectivity index, population growth rate

1 Introduction

Freshwater ecosystems are in severe peril worldwide due to habitat degradation and fragmentation. Unlike terrestrial habitats, river systems are particularly susceptible to fragmentation due to their dendritic network geometry, i.e. the hierarchical arrangement of branching stream reaches [1, 2]. Populations inhabiting these dendritic networks have, by nature and topology, limited access to large parts of the watershed, even in the absence of any disconnecting structures [3–5].

Human development often adds disconnecting structures (e.g. dams or culverts) for transportation, energy generation, protection, or leisure. Nowadays, only a third of the world's largest rivers remain free-flowing from source to mouth [6]. While these developments have clear benefits to humans, they also have obvious effects on the geomorphological aspects of rivers as well as on their fauna and flora. For example, dams regulate flow speed and water level, modify sediment and nutrient supply in reaches upstream and downstream, and can pose an insurmountable obstacle for migrating fish, diadromous and potadromous [7]. The effects of damming on fish populations have been well documented, either through changes in patch occupancy [8], asymptotic growth rate [9, 10], extinction risk [1, 3, 11] or population demogenetics [3].

Great efforts are underway to understand the effects of human-imposed dispersal barriers on the fate of biological populations. Network-theoretic approaches are being used increasingly to evaluate and explore the effects of obstacles on ecosystem function in terrestrial and aquatic ecosystems [12]. Resulting insights can be applied in development planning and conservation prioritization. A key focus is on *habitat connectivity* as an attempt to capture the existence and importance of dispersal pathways in spatially distributed habitat patches. Many indices exist, on the landscape level or patch level, to measure in some sense how connected one individual patch or the entire network of patches are [4, 12–17]. The intuitive common idea being promoted is that a higher connectivity index represents better conditions for the respective populations [4, 5, 15].

A recent review devoted specifically to connectivity metrics for watersheds explores the relationships between eight different connectivity metrics, some of which are global (a single metric for a watershed) some are local (a value for each patch in the watershed) [18]. They found that so-called "path-counting" metrics represent "an organisms ability to disperse throughout the watershed" and may therefore be used to assess the impact of barriers. All the metrics studied in [18] assume that each barrier is completely impassable, dividing a habitat in two disconnected sub-habitats. Many barriers, however, are somewhat passable [19]. A relatively recent path-counting metric that allows for partial passability is the *dentritic connectivity index* (DCI) [4]. Clearly, passability is species specific, and so the definition of this index was specialized [4] depending on the life history of the fish species under consideration: DCI_P for potadromous (migrating within freshwater) and DCI_D diadromous (migrating between fresh water and sea) species. In either case, DCI is a network-scale measure of connectivity, specific to freshwater systems, simple enough to examine the effects and interactions of multiple barriers and their permeability, i.e. the movement probability of individuals between sections connected by the obstacles [4, 16, 20].

What is missing for DCI is a detailed study of the relationship between the value of the index and meaningful population-level characteristics, such as persistence conditions or mean extinction times. In fact, such studies are largely missing for many indices applied to connectivity [12] and other areas, e.g. biodiversity [21]. A first step in uncovering the relation between structural connectivity (as measured by most indices) and functional connectivity (as expressed by population characteristics) was to compare the results of a movement-only, patch-occupancy simulation model with DCI [8]. In the present work, we include population growth and survival as well as a more detailed description of separate aspects of movement barriers into a spatially explicit patch model. We compare how movement barriers affect population persistence conditions, as measured by the long-term population growth rate, and DCI for different network geometries. Incorporating demographics to understand population persistence is obviously necessary, since persistence requires that an individual, on average, replaces itself over its lifetime [22]. Movement barriers in rivers not only inhibit migration, they often also are a significant source of direct mortality (e.g. power-generating dams) or indirect stress and increased energy expenditure of fish (e.g. fish ladders) that needs to be considered to understand demographic outcomes.

Our model is a strategic, generation-based model for a hypothetical potadromous fish species in randomly generated watersheds. We represent reaches of the river or stream as patches in our model and project changes in the density of the population on each patch

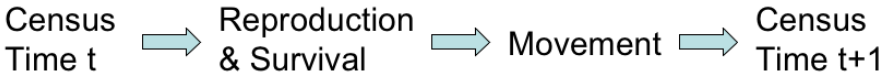


Figure 1: The life cycle of the model organism. We census the population after movement and before reproduction and survival.

through demographics and migration forward in time. The dominant eigenvalue of the resulting projection matrix then represents the asymptotic population growth rate; if it is greater than unity, then the population persists, if not, it becomes extinct [23]. Similar matrix models were previously applied to fish populations by various authors [9, 10, 24, 25] but with somewhat different goals. We give a detailed description of the model, the aspects of a barrier, and the generation of the network structure in the next section. We then explore in detail how the location of a single obstacle affects the population growth rate, and whether and to what extent this change can be predicted by a corresponding change in DCI. We find that only certain aspects of functional connectivity can be captured by DCI and argue that other known structural metrics are unlikely to capture those details. We advocate that more mechanistic models are necessary to predict the ecological impact of disersal barriers in watersheds or to prioritize conservation efforts.

2 Model and Methods

We model the spatial population dynamics of a potadromous fish species in a dendritic river network. We represent each reach in the network as a patch of primary habitat where individuals reproduce and survive (see below). Direct connections between reaches are migration links between patches. The population density in each patch changes from year to year as individuals first reproduce locally and then migrate between patches. In a network of n patches, we denote the population density in patch i and year t as $N_{i,t}$. These densities change from year to year due to population dynamics and migration (see Figure 1) according to the equation

$$N_{i,t+1} = \sum_{j}^{n} c_{i,j} g_j(N_{j,t}) N_{j,t}. \tag{1}$$

Per capita survival and offspring production may depend on population density and patch attributes and are denoted by $g_j(N_{j,t})$. The probability that an individual, initially located in reach j resides in patch i at the end of the season is denoted by $c_{i,j}$.

Under the assumption that there is no Allee effect [26], we linearize model (1) at low density to evaluate conditions for population persistence. We denote $g_j'(0) = r_j + s_j$, where r_j is the per-capita number of offspring produced at site j and s_j is the survival probability in that reach. The linearized model then becomes

$$N_{i,t+1} = \sum_{j}^{n} c_{i,j}(r_j + s_j)N_{j,t}. \tag{2}$$

Using the (column) vector $\mathbf{N}(t) = (N_{1,t}, \dots, N_{n,t})^T$ of population densities in each patch, we can write the linear model conveniently in matrix form as

$$\mathbf{N}(t+1) = B\mathbf{N}(t) \tag{3}$$

where the projection matrix B is given by the product of the migration matrix $C = (c_{i,j})$ and the diagonal matrices for production and survival, i.e.

$$B = C[R + S] \quad \text{with} \quad R = \text{diag}(r_j), \quad S = \text{diag}(s_j). \tag{4}$$

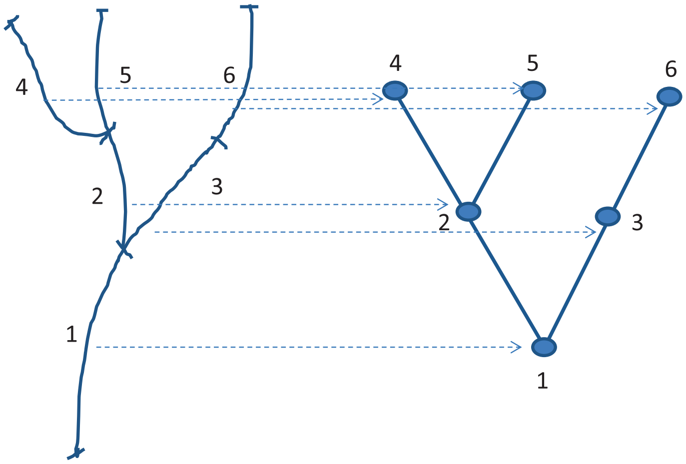
Before we can derive the exact form of the migration matrix, we explain in more detail the representation of reaches in the watershed.

2.1 Graphs of dendritic networks

A river network can be represented as a spatial graph [27]. We represent a river reach, or a suitable part thereof, by a node that is attributed with physical and ecological characteristics corresponding to the reach. A connection between reaches corresponds to an edge in the graph (Figure 2). While reaches 1, 2, 4, 5 in this Figure are delineated by confluences, reaches 3 and 6 could be separated by a physical disruption, such as a waterfall or culvert. Alternatively, the separation between 3 and 6 could be introduced to make all patches correspond to roughly similar length sections of the river network. The dentritic structure of the river network results in a tree graph [1, 2, 11]. We choose the river mouth to be the root of the tree.

The geometry of a (dendritic) network with n nodes is encapsulated in the adjacency matrix, A, a binary $n \times n$ matrix. This matrix is the fundamental structure of the migration matrix. Entries a_{ij} equal to one indicate a connection between reaches i and j, whereas zero entries indicate that reaches i and j are not adjacent, see Figure 2. By convention, diagonal elements are zero.

We consider the situation where each reach is adjacent to at most two upstream reaches. The simplest network then is a linear network, where each reach connects to exactly one upstream reach, the most complex is the complete binary network with exactly two. We generate intermediate geometries numerically according to a stochastic branching process [3]. Starting from the root, the tree graph is generated using a probability triplet, indicating the probabilities of a reach connecting to zero, one or two reaches upstream. The number of reaches and the height of the graph can vary. For example, networks in Figure 2(b) and Figure 3(a) can both be generated with the triplet $(0, 0.5, 0.5)$ and height 3, but have a different number of reaches. We constrain the stochastic generation process to triplets of the form $(0, \beta, 1 - \beta)$, where β is the probability of having one reach upstream. When $\beta = 0$, the complete binary tree is generated, and when $\beta = 1$, we get the linear network. We then



(a) (b)

$$A = \begin{pmatrix} 0 & 1 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \end{pmatrix}$$

(c)

Figure 2: (a) A river network with 6 reaches. (b) Spatial graph representation of the river network. (c) The corresponding adjacency matrix.

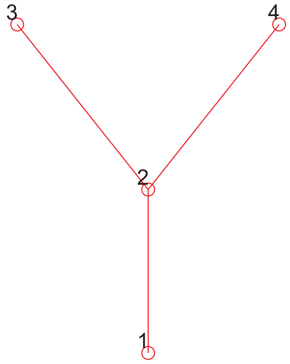
generate a graph until it contains a given height or number of nodes. We understand the simpler situations such as in Figures 2 and 3 as “modules” of a larger network, similar to the decomposition of foodwebs into building blocks [28].

2.2 The migration matrix C – no obstacles

As a first step to defining the migration matrix C, we model between-patch movement in the absence of obstacles. We distinguish between upstream and downstream movement. We obtain the “uninhibited movement matrix” M from the adjacency matrix A by multiplying each nonzero element in A with the appropriate downstream $(d_{i,j},\ i < j)$ or upstream $(u_{i,j},\ i > j)$ movement probability. The column sums in matrix M are bounded by unity. Matrix M for the simple 4-reaches network in Figure 3 is given by

$$M = \begin{pmatrix} 0 & d_{1,2} & 0 & 0 \\ u_{2,1} & 0 & d_{2,3} & d_{2,4} \\ 0 & u_{3,2} & 0 & 0 \\ 0 & u_{4,2} & 0 & 0 \end{pmatrix}. \tag{5}$$

To obtain migration matrix C from matrix M, we need to add the diagonal elements that represent the probability that an individual does not move. In the absence of mortality, C is a stochastic matrix, i.e., the column sums of C are one. We only make an exception to this rule in the first column where we consider two scenarios. In the “closed network”-scenario individuals do not leave the river network at the mouth, and the column sum in the first column is one. In the “open network”-scenario, individuals will leave the system through the river mouth, and the $(1,1)$-entry of C is zero. We regard these two cases as extreme



(a)

$$A = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{pmatrix}$$

(b)

Figure 3: (a) A dendritic graph representing a river network of 4 reaches, (b) The corresponding adjacency matrix to the graph on the left

cases; for a partially open network, one can choose any probability between the two cases. Hence the migration matrix C in the absence of migration obstacles is given by

$$C = \begin{pmatrix} * & d_{1,2} & 0 & 0 \\ u_{2,1} & 1 - d_{1,2} - u_{3,2} - u_{4,2} & d_{2,3} & d_{2,4} \\ 0 & u_{3,2} & 1 - d_{2,3} & 0 \\ 0 & u_{4,2} & 0 & 1 - d_{2,4} \end{pmatrix} \tag{6}$$

where

$$* = \begin{cases} 0 & \text{if the system is open} \\ 1 - u_{2,1} & \text{if the system is closed} \end{cases} \tag{7}$$

With this definition, individuals effectively move at most one patch up- or downstream per year. For more mobile species, one can use $\widetilde{C} = C^k$ for some $k > 1$ as the migration matrix. These two scenarios correspond to movement based on local versus global knowledge [8].

2.3 The migration matrix C – with obstacles

An obstacle or barrier, such as a dam, a culvert, or a hydropower station, can modify the probability of upstream and downstream movement between reaches, and it can also induce mortality in the movement process. To each obstacle we assign an upstream and downstream passability value (α_u and α_d, respectively, $0 \leq \alpha_u, \alpha_d \leq 1$), representing the proportion of individuals that can successfully cross the obstacle in the corresponding direction [4]. If the passability value is 1, then the obstacle is completely passable in the given direction. Contrarily, when the passability value is 0, the obstacle does not allow any transit through it. We represent the passability values of all obstacles in a passability matrix O. Matrix

O is obtained from the adjacency matrix A by replacing the corresponding nonzero entries with the passability values. For notational convenience, we set the diagonal elements to one, i.e. $o_{i,i} = 1$. Accordingly, the probability of failing to cross an obstacle is $1 - o_{i,j}$ for all nonzero entries $o_{i,j}$. We define the failure of passing matrix as $\tilde{O}$. If, for example, an obstacle is placed between reaches 2 and 3 in the simple network in Figure 3, then these matrices are given by

$$O = \begin{pmatrix} 1 & 1 & 0 & 0 \\ 1 & 1 & \alpha_d & 1 \\ 0 & \alpha_u & 1 & 0 \\ 0 & 1 & 0 & 1 \end{pmatrix} \quad \text{and} \quad \tilde{O} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 1-\alpha_d & 0 \\ 0 & 1-\alpha_u & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \tag{8}$$

Individuals who fail to cross an obstacle either stay in the reach from which they attempted to leave or die. Mortality can arise from the structure itself (e.g. fish being sucked into turbines at power-generating dams) or from increased energy expenditure in the attempt to cross the obstacle. We collect these mortality values in a matrix E where entry $e_{i,j}$ is the probability that an individual will die in the attempt to cross the obstacle from reach j to reach i. Mortality may depend on direction. Again, for a hypothetical obstacle between reaches 2 and 3 in the simple network in Figure 3, matrix E is given by

$$E = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & e_d & 0 \\ 0 & e_u & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \tag{9}$$

The resulting migration matrix C arises from careful bookkeeping of individual movement. For example, an individual can be in patch 2 if it moved upstream from patch 1 (with probability $u_{2,1}$), or downstream from patch 4 (with probability $d_{2,4}$), or successfully passed the obstacle downstream from patch 3 (with probability $\alpha_d d_{2,3}$), or it was already in patch 2 and stayed (with probability $1 - d_{1,2} - \alpha_u u_{3,2} - (1-\alpha_u) e_u u_{3,2} - u_{4,2}$). The latter probability is obtained by considering individuals that did not move downstream to patch 1 nor upstream to patch 4, nor successfully got to patch 3 upstream, nor died while trying to get to patch 3 upstream. Based on these consideration, matrix C (for a closed network) is given by

$$C = \begin{pmatrix} 1 - u_{2,1} & d_{1,2} & 0 & 0 \\ u_{2,1} & 1 - d_{1,2} - \alpha_u u_{3,2} - (1-\alpha_u) e_u u_{3,2} - u_{4,2} & \alpha_d d_{2,3} & d_{2,4} \\ 0 & \alpha_u u_{3,2} & 1 - \alpha_d d_{2,3} - (1-\alpha_d) e_d d_{2,3} & 0 \\ 0 & u_{4,2} & 0 & 1 - d_{2,4} \end{pmatrix}. \tag{10}$$

In terms of matrices $\Delta_1 = \tilde{O} \circ E \circ M$ and $\Delta_2 = O \circ M$, the migration matrix C can be conveniently written as

$$C = \Delta_1 + I - \operatorname{diag}\left(\sum_i (\Delta_1 + \Delta_2)_{i,j} \right). \tag{11}$$

Here, ∘ denotes the Hadamard product of entrywise multiplication of matrices.

The extension of this procedure to several obstacles is straight forward. In this work, we concentrate on the effect of adding (or removing) a single obstacle from a network.

2.4 Defining connectivity

There is a great variety of different indices to measure connectivity in general networks [12, 13]. Many indices are purely topological in that they consider only the existence of connections between patches. Those that include, in addition, patch attributes and at least to some extent also distances, are typically much more informative [17]. For a dentritic network, such indices tend to be too coarse. While terrestrial networks often contain many different paths between any two patches, there is only a single unique path connecting any two patches in a dentritic network. As a result, breaking any connection in a connected dentritic network will lead to two disconnected sub-networks, whereas a connected terrestrial ecological network often remains connected even if a connection is removed. Empirically more relevant is the observation that many barriers in watersheds are actually not complete impassable [19].

A relatively recent measure, developed specifically for watersheds and dentritic networks is the "dentritic connectivity index" DCI [4]. It is based on the probability that a fish can move between any two given points in the network. Hence, the index depends on movement behavior and includes the "strength" of a connection by looking at probabilities of movement. The idea behind this index for a potadromous species is the following. Suppose that there are K barriers, dividing a watershed into D sections. Denote the length of section j by L_j and the upstream and downstream passability of the m^{th} barrier by $\alpha_{u,m}$ and $\alpha_{d,m}$, respectively. For any two sections of the watershed, one multiplies the passabilities of all barriers that lie between these two sections as the total probability of passage between these two sections. The dentritic connectivity index for potadromous species is then given by

$$DCI_P = \sum_{i=1}^{D} \sum_{j=1}^{D} \left(\prod_{m=1}^{K} \alpha_{u,m}\alpha_{d,m} \right) \frac{L_i}{L}\frac{L_j}{L} \times 100, \tag{12}$$

where L denotes the total length of the system, see equations (2) and (3) in [4]. The value of $K = K(i, j)$ depends on the two sections chosen.

In the absence of obstacles to fish movement, DCI_P is equal to 100. Adding obstacles to the network decreases the connectivity index, unless obstacles are completely passable [4]. Other measures of habitat quality can replace length. In what follows, we scale the DCI_P so that the maximum corresponding value is 1.

2.5 Relating network connectivity to population persistence

To evaluate the effects of migration obstacles on the persistence of fish populations, we compare and contrast how the population growth rate of model (2) and the DCI_P vary with changes in obstacle location and other attributes (e.g. passability and mortality). The population growth rate is the dominant eigenvalue λ of the projection matrix B. When λ is greater than unity, then the population will grow, otherwise, it will decline. An alternative measure for population persistence is the reproduction number R_0 that, for certain life-cycle models, can be obtained in a relatively simple and elegant way by graph-reduction arguments [29]. This method does not simplify calculations in our case, and the dominant eigenvalue gives additional information about time scales.

As the model contains many parameters, we consider certain strategically chosen simplified scenarios. In the baseline scenario, all reaches are of the same quality. However, river reaches generally differ in many aspects, such as river bed quality, primary producers, or temperature, which may enhance or reduce growth rates and/or survival probabilities for the fish population. For example, a typical classification distinguishes between warm-water loving species and cold-water loving species. Since water temperature generally increases downstream, the former do better downstream and the latter upstream. As two alternative scenarios, we therefore choose one where growth conditions are better upstream and one where they are better downstream.

For simplicity, we assume that all reaches located within the same level k (i.e. distance from the root of the tree or mouth of the river) are identical with respect to habitat quality.

In our dynamic model, we express habitat quality through parameters r_j, where higher values correspond to better conditions. For the calculation of the DCI_P, we express habitat quality as the length l_j of reach j. The length of a segment L_j is then the combined length of all reaches within a segment. For simplicity, we assume that all reaches located within the same level k are identical with respect to habitat quality. In particular, we write r_k and l_k for the habitat quality or length of any reach with distance $k-1$ from the root. To simplify matters even more, we introduce a single parameter that indicates how habitat quality changes between levels. We assume that the relative changes are constant between levels and write

$$\rho = \frac{r_{k+1}}{r_k} = \frac{l_{k+1}}{l_k}. \tag{13}$$

The base-line scenario of equal habitat quality everywhere is given by $\rho = 1$. When conditions are better upstream, we have $\rho > 1$ and when they are better downstream then $\rho < 1$. We then compare the qualitative behavior of λ and DCI_P in these three scenarios.

3 Results

We examine how the growth rate (λ) and the dentritic connectivity index (DCI_P) depend on the location of an obstacle in the system. We consider the three scenarios of a homogeneous network ($\rho = 1$), a network with better upstream conditions ($\rho > 1$) and a network where downstream conditions are better ($\rho < 1$). We investigate the influence of passability and mortality and river mouth conditions in each case.

We refer to the location of a barrier according to the level or height of the tree at which the obstacle is placed. In a linear network, there is only a single connection between any two levels, hence, there is a unique location for the barrier. In a complete binary tree, there are 2^k possible locations to place an obstacle at level k. By the symmetry of the complete binary tree, the growth rate and DCI_P will depend only on the level. In a randomly generated tree, there can be up to 2^k obstacle locations at level k. For each level k and probability triplet $(0, \beta, 1 - \beta)$, we generated 50 networks of height 7 and recorded the average values of λ and DCI_P.

We begin with the effects of obstacle location on population growth rate. We choose the growth rate at the river mouth to equal $r_1 = 1.64$ and the survival probability to $s_j = 0.5$. We assumed that the probability of leaving a patch is 0.5 and that dispersal is unbiased, i.e. $d_{i,j} = u_{i,j} = 0.25$.

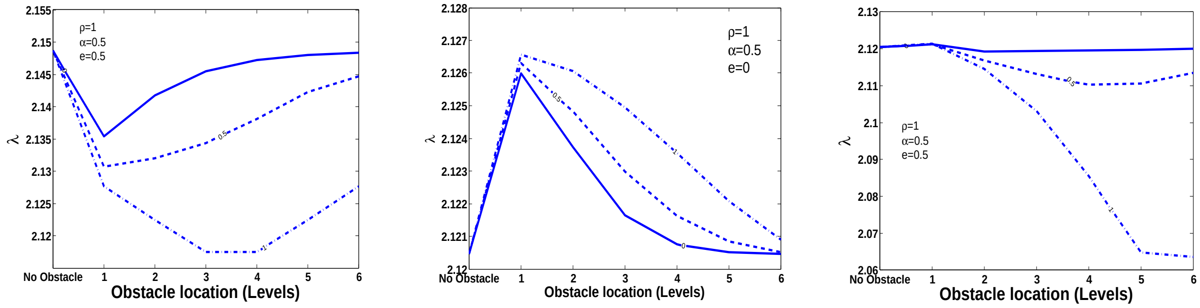
3.1 Homogeneous reaches ($\rho = 1$)

In a closed river system, when all reaches are of the same quality and there is no mortality associated with the barrier, the barrier or its location does not affect the population growth rate. Even though movement is affected, λ remains constant since conditions are the same everywhere.

If there is mortality at the obstacle ($e \neq 0$), the growth rate is lower than without the obstacle, and the actual value depends on location, see Figure 4, left panel. The lowest value of λ for the complete binary tree ($\beta = 0$) occurs when the obstacle is located at the first (i.e. lowest) level. For the linear network ($\beta = 1$), the lowest value of λ occurs when the barrier is in the middle of the network. (We confirmed this result numerically for linear networks of various sizes, only the network of height 7 is shown.) Thus, in both cases, the negative impact of the obstacle is largest when it separates the network into two evenly-sized parts. For randomly generated networks ($0 < \beta < 1$), the averaged population growth rate is in between the linear and the complete binary case. The obstacle location that has the most negative impact on growth rate depends on mortality and β. Increasing passability (α) will increase the growth rate since fewer individuals face mortality (plot not shown).

In an open network, an obstacle without mortality increases the growth rate for any location, and the highest growth rate occurs when the obstacle is located in the lowest level, independent of network topology, see Figure 4, middle panel. The obstacle prevents individuals from dispersing to the river mouth where they would leave the network. We refer to this mechanism as the "retention effect" of the obstacle. The effect is larger when the obstacle is placed close to the mouth. As the passability of the obstacle increases, λ decreases. As before, the averaged growth rate of randomly generated networks is bounded by the growth rate of the linear and the complete binary topology.

When an obstacle with mortality is placed into an open network, the resulting growth rate depends on the net effect between mortality (reducing λ) and retention (increasing λ), see Figure 4, right panel. When mortality is low enough, the retention effect is stronger when the obstacle is placed near the mouth. When the obstacle is placed higher up in the network, individuals face mortality in both directions: downstream from the mouth, upstream from the obstacle. This effect is particularly strong in the linear topology and is diluted in the complete binary case. The growth rate for random networks is, again, in between the two extremes. When obstacle mortality is high, the retention effect is too weak, and the growth rate will always be below the default case without obstacles (plot not shown).



(a) (b) (c)

Figure 4: Relationship between the asymptotic growth rate (λ) and obstacle location in a network for the linear ($\beta = 1$, dash-dot), complete binary ($\beta = 0$, solid) and random ($\beta = 0.5$, dashed) topology. **Panel (a):** obstacle mortality in a closed system has the most negative effect when the network is partitioned into two similar-sized parts ($e = 0.5$). **Panel (b):** an obstacle without mortality induces the retention effect, which is strongest when the obstacle is near the mouth ($e = 0$). **Panel (c):** The net effect of retention and mortality in an open network ($e = 0.5$). In all cases, passability is $\alpha = 0.5$.

3.2 Reach quality increases downstream ($\rho < 1$)

When downstream reaches provide better habitat, an obstacle without mortality will increase the population growth rate in any network topology, even in a closed network. The effect is the strongest when the obstacle is at the lowest level, see Figure 5, top left. Similar to the retention effect, an obstacle at low levels traps individuals in the reaches of high quality and thereby increases λ. In fact, with the chosen parameters, the growth rate in patches of level 4 and up is less than unity. Only in the highest level do we have a net loss as $r_k + s_k < 1$. As the obstacle is moved upstream or passability is increased, the trapping effect is diminished and λ decreases.

When the obstacle engenders high enough fish mortality, we get completely opposite results (Figure 5, top right). The growth rate is lower than without obstacle, and the lowest value occurs when the obstacle is at the lowest level. As more individuals will be located in the downstream patches, they are more prone to obstacle induced mortality if they disperse. In this case, the more passable the obstacle, the higher the λ, because fewer individuals fail to successfully cross the obstacle and risk death. As we can expect, λ decreases with higher obstacle induced mortality.

When $\rho < 1$ and the system is open, the best growth conditions are downstream where the risk of loss is also the highest. An obstacle without mortality in the first level prevents individuals from reaching the best habitat and also from leaving the system. For intermediate passability values, the latter effect is stronger than the former, i.e. the growth rate is higher with the obstacle than without, see Figure 5, bottom left). The effect is much weaker when the obstacle is placed higher upstream. The reason is that individuals above the obstacle are in low growth quality habitats, while those below the obstacle face loss downstream. Similar to the closed network case, a less passable obstacle results in a higher λ, preventing more individuals from dispersing to the river mouth.

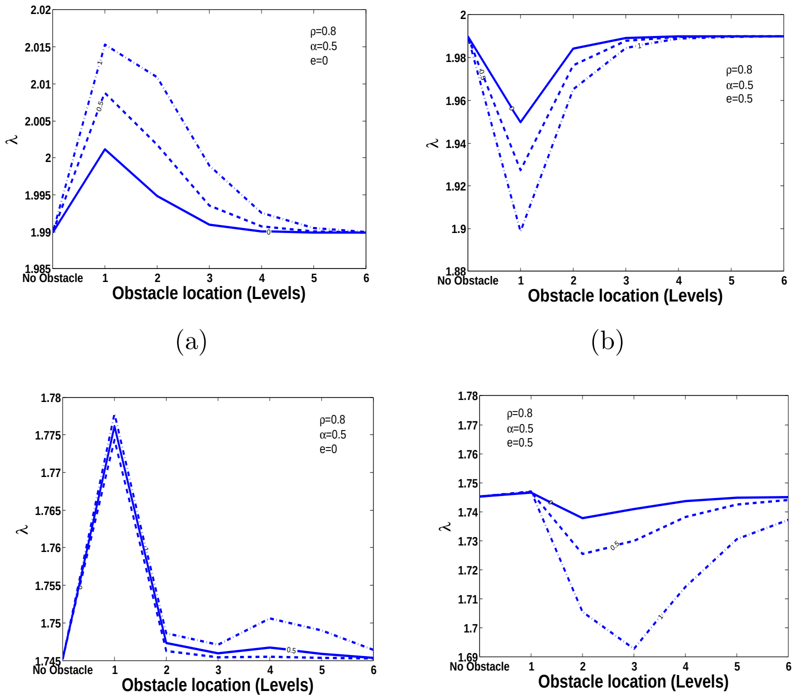
Finally, if an obstacle in an open network induces fish mortality ($e \neq 0$), the retention effect of the obstacle in the first level is still present for low enough passability and mortality, and for any network topology, see Figure 5, bottom right. When the obstacle is located further from the mouth, the retention effect is weaker than the negative effects of mortality and open network. For the complete binary tree ($\beta = 0$), the lowest value of λ occurs at level 2, whereas it occurs at level 3 for the linear network ($\beta = 1$). Through simulations on larger networks, we found that these particular locations are independent of network height (plots not shown). Aside from the first level location, λ increases with increasing passability. In general, λ decreases when obstacle mortality is higher.

3.3 Reach quality increases upstream ($\rho > 1$)

For some fish species, the colder upstream reaches provide better habitat and maybe even a refuge against competition [30]. In this case, the difference between open and closed networks with respect to growth rate and obstacle location is marginal. With no obstacle-induced fish mortality ($e = 0$), λ increases as the obstacle is placed in higher levels, since individuals are trapped in patches of high quality. However, only for the linear topology ($\beta = 1$) does the highest growth rate occur with the obstacle in the highest level. For all non-linear topologies ($\beta < 1$), λ is the highest when the obstacle is in the second last level (see Figure 6, left panel). In the linear network, there is only one highest-quality patch, and with the obstacle just below it, individuals are trapped in the best growth conditions. In other topologies, an obstacle in the highest level traps individuals only in one of several best-quality patches. Individuals will still move away from all other high-quality patches, thereby reducing overall growth rate. An obstacle placed in the downstream levels has virtually no effect on λ since it is not harmful, but at the same time it locks individuals in low-growth conditions, obstructing them from moving to better habitats. Furthermore, as we have already seen in the other cases, λ is higher when the passability of the obstacle is lower, impeding more individuals from leaving the higher quality patches.

When the obstacle induces fish mortality ($e \neq 0$), then the positive trapping effect disappears. In non-linear topologies, the decrease in λ is very small and noticeable only for upstream locations. For the linear network however, λ drastically decreases as the obstacle location is moved upstream (see Figure 6, right panel). Essentially, the single best-quality patch carries a high mortality risk from the obstacle and loses its beneficial effect on population growth. As before with mortality, λ is higher for high passability values, allowing more individuals to safely traverse the obstacle. Clearly, increased mortality decreases λ in the linear network. For non-linear topologies, the sensitivity of λ with respect to mortality is marginal since there are so many high-quality patches that support population growth.

For an open network, the loss at the river mouth has no qualitative effect on these results,



(a) (b)

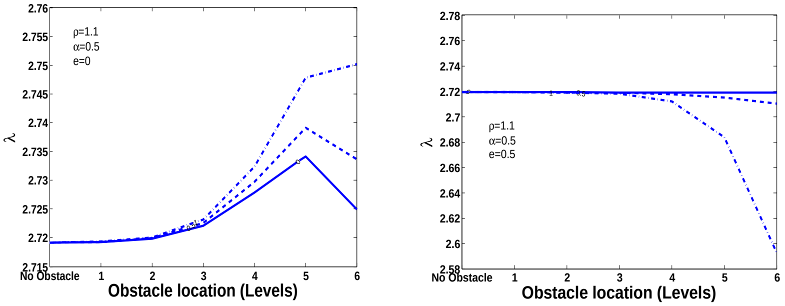
(c) (d)

Figure 5: Relationship between the asymptotic growth rate (λ) and obstacle location in a network when downstream reaches are of higher quality. **Panel (a):** In a closed network, λ increases as a barrier traps individuals in the high-quality reach downstream ($e = 0$). **Panel (b):** With high enough obstacle mortality, the trapping effect disappears ($e = 0.5$). **Panel (c):** The trapping effect is also present in an open network ($e = 0$). **Panel (d):** Obstacle mortality in an open network can lead to mixed results: an obstacle in the first level is beneficial, in the second ($\beta = 0$) or third ($\beta = 1$) level it is the most devastating for population growth. Parameter values are $\rho = 0.8$ and $\alpha = 0.5$. Other parameters are as in the previous figure.

even when the obstacle location is in level 1. The retention effect disappears, and only the better growth conditions control the results.

3.4 Connectivity Index DCI_P

While the dentritic connectivity index (DCI_P) measures how barriers inhibit fish movement between sections in a watershed, it does not account for demographic dynamics, specifically not for mortality related to obstacles. It does, however, account for some aspect of habitat quality by considering length of a section, where longer sections correspond to higher quality. We calculated the DCI_P as a function of obstacle location in the three different settings of (a) homogeneous habitat quality ($\rho = 1$), (b) decreasing habitat quality upstream ($\rho < 1$), and (c) increasing habitat quality upstream ($\rho > 1$).



(a) (b)

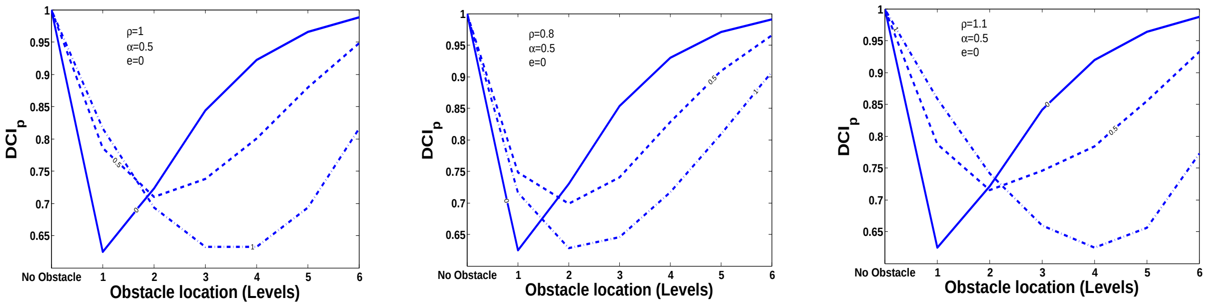
Figure 6: Relationship between the asymptotic growth rate (λ) and the obstacle location in a network when upstream reaches are of higher quality. **Panel (a):** When there is no obstacle mortality, λ increases with level, except the highest level for non-linear topologies. **Panel (b):** When there is mortality, λ decreases with level, most strongly in the linear case and imperceptibly for the complete binary network. Parameters and line styles are as in previous figures.

The greatest reduction in DCI_P arises when the obstacle separates the network into two sections of (roughly) equal lengths (or quality), see Figure 7. For the complete binary network ($\beta = 0$), this location is at the lowest level, for the linear network ($\beta = 1$), it is at some intermediate level. When the habitat is homogeneous, the location is the middle level, when habitat quality is better downstream (upstream) the location is shifted downwards (upwards). The average DCI_P for 50 randomly generated networks shows an intermediate behavior between the two extreme cases.

Clearly, DCI_P decreases as the obstacle passability decreases. Obviously, the effects of open versus closed networks or of obstacle mortality cannot be evaluated with this index.

4 Discussion and conclusions

As more and more network-theoretic approaches are being employed to study the effects of movement barriers and habitat degradation on ecosystem function, the great challenge becomes "to determine how the connectivity structure of habitat networks constrains and enables ecological and evolutionary processes at various levels of biological organization" [12]. With this study, we contribute to this endeavor a comparison between two ecosystem-scale measures, namely (i) the long-term growth rate (λ) of a population dynamics model, and (ii) the dentritic connectivity index (DCI_P). More specifically, we evaluate the effect of the location of a single movement barrier in a watershed on these two quantities. The three most important insights from the population dynamics model are (i) that the effects in a randomly generated network are in some sense bounded by the effect in a linear and a complete binary network of the same height; (ii) that barriers can be beneficial to a population through a retention or trapping effect; and (iii) that mortality at an obstacle is the determining



(a) (b) (c)

Figure 7: Relationship between the dendritic connectivity index DCI_P and the obstacle location in a network with different distribution of habitat quality. **Panel (a):** Homogeneous habitat ($\rho = 1$). **Panel (b):** Habitat quality increases downstream ($\rho = 0.8 < 1$). **Panel (c):** Habitat quality increases upstream ($\rho = 1.1 > 1$). In the absence of any obstacle, $DCI_P = 1$. Passability parameters are identical for the upstream and downstream direction ($\alpha = 0.5$).

factor of the negative effects of the obstacle on population growth. The DCI_P can capture these effects only to a certain (limited) degree. The relative size of the effects depends on parameter values, and a thorough sensitivity analysis will be required when empirical data are available for any species. At this point, we only note that for the chosen parameters, the typical maximal increase in population growth rate is an order of magnitude smaller that the maximal decrease.

To guarantee population persistence, an individual has to at least replace itself within a lifetime. In networks, not only the connectivity but viable reproduction "multiplied" by connectivity is the crucial quantity [22]. The importance of "loops" (e.g. ways to return to a patch) in the network topology has been stressed for terrestrial systems [31] and marine systems [22]. In river networks, loops can exist – and a population can persist – only when individuals move up- *and* downstream [32, 33]. Accordingly, the location of a barrier will determine how many loops it affects and therefore, how important it is for the persistence of a population. Because the path structure in a dentritic network is simple, a barrier affects more loops when it is located near the "middle" of the network. For a linear network, this location is halfway, for a complete binary network, it is the root. When habitat quality is changes along a gradient, this "middle" location changes accordingly.

Previous studies with population dynamics models considered only a complete binary network of 15 patches, and modeled dams and channelization as complete removal of patches [9, 24]. Fish moved on a fast time-scale through the entire (available) network. By contrast, we explored random topologies and slow-moving individuals. For a closed network, we arrive at the same result as in [9, 24] that a dam at the lowest level in the network has the most devastating effect on population growth. This commonality indicates a generic effect, independent of modeling approach. Our results are much more general (by allowing intermediate passability and considering random topologies) and more detailed (including obstacle mortality). From the comparison of all these different scenarios, we speculate that the size of the remaining fragments and the interaction between movement and mortality rather than the level of disturbance seems to be the driving force.

We chose a population dynamics framework where population persistence emerges from the interplay of reproduction and mortality. We argue that this approach is valid is relatively stable hydrological conditions. An alternative approach considers colonization-extinction dynamics in highly variable environments, such as desert streams [1]. The importance of fragment size has been explored in the resulting stochastic patch-occupancy models either with [1,11] or without [8] population dynamics. The size of fragments or the largest connected component is also often the focus for prioritization in dam removal [34–37].

In patch-occupancy models, barriers and fragmentation typically results in population decline. Most uses of connectivity indices assume that barriers and fragmentation have negative effects on populations. Our study is the first to tease apart the effects of movement limitation from obstacle mortality. For that reason, we found the retention or trapping effects that can alleviate the negative effects of an obstacle with mortality. This positive effect of limiting migration is one of four recently advocated by Rahel [38], others being protection against invasive species, against disease, and eliminating hybridization. All these effects could be tested in an extension of our modeling framework. Incorporating (some of) these effects into patch-occupancy models is a challenge for the future.

Our strategic model focused on the effect of movement barriers while considering individuals with a very simple life cycle (growth to maturity in one year). Some previous models considered two [25] or three [9, 24] life stages. In addition, we only considered the scenario that upstream and downstream movement probabilities are equal, whereas many real populations show upstream-biased movement of adults [8] and potentially downstream-biased movement of early life stages [39]. A relatively simple first step to include differential upstream and downstream mobility in our model is to consider dispersal of the young-of-the-year separately. We modify equation (2) to

$$N_{i,t+1} = \sum_{j}^{n} (c_{i,j} s_j N_{j,t} + \tilde{c}_{i,j} r_j N_{j,t}) \tag{14}$$

where $c_{i,j}$ are the movement probabilities of adults as before and $\tilde{c}_{i,j}$ are the movement probabilities of juveniles. We still assume maturation within one year. While a complete study of this model is beyond the scope of this paper, we illustrate one effect under the extreme assumption that juveniles drift downstream only ($d_{juv} = 1$ and $u_{juv} = 0$), and that obstacles are completely passable for juveniles in the downstream direction.

In an open network with homogeneous reach quality, an obstacle in the first level still increases growth rate through a retention effect (for adults). At higher levels, however, the obstacle has a negative effect, stronger for the linear topology and weaker for the complete binary case, see Figure 8. This negative effect is not present in the comparable scenario without juvenile movement bias (Figure 4, middle panel). However, the qualitative behavior compares closely with the scenario that habitat quality decreases upstream (Figure 5, bottom right). Indeed, this similarity is not so surprising considering that if juveniles leave their native reach and travel downstream, then the contribution of upstream reaches to reproduction is reduced.

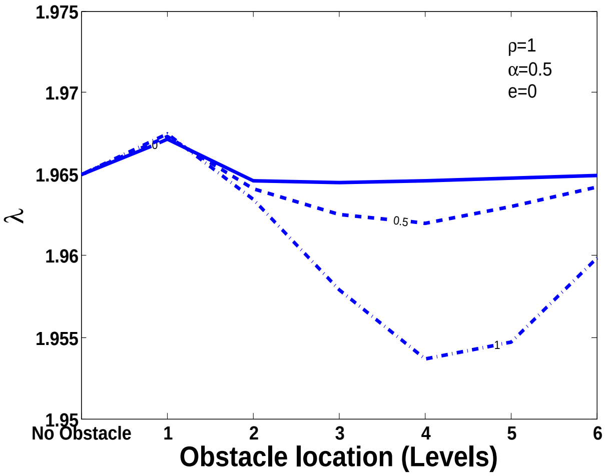


Figure 8: Relationship between the asymptotic growth rate (λ) and the obstacle location in an open network when juveniles exhibit a strong downstream bias ($d_{juv} = 1$ and $u_{juv} = 0$). Reaches are of equal quality ($\rho = 1$) and there is no obstacle mortality ($e = 0$). Passability for adults is $\alpha = 0.5$ and for juveniles $\alpha_{juv} = 1$.

The dentritic connectivity index (DCI_P) is a network-level index that measures not only the existence of a link between patches but also how hard it is to move between sections in a network with barriers [4]. Dentritic networks differ significantly from most terrestrial networks in that there is only one path between any two points in a dentritic network so that each new barrier will create a new section in the network. We saw that the DCI_P can capture certain effects of movement barriers on population dynamics but not all. When multiple life-stages involve multiple dispersal behaviors, a single network-level index is more unlikely to capture the resulting population dynamic effects. Patch-models for dispersal in the absence of growth and mortality, also found that DCI_P is only partly correlated with results [8]. While we used only DCI for comparison, it is clear that certain, potentially crucial, aspects of population growth cannot be captured by any structural indices. There is, therefore, a need to develop new indices for connectivity in dentritic networks and simultaneously systematically investigate their effect on population dynamic processes. This effect will strongly depend on migration characteristics and habitat requirements. Many indices have been developed for terrestrial networks [12], but even for those, the connection to population dynamics is not always clear. Some of these indices have been applied to river systems, for example the network-level "integral index of connectivity" (after which the DCI is modeled) and the measure of "betweenness-centrality" as an indicator of the importance of a given patch [15,16]. These measures could and should be compared to population dynamics indices such as reproductive value [23] or metapopulation capacity [40]. Probably more importantly, one needs to develop indices for the importance of a connection between patches in a similar fashion.

Real river systems often contain not only one but many migration barriers for fish. Our modeling approach readily extends to include several barriers, and exploring the combined effect is our ongoing research work. The principles of retention/trapping and mortality are combined and create an overall effect. Probably more crucially, some attributes of habitat quality are being transported downstream, an effect that is mostly absent from terrestrial ecosystems. Dams and culverts not only affect fish movement, they can also change the abiotic conditions in a stream or river by changing temperature, flow and other aspects. Including this downstream influence in modeling population dynamics in dentritic networks is another challenge for future theory.

Competing interests

We have no competing interests.

Authors' contributions

FL and AH conceived of the study; all three authors designed the study; YS carried out the analysis and drafted the manuscript; FL and AH critically edited the manuscript. All authors gave their final approval for publication.

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Appendix

The Matlab files used for calculations and to create the plots in this work are available from the journal website. The executable main file is named `SingleObstacle_MainFile.m`; all other files are function files that feed into this main file.

References

[1] William F Fagan. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, 83(12):3243–3249, 2002.

[2] Evan H Campbell Grant, Winsor H Lowe, and William F Fagan. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, 10(2):165–175, 2007.

[3] Jacques Labonne, Virginie Ravigné, Bruno Parisi, and Cédric Gaucherel. Linking dendritic network structures to population demogenetics: the downside of connectivity. *Oikos*, 117(10):1479–1490, 2008.

[4] David Cote, Dan G Kehler, Christina Bourne, and Yolanda F Wiersma. A new measure of longitudinal connectivity for stream networks. *Landscape Ecology*, 24(1):101–113, 2009.

[5] Mark Padgham and J Angus Webb. Multiple structural modifications to dendritic ecological networks produce simple responses. *Ecological Modelling*, 221(21):2537–2545, 2010.

[6] World Wildlife Fund. Free-flowing rivers: Economic luxury or ecological necessity?, 2006.

[7] Graeme S Cumming. The impact of low-head dams on fish species richness in wisconsin, usa. *Ecological Applications*, 14(5):1495–1506, 2004.

[8] J.S. Perkin, K.B. Gido, O. Al-Ta´ ani, and C. Scoglio. Simulating fish dispersal in stream networks fragmented by multiple road crossings. *Ecological Modelling*, 257:44–56, 2013.

[9] S Charles, R Bravo de La Parra, JP Mallet, H Persat, and P Auger. Population dynamics modelling in an hierarchical arborescent river network: an attempt with salmo trutta. *Acta biotheoretica*, 46(3):223–234, 1998.

[10] S Charles, R Bravo De La Parra, J-P Mallet, H Persat, and P Auger. Annual spawning migrations in modelling brown trout population dynamics inside an arborescent river network. *Ecological modelling*, 133(1):15–31, 2000.

[11] William F Fagan, Evan H Campbell Grant, H Lynch, and Peter J Unmack. Riverine landscapes: ecology for an alternative geometry. *Spatial ecology*, pages 85–100, 2009.

[12] Bronwyn Rayfield, Marie-Josée Fortin, and Andrew Fall. Connectivity for conservation: a framework to classify network measures. *Ecology*, 92(4):847–858, 2011.

[13] Justin M Calabrese and William F Fagan. A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment*, 2(10):529–536, 2004.

[14] Joern Fischer and David B Lindenmayer. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, 16(3):265–280, 2007.

[15] Tibor Erős, Dénes Schmera, and Robert S Schick. Network thinking in riverscape conservation–a graph-based approach. *Biological Conservation*, 144(1):184–192, 2011.

[16] Tibor Erős, Julian D Olden, Robert S Schick, Dénes Schmera, and Marie-Josée Fortin. Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landscape ecology*, 27(2):303–317, 2012.

[17] Atte Moilanen and Marko Nieminen. Simple connectivity measures in spatial ecology. *Ecology*, 83(4):1131–1145, 2002.

[18] Urmila Malvadkar, Frederick N Scatena, and Miguel Leon. A comparison of connectivity metrics on watersheds and implications for water management. *River Res. Appl.*, 31(2):256–267, 2015.

[19] Marc Pépino, Marco A Rodríguez, and Pierre Magnan. Fish dispersal in fragmented landscapes: a modeling framework for quantifying the permeability of structural barriers. *Ecological Applications*, 22(5):1435–1445, 2012.

[20] Aimee H Fullerton, Kelly M Burnett, E Ashley Steel, Rebecca L Flitcroft, George R Pess, Blake E Feist, Christian E Torgersen, Daniel J Miller, and Beth L Sanderson. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshwater Biology*, 55(11):2215–2237, 2010.

[21] Michael A McCarthy, Alana L Moore, Jochen Krauss, John W Morgan, and Christopher F Clements. Linking indices for biodiversity monitoring to extinction risk theory. *Conservation Biology*, 28(6):1575–1583, 2014.

[22] A. Hastings and L.W. Botsford. Persistence of spatial populations depende on returning home. *Proc. Natl. Acad. Sci. USA*, 103(15):6067–6072, 2006.

[23] Hal Caswell. *Matrix population models*. Wiley Online Library, 2001.

[24] Sandrine Charles, Rafael Bravo de la Parra, Jean-Paul Mallet, Henri Persat, and Pierre Auger. A density dependent model describing *salmo trutta* population dynamics in an arborescent river network. effects of dams and channelling. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie*, 321(12):979–990, 1998.

[25] Emma E Goldberg, Heather J Lynch, Michael G Neubert, and William F Fagan. Effects of branching spatial structure and life history on the asymptotic growth rate of a population. *Theoretical Ecology*, 3(3):137–152, 2010.

[26] F. Courchamp, L. Berec, and J. Gascoinge. *Allee effects*. Oxford Univ. Press, 2008.

[27] MRT Dale and M-J Fortin. From graphs to spatial graphs. *Annual Review of Ecology, Evolution, and Systematics*, 41(1):21, 2010.

[28] Kevin McCann. *Food Webs*, volume 50 of *Monographs in Population Biology*. Princeton University Press, 2011.

[29] T. de Camino-Beck and M.A. Lewis. A new method for calculating net reproductive rate from graph reduction with applications to the control of invasive species. *Bull. Math. Biol.*, 69:1341–1354, 2007.

[30] T.E. McMahon, A.V. Zale, F.T. Barrows, J.H. Selong, and R.J. Danehy. Temperature and competition between bull trout and brook trout: A test of the elevation refuge hypothesis. *Trans. Am. Fish. Soc.*, 136:1313–1326, 2007.

[31] Y. Artzy-Randrup and L. Stone. Connectivity, cycles, and persistence thresholds in metapopulation networks. *PLoS Comp. Biol.*, 6(8):e1000876, 2010.

[32] J. Sarhad, R. Carlson, and K.E. Anderson. Population persistence in river networks. *J. Math. Biol.*, 69:401–448, 2014.

[33] F. Lutscher, E. Pachepsky, and M.A. Lewis. The effect of dispersal patterns on stream populations. *SIAM Appl. Math*, 65(4):1305–1327, 2005.

[34] M.J. Kuby, William F. Fagan, C.S. ReVelle, and W.L. Graf. A multiobjective optimization model for dam removal: An example trading off salmon passage with hydropower and water storage in the Willamette basin. *Adv. Water Res.*, 28(8):845–855, 2005.

[35] Jesse R O'Hanley. Open rivers: Barrier removal planning and the restauration of free-flowing rivers. *J. Environ. Management*, 92:3112–3120, 2011.

[36] Stephanie R Januchowski-Hartley, Peter B McIntyre, Matthew Diebel, Patrick J Doran, Dana M Infante, Christine Joseph, and J David Allan. Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. *Front. Ecol. Environ.*, 11(4):211–217, 2013.

[37] P. Branco, P. Segurado, J.M. Santos, and M.T. Ferreira. Prioritizing barrier removal to improve functional connectivity in rivers. *Journal of Applied Ecology*, 2014.

[38] Frank J Rahel. Intentional fragmentation as a management strategy in aquatic systems. *BioScience*, 63(5):362–372, 2013.

[39] M.B. Morrissey and M.M. Ferguson. Individual variation in movement throughout the life cycle of a stream-dwelling salmonid fish. *Molecular Ecology*, 20(2):235–248, 2011.

[40] O. Ovaskainen and I. Hanski. Spatially structured metapopulation models: Global and local assessment of metapopulation capacity. *Theor. Pop. Biol.*, 60:281–302, 2001.