



A simple method to assess the fragmentation of freshwater fish meta-populations: Implications for river management and conservation

Amaia A. Rodeles^{*,1}, David Galicia², Rafael Miranda³

Department of Environmental Biology, University of Navarra, C/ Iruñaldea 1, Pamplona, Spain

ARTICLE INFO

Keywords:

Dam prioritization
Fish dispersal
Fish meta-populations
River fragmentation
Meta-population connectivity
River conservation

ABSTRACT

Rivers are very vulnerable to fragmentation caused by the presence of man-made barriers. To restore river basin connectivity, numerous indices have been developed to calculate river fragmentation and optimise barrier mitigation actions. These methods usually calculate connectivity for whole river basins, but sometimes it is useful to analyse the connectivity for certain elements of interest. The main goal of this study was to develop a simple method to calculate the connectivity of specific riverine habitats or fish meta-populations.

The framework of the Dendritic Connectivity Index (DCI) created by Cote et al. in 2009 was changed to develop the Population Connectivity Index (PCI). This index would depend on the number of populations, the total river length occupied by each population, the distance between populations, the dispersal capability of the fish species and the presence of barriers in the river. The outcome of the index is a percentage that measures the degree of connectivity in a meta-population. The PCI was tested in four Iberian fish species with different dispersal capabilities: *Salmo trutta*, *Luciobarbus comizo*, *Anaocypris hispanica* and *Cobitis vettonica*.

The results show a natural connectivity between populations (without considering dams) of 7.95–47.48%. The most connected meta-population was *L. comizo* while the most naturally fragmented meta-population was *A. hispanica*. When large impassable dams were added to the index the results show a connectivity of 2.19–16.48%. Dams reduce connectivity between 5.37 and 30.99 points. Dams were ranked according to their impact in the fragmentation of each studied meta-population.

This PCI allows to find out naturally isolated fish meta-populations and to assess the impact of dams in the fragmentation of fish meta-populations. It can also be used in dam prioritization decisions such as dam removals and new dam location selection. It also can aid in the creation of river ecological corridors between endangered or important fish populations.

1. Introduction

Dams have multiple impacts on riverine organisms, especially on freshwater fish species as they are totally constrained to the river streams (Gido et al., 2016). Nowadays, there are more than 45,000 large dams all over the world, with hundreds more under construction (Zarfl et al., 2014). All of these dams regulate more than 50% of all major world river systems and water flow (Nilsson et al., 2005; Vörösmarty et al., 2010). These obstacles to fish movement reduce the connectivity of the river and between fish populations. A single barrier such as a dam may be enough to completely block the movement of fish between

segments, totally isolating adjacent populations (Campbell Grant et al., 2007).

Diadromous fishes are the most impacted, as obstacles block their migrations upstream from the sea to reproduce (Clavero and Hermoso, 2015; Garcia de Leaniz, 2008; Nieland et al., 2015). However, potamodromous fishes are also affected, as they usually travel between feeding and reproduction grounds (Benitez et al., 2015; Ferguson et al., 2011; Lucas and Batley, 1996; Ovidio and Philippart, 2002). Even resident fishes, which move generally short distances, are impacted as river segment isolation caused by the presence of dams has impacts in the structure of fish populations and communities and can lead to the

* Corresponding author.

E-mail address: aangulo@alumni.unav.es (A.A. Rodeles).

¹ <https://orcid.org/0000-0003-4109-6777>.

² <https://orcid.org/0000-0002-2585-9888>.

³ <https://orcid.org/0000-0003-4798-314X>.

extirpation of entire populations within decades (Horreo et al., 2011; Morita and Yamamoto, 2002; Vera-Escalona et al., 2018; Yamamoto et al., 2004).

To better understand the effect of man-made obstacles such as dams in river connectivity, different methods have been developed. Some tools are simple and rank dams according to their passability, without considering the effects of the accumulation of barriers in the river network (Kemp and O'Hanley, 2010). Others are more complex and consider dams as part of a bigger system (Erös et al., 2011). In general, river basin connectivity assessment needs at least three variables: a river network, the position of each dam in the network (with a measure of passability) and a measure of river habitat. With these three variables different connectivity indices can be calculated (Cote et al., 2009; Grill et al., 2015; McKay et al., 2013). The outcome of these indices is the percentage of a river basin available to organisms. Connectivity indices are generally calculated with segment length as a proxy for river habitat. However, other variables such as habitat quality or stream size can be added to a connectivity index to emphasize different river characteristics important to certain species (Diebel et al., 2015; Grill et al., 2014; Rodeles et al., 2019).

River connectivity indices are usually applied in dam mitigation prioritization (McKay et al., 2017) and are calculated for entire river basins, no matter segment characteristics or quality for species development. However, in some instances, other connectivity frameworks may be useful: connectivity studies on terrestrial ecosystems are performed for certain types of habitat or populations. Connectivity is thus usually measured as the probability of an organism of the species of interest crossing between suitable habitat patches successfully (Galpern et al., 2011; Taylor et al., 1993; Tischendorf and Fahrig, 2000). This connectivity is essential for the long-term survival of *meta*-populations and thus species conservation (Hanski and Gilpin, 1991; Levins, 1968; MacArthur and Wilson, 1967). Some terrestrial connectivity methods have been applied to river fish populations (Schick and Lindley, 2007) but they are generally complex and are not widely used.

We wanted to develop a simple connectivity index to calculate the connectivity of fish species *meta*-populations. The proposed index is adapted to the river structure and includes barrier accumulation impact in connectivity. Moreover, it can be easily used to prioritise dam mitigation actions.

The Iberian Peninsula is an interesting place to study river connectivity and its effects on fishes as it contains more than a thousand large dams and numerous endangered endemic freshwater fish species (Maceda-Veiga, 2013). This article will present the theoretical framework of a simple *meta*-population connectivity index (PCI) developed using examples from Iberian endangered fishes. This new index may be useful to calculate the impact of obstacles in the connectivity of fish *meta*-populations and to find the barriers with the highest effect in population connectivity in order to inform management and conservation actions.

2. Methods

2.1. Iberian Peninsula and fish species

The Iberian Peninsula is in southwestern Europe, surrounded by the Atlantic Ocean to the west, the Cantabrian Sea to the north and the Mediterranean Sea to the east and south (Fig. 1). It is isolated from mainland Europe by the Pyrenees. The Mediterranean climate, with warm and dry summers and wet winters, dominates the majority of the Iberian Peninsula while humid and temperate Atlantic climate is present along the north coast (Rivas-Martínez, 1987). The Iberian Peninsula is crossed by numerous mountain ranges. The isolation from mainland Europe, the clash of climates and its varied geography have led to the evolution of numerous endemic freshwater fish species, many of them restricted to one river basin or sub-basin (Antunes et al., 2016). More than 60% of native and endemic Iberian fish species are under some degree of threat according to the International Union for the Conservation of Nature (IUCN 2019).

At the same time, there are around 1000 large dams (>1 hm³ of capacity) and thousands of small dams and weirs scattered through Iberian rivers (Antunes et al., 2016). More than 50% of Iberian fish species are threatened by water storage and extraction (Maceda-Veiga, 2013). Due to this, the Iberian Peninsula is an excellent place to study river and fish population connectivity.

We tested the new fish Population Connectivity Index using data of four species with different dispersal capacities as examples: *Salmo trutta* Linnaeus 1758, *Luciobarbus comizo* (Steindachner 1864), *Anaocypris hispanica* (Steindachner 1866), and *Cobitis vettonica* Doadrio & Perdiges

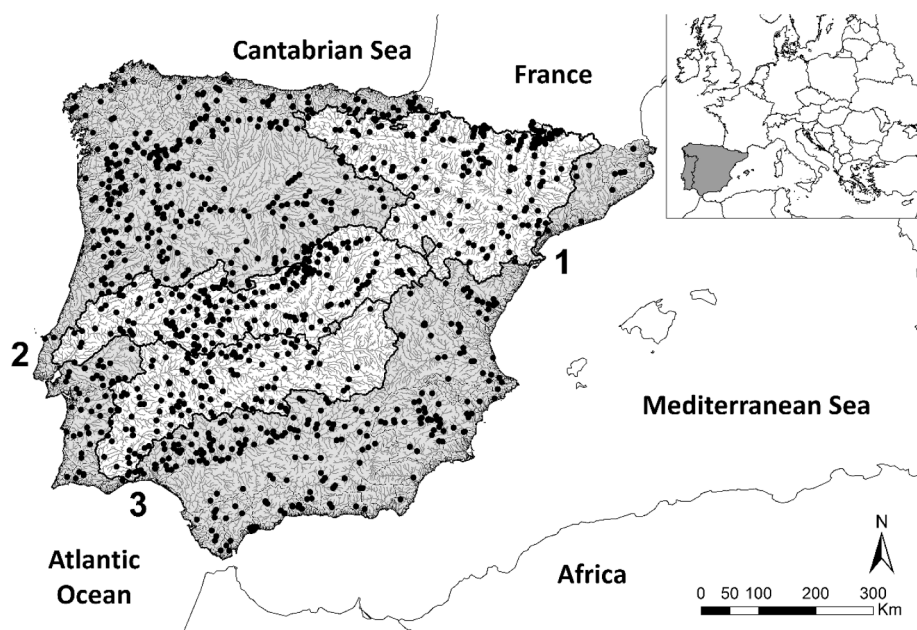


Fig. 1. The Iberian Peninsula, with its large dams (black dots, MAGRAMA, 2004). The river basins studied in this paper are highlighted in white. 1: Ebro, 2: Tagus and 3: Guadiana.

1997. *Salmo trutta* is a large salmonid with high swimming and leaping capacity, capable of large migrations from feeding to reproduction grounds. *Luciobarbus comizo* is a large barbel endemic of various large Iberian river basins (Doadrio et al., 2011), capable of large migrations during reproduction season. *Anaocypris hispanica* is a small potamodromous cyprinid. Lastly, *C. vettonica* is a small benthonic sedentary fish, endemic of a few river basins of the Iberian Peninsula. As a model, each these four species were studied in one river basin (Table 1).

2.2. Population modelling

As a proxy for fish populations, habitat suitability models were fitted for fish species in each major river basin. Presence and absence data was provided by the Iberian Society of Ichthyology (SIBIC, 2015), while raster environmental variables (30 arc-seconds resolution) were downloaded from <http://www.earthenv.org/streams> (Domisch et al., 2015). These variables are based on WorldClim (Hijmans et al., 2005) and consider the spatial structure of river networks, modifying the environmental data according to the position of each cell in the river basin. A correlation analysis was performed on all bioclimatic, elevation and soil variables and the ones with a correlation > 0.7 were removed, one by one, trying to keep the least correlated and most diverse and ecological relevant set of parameters. As uncorrelated variables may still be related, a Variance Inflation Factor (VIF) assessment was also performed, removed the variables with a VIF > 5. To create simple potential habitat models adequate to the number of occurrences available, five environmental variables were selected as the independent variables for the models: BIO10 (mean temperature of warmest quarter), BIO11 (mean temperature of coldest quarter), BIO12 (annual precipitation), BIO15 (precipitation seasonality) and pH. Species suitable habitat models were calculated for the river basins they were present on. Of the four fish species selected, *C. vettonica* did not have enough presence points (< 20) to fit a model, so its suitable habitat was described using the appropriate literature (Doadrio, 2001; Doadrio et al., 2011; Kottelat and Freyhof, 2007).

Models were calibrated using the software R v3.4.2 (R Core Team, 2015) with the packages *raster* (Hijmans et al., 2016) and *BIOMOD2* (Thuiller et al., 2016). Spatial autocorrelation was diminished by removing presence points located in a same cell or in adjacent cells (Komori et al., 2020; Veloz, 2009). Ten runs of the nine available statistical models (Generalized Boosted Model, Generalized Linear Model, Generalized Additive Model, Classification Tree Analysis, Artificial Neural Network, Surface, Range Envelope, Flexible Discriminant Analysis, Multivariate Adaptive Regression Splines and Random Forest) were done with 80% of presences and absences. The other 20% was used for testing. For more information about the characteristics of the models, see Guisan et al. (2017). Because not all models perform equally for every species, ensemble models that average the results of all models

Table 1

Fish species studies with their IUCN category, maximum length and estimated probability of dispersion. The river basins in which they were studied are also added.

Family	Species	IUCN category	Maximum size (cm)	Prob. disp. (10 km)	River basin
Cobitidae	<i>Cobitis vettonica</i>	Endangered	13	0.3	Tagus
Salmonidae	<i>Salmo trutta</i>	Least Concern*	60**	0.9	Ebro
Cyprinidae	<i>Luciobarbus comizo</i>	Least Concern	100	0.8	Tagus
Cyprinidae	<i>Anaocypris hispanica</i>	Endangered	10	0.5	Guadiana

*Vulnerable in Spain (Doadrio et al., 2011).

**Freshwater form.

were created (Guisan et al., 2017; Segurado and Araújo, 2004). All models with Area Under the Curve (AUC) > 0.7 were selected to create the ensemble by calculating the mean of the models weighted by their AUC. All ensembles had an AUC > 0.8. A cut-off threshold that maximizes the true skill statistic (TSS) was selected to transform the continuous ensemble model into a binary one (suitable/non-suitable). Binary suitability raster maps were created.

A line shapefile of Iberian river networks was downloaded from HydroSHEDS (Lehner et al., 2008). In ArcMap 10.6 (ESRI, 2011) all river segments that contained at least one suitable raster cell of the ensemble models was classified as suitable. This was calculated for the four analysed species (Fig. 2).

2.3. Population connectivity index

The new Population Connectivity Index (PCI) is based in the Dendritic Connectivity Index for potamodromous fish species (DCI_p, Cote et al., 2009). This index considers the length of river sections between dams, the passability of each dam and their cumulative impact between sections. It can be expressed as:

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

where n is the number of sections (number of dams + 1), c_{ij} is the cumulative passability of all dams between sections i and j , l_i is the length of section i , l_j is the length of section j , and L is the total length of the river basin.

In our Population Connectivity Index, a population area is defined as the sum of the lengths of all the suitable river segments that are interconnected, i.e., not separated by dams. Thus, l_i and l_j are the total area (length) of populations i and j of a particular species in a river basin, and L is the sum of all populations' areas (suitable habitats) in the river basin. In this paper suitable river segments were used indistinctly as fish populations. Populations are treated as nodes connected by edges represented by c_{ij} . The parameter c_{ij} measures the dispersal capability of the studied fish species corrected by the minimum distance (d) and the cumulative passability (B) of the M barriers (p) between the populations i and j . If there is an impassable dam between populations i and j , $B = 0$ and $c_{ij} = 0$. If there are no dams between populations i and j , $B = 1$.

$$B_{ij} = \prod_{m=1}^M p_m \quad (2)$$

The dispersal capability of a species is defined here as the mean distance that can be travelled successfully by its individuals. The dispersal capability varies from one species to another (Tischendorf and Fahrig, 2000). As the dispersal capability of our fish species is not well studied, we used a probability of dispersal (PD) based in size and swimming capability as proxy (Table 2). PD is a number between 0 (no capable of dispersal) and 1 (totally capable of dispersal) that describes the probability of a fish travelling a certain distance. In this case PD refers to the probability of fish travelling 10 km.

PD can be replaced by any other dispersal capability value. The PD is elevated by the distance between populations. Following the work of Schick and Lindley (2007) we proposed an exponential relationship between the probability of dispersal and distance as shown in the following equation:

$$c_{ij} = B_{ij} PD^{d_{ij}} \quad (3)$$

The parameter c_{ij} between two fish populations i and j is the PD of the species raised to the minimum distance d that separates the two populations. In our example, fishes travel short distances more easily than long distances. Other studies also use an exponential relationship between distance and dispersion (Fullerton et al., 2011; Schick and Lindley, 2007). However, the relationship between PD and d can be changed

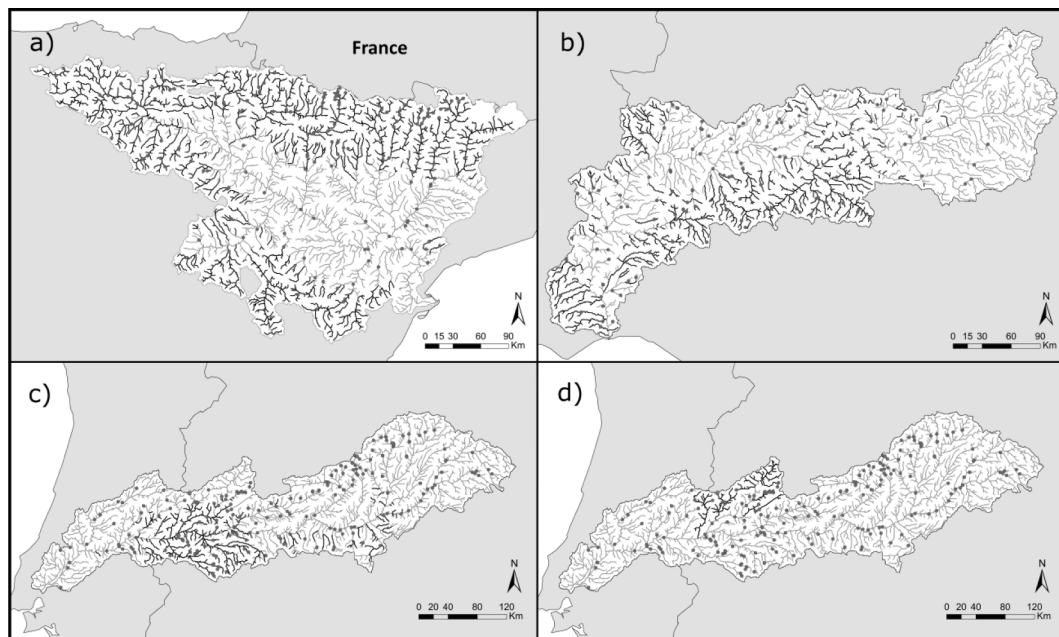


Fig. 2. Suitable river segments (dark lines) for a) *Salmo trutta* in the Ebro River basin, b) *Anaocypris hispanica* in the Guadiana River basin, c) *Luciobarbus comizo* in the Tagus River basin, d) *Cobitis vettonica* in the Tagus River basin. Dams are represented as grey points and unsuitable segments as light grey lines.

Table 2

Probability of dispersal assumed for the main groups of Iberian freshwater fishes, with their maximum total size and estimated swimming capabilities. Some Iberian genus and species are added as examples.

PD	Fish characteristics	Iberian examples	References
0.9	High swimming and leaping capacity	Salmonids	2, 3, 9, 10, 15, 18
0.8	Medium swimming and leaping capacity. Size ≥ 35 cm	<i>Luciobarbus</i> , <i>Pseudochondrostoma</i>	1, 7, 14, 15, 16
0.7	Medium swimming and leaping capacity. $25 \text{ cm} \leq \text{size} < 35 \text{ cm}$	<i>Barbus</i> , <i>Parachondrostoma</i>	2, 8, 9, 10, 13
0.6	Medium swimming and leaping capacity. $15 \text{ cm} \leq \text{size} < 25 \text{ cm}$	<i>Iberochondrostoma</i>	6, 19, 20, 21
0.5	Medium swimming and leaping capacity. $10 \text{ cm} \leq \text{size} < 15 \text{ cm}$	<i>Phoxinus</i> , <i>Anaocypris</i>	2, 3, 9, 13
0.4	Medium swimming and leaping capacity. Size < 10 cm	<i>Aphanius</i>	5, 12, 13
0.3	Benthonic. Low swimming and leaping capacity	<i>Barbatula</i> , <i>Cottus</i> , <i>Cobitis</i>	2, 4, 11, 17, 18

[1] Alexandre et al. (2014); [2] Baudoin et al. (2015); [3] Holthe et al. (2005); [4] Knaepkens et al. (2007); [5] Latorre et al. (2020); [6] Mameri et al. (2020); [7] Mateus et al. (2008); [8] O'Steen and Bennett (2003); [9] Ordeix et al. (2011); [10] Ovidio and Philippart (2002); [11] Pavlov (1989); [12] Rubio-Gracia et al. (2020a); [13] Rubio-Gracia et al. (2020b); [14] Sanz-Ronda et al. (2015); [15] Sanz-Ronda et al. (2016); [16] Silva et al. (2012); [17] Stahlberg and Peckmann (1987); [18] Tudorache et al. (2008); [19] Corse et al. (2015); [20] Pires and Magalhães (2013); [21] Santos and Ferreira (2008).

and adapted to other dispersal situations (e.g. a lineal relationship between distance and probability of dispersal).

2.4. Index calculation

For the calculation of the PCI, four georeferenced geographic layers are needed. The first is the dam location layer with their coordinates. Here, large dams (defined as impounding more than 1 hm^3) were used (MAGRAMA, 2004). The second is a river basin layer with segments separated by their junctions and dams. Sections (groups of segments

between two dams) have to be calculated and uniquely numbered. The third is the *meta*-population layer, with segments divided by their junctions and dams. Population segments need to have a unique population ID and population length. The last layer contains the suitable habitat or population nodes. These nodes are located in the junctures between suitable and non-suitable habitat and have their coordinates, and the ID of the section and population they belong to (Fig. 3).

Populations are treated as the nodes of a graph, connected by edges that in these examples can be i) a dam with passability = 0, or ii) the minimum length along the river between the external limits of the populations' range corrected by the dispersal capability of the species. River section and population ID was calculated in R (R Core Team, 2015) using the packages *raster* (Hijmans et al., 2016) and *igraph* (Igraph Core Team, 2015). Nodes were created in ArcMap (ESRI, 2011). Distances between population nodes were calculated in R with the package *riverdist* (Tyers, 2017).

With all this information, natural PCI was calculated in R for each of the fish species in the selected river basins (Fig. 3a). After that, PCI was calculated adding the river basin dams (Fig. 3b). Then, the same PCI was calculated removing one dam of the river basin at a time. The increment in PCI resulting from the removal of each dam was calculated as the difference between the new PCI and the PCI with all dams. Lastly, dams were ranked according to their impact to the overall connectivity of each species *meta*-population (the full list of dams can be seen in the Appendix 1).

The R scripts used for the analyses are available in the Appendix 2.

3. Results

The fragmentation of all four studied fish species *meta*-populations increased between a 48.7% and a 190% when natural populations were divided by dams. Meanwhile the mean length of the populations decreased 32.8–65.5% when impassable dams were considered. *Cobitis vettonica* has only 10 natural populations and is the most impacted species, as dams divide them in 29 smaller populations 65.5% shorter than natural populations (Table 3). Attending to number and length of populations *S. trutta* is the second most impacted fish species as its natural populations are divided by 133 dams. *Anaocypris hispanica* is the least impacted fish species when we look at number and length of its

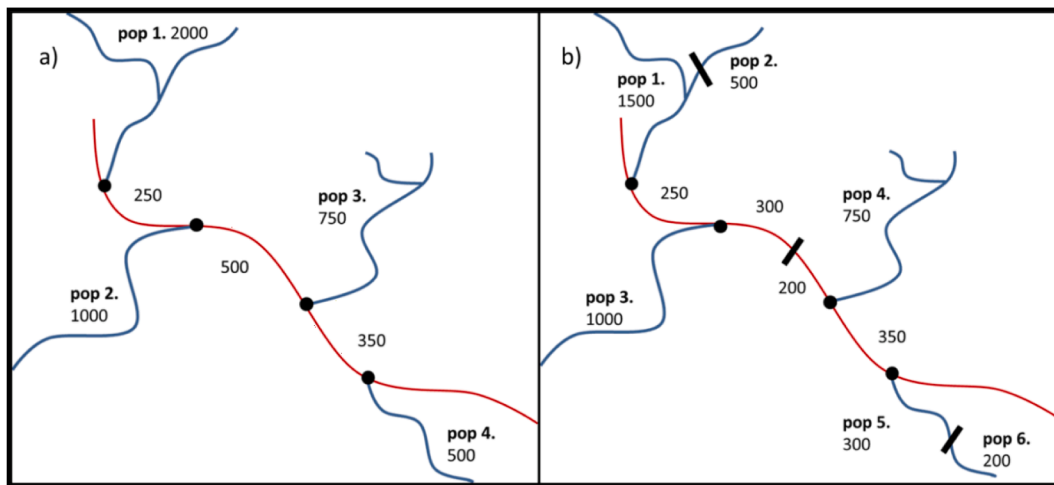


Fig. 3. Simplified example of the data needed for the calculation of a) natural populations PCI and b) PCI with dams added to the river network. Segments need to be grouped in unique populations. Total length of populations, location of dams and inter-population segments' length are necessary to calculate PCI. In this simple example, using $PD = 0.5$ and a logarithmic relationship between PD and distance, the a) natural PCI = 32.18%; while b) PCI = 23.21% when impassable dams are included.

Table 3

Descriptive characteristics of the four studied meta-populations (number of populations, total population length, mean population length) and their respective PCI results. Results for both natural populations and dam-isolated populations are given. All length measurements are given in km. PD information can be found in Table 2. The PCI was estimated according to the proposed equation in the Material and Methods section.

River basin	Species	PD	Total pop length	Natural populations			Fragmented populations		
				Number of pops	Mean pop length	PCI	Number of pops	Mean pop length	PCI
Tagus	<i>Cobitis vettonica</i>	0.3	845.82	10	84.58	20.09	29	29.17	14.36
Tagus	<i>Luciobarbus comizo</i>	0.8	2520.32	70	36.00	47.48	120	21.00	16.48
Guadiana	<i>Anaocypris hispanica</i>	0.5	4468.79	117	38.19	7.95	174	25.68	2.59
Ebro	<i>Salmo trutta</i>	0.9	8961.47	89	100.69	19.3	222	40.37	2.19

populations.

Natural PCI outcomes ranged from 7.95% to 47.48% depending on the species (Table 3). The most naturally connected species meta-population is *L. comizo*. On the other hand, *A. hispanica* has the least connected meta-population. *Cobitis vettonica*, which has the lowest PD, had low PCI numbers even when there are only 10 natural populations (Table 3). Adding dams to the PCI reduced the connectivity results. The most affected species is *L. comizo*, with a PCI almost 31 points lower

compared to its natural connectivity. *Cobitis vettonica* and *A. hispanica* meta-populations were not very affected by dams, with reductions in PCI of 5 points.

When dams in the meta-population area of influence were removed one at a time, the observed PCI increase varied considerably. The most impacting dam is “José María de Oriol (Alcántara II)”, which divides a large *L. comizo* population in two (Table 4, Fig. 2c). In general, the most impacting dams affect *L. comizo* and *C. vettonica* in the Tagus river basin.

Table 4

The five most impacting dams for each fish species meta-population, ranked from most to least impacting. The increment in the PCI is given in points. The potential of dispersion (PD) of fish species was considered according to Table 2. The PCI was estimated according to the proposed equation of Material and Methods section.

River basin	Fish species	Name	Longitude	Latitude	PCI Increment (points)
Tagus	<i>Luciobarbus comizo</i>	José María De Oriol (Alcántara II)	-6.8899	39.7267	13.75
Tagus	<i>Luciobarbus comizo</i>	Encín	-6.4278	39.9554	2.41
Tagus	<i>Luciobarbus comizo</i>	Santa Marta De Magasca	-6.0784	39.5221	1.43
Tagus	<i>Luciobarbus comizo</i>	Torrejón Tiétar	-5.9891	39.8441	0.57
Tagus	<i>Luciobarbus comizo</i>	Torrejón Tajo	-5.9836	39.8362	0.48
Tagus	<i>Cobitis vettonica</i>	Besagueda	-7.0778	40.1414	0.97
Tagus	<i>Cobitis vettonica</i>	Rivera De Gata (Main)	-6.6325	40.1340	0.79
Tagus	<i>Cobitis vettonica</i>	Jerte (Jerte Plasencia)	-6.0407	40.0592	0.14
Tagus	<i>Cobitis vettonica</i>	Gabriel y Galán	-6.1301	40.2243	0.13
Tagus	<i>Cobitis vettonica</i>	Manufacturas Béjar	-5.7464	40.3951	0.11
Ebro	<i>Salmo trutta</i>	Cereceda	-3.4676	42.7867	0.26
Ebro	<i>Salmo trutta</i>	Leiva	-3.0501	42.5053	0.23
Ebro	<i>Salmo trutta</i>	Cillaperiata	-3.3575	42.7840	0.11
Ebro	<i>Salmo trutta</i>	Oliana	1.2970	42.0933	0.08
Ebro	<i>Salmo trutta</i>	Ullivarri	-2.6124	42.9291	0.08
Guadiana	<i>Anaocypris hispanica</i>	Mendoza	-4.9255	38.7054	0.78
Guadiana	<i>Anaocypris hispanica</i>	La Colada	-5.0112	38.5469	0.25
Guadiana	<i>Anaocypris hispanica</i>	Castilseras	-4.7975	38.7417	0.16
Guadiana	<i>Anaocypris hispanica</i>	Caia	-7.1413	39.0022	0.05
Guadiana	<i>Anaocypris hispanica</i>	Aroche (Valdesotellas)	-6.9764	37.9887	0.05

The increment in *meta*-population connectivity due to one dam removal is generally low, with only three dam removals increasing the PCI in more than one point.

4. Discussion

River connectivity indices have become a common tool to assess the fragmentation of river basins and help in barrier mitigation prioritization. However, these indices are generally used to calculate connectivity for a whole river network, considering a continuous habitat between the headstreams and the river mouth (Cote et al., 2009; Grill et al., 2014; McKay et al., 2013).

Our PCI index is developed to analyse connectivity for certain habitat characteristics or *meta*-populations for aquatic-obligated organisms like fish. In terrestrial ecosystems, connectivity is measured between the studied habitat patches (e.g. connectivity of forest patches across croplands or protected areas). These habitats are often suitable for a species of interest or ecosystems of high conservation value. The connectivity is thus measured between those habitats of interests, not the totality of habitats (Bunn et al., 2000; Galpern et al., 2011; Pascual-Hortal and Saura, 2006). This methodology has many applications such as creating networks of connected areas for the conservation of certain species or establishing efficient ecological corridors between high biodiversity areas (Galpern et al., 2011).

Freshwater organisms such as fishes realize certain ecological niches (determined by environmental and biological variables such as water temperature, flow, substrate, pollution, presence of predators, etc.) and have different dispersal capabilities (Wiens, 2002). This capability depends on multiple factors such as the swimming power of the fish and the length and characteristics of the non-suitable habitat that has to be crossed (Crook et al., 2015). Potamodromous fish populations separated by large distances of non-suitable habitat are usually more isolated than closer populations although the degree of isolation for the same inter-population distance depends on species-specific characteristics (Dunham and Rieman, 1999; Heino et al., 2015; Tischendorf and Fahrig, 2000).

The PCI only considers the connectivity of habitats of interest or *meta*-populations instead of the connectivity of the whole river basin. It does not depend on graph theory, making it more approachable and it requires a small number of easily collected variables, thus making the index calculation simple and easy to adapt to different situations and scales. The PCI is a simple method to identify naturally isolated fish populations. For example, the PCI can put numbers to the degree of isolation of *S. trutta* populations, which are very fragmented and located in cold and oxygen-rich mountain streams (Elliott and Elliott, 2010; Jonsson and Jonsson, 2011, Fig. 2a). According to the PCI results, *S. trutta* natural *meta*-population connectivity is only a 17.11%, probably due to the large distances separating populations.

This index also allows the inclusion of artificial barriers to understand their impacts in the connectivity of different habitats and populations and assess the impact of each individual dam (Table 4). More naturally isolated fish populations may be less susceptible to dam fragmentation than more connected *meta*-populations as suggested by the PCI results of *L. comizo*. This well connected *meta*-population was heavily fragmented by barriers, with a PCI reduction of more than 30 points (Table 3). *Cobitis vettonica* and *A. hispanica* have the lowest PCI reductions when dams are added, possibly due to their low dispersal capacities or necessities (Table 3). This may suggest that fish species with lower dispersal capability may also be less impacted by the presence of dams between populations, because they would not cross the large distances between them (Doadrio, 2001; Doadrio et al., 2011). Moreover, in naturally isolated *meta*-populations such as *C. vettonica* and *S. trutta*, barriers dividing a population in smaller isolated parts are more impacting than barriers located on the river stretches between populations. This suggests that the degree of connectivity between populations determines the effect of each barrier and governs the selection

of the most impacting obstacles for removal or mitigation.

Dams impacting different species or higher-quality habitat may be found out and their effects mitigated. If economic, social and environmental factors allow it, the dam may be removed to restore river connectivity. However, dam removal needs to be carefully studied because some dams may prevent further colonization of freshwater invasive species (Milt et al., 2018; Rahel, 2013). Moreover, toxic sediments and hydromorphic changes need to be assessed beforehand to avoid degradation of the freshwater ecosystems upstream and downstream of the dam (Gangloff, 2013; Stanley and Doyle, 2003). There are other partial connectivity restoration solutions that do not require the removal of the barriers, such as the construction of fishways to allow fish passage and thus the reconnection of populations (Seliger and Zeiringer, 2018).

The PCI may also be used to assess the vulnerability of *meta*-populations and individual isolated populations with the aim to create river ecological corridors. These river corridors would be unfragmented river segments that ensure the connectivity of essential fish communities or habitats. Connectivity is essential for the appropriate selection of protected river areas (Erös et al., 2018; Hermoso et al., 2011) and PCI may help in the assessment of valuable connected river segments. However, due to its nature, PCI is built for specific species and *meta*-populations and its results can't be applied to manage entire river networks. This index is complementary to river basin connectivity indices and they could be applied together to create a complete picture of connectivity for freshwater fish in a river network.

There are some challenges to the application of the PCI, that should be addressed before using it for freshwater fish management. The most important one is the accurate estimation of fish dispersal capabilities. Connectivity at *meta*-population scales is driven by the movement of individuals. Migration movements between fish species are very variable (Crook et al., 2015). Is the species migration obligated? Is the migration directional, such as a spawning migration upstream? What are the physiological capabilities of the species? Is there a passive larvae movement or adult active migration? When is the migration occurring? Dispersal has to be empirically studied and understood for each species and even population, as individual evolution and environmental factors play a role in movement (Lowe and McPeck, 2014).

Our PCI model relies in very broad qualitative dispersal categories. These are assigned according to the fish species size and swimming capabilities similar to the ones used in some dam passability indices (Solà et al., 2011). The connectivity study is thus simplified and more approachable but the results are less accurate. As we do not know the dispersal capabilities of fish species we cannot comprehend how they are related to distance. We assumed an exponential relationship where fish is more likely to move short distances than large stretches as was in other studies (Schick and Lindley, 2007). However, this assumption can be easily replaced by others that reflect reality more accurately.

River habitat characteristics is also related to the dispersal capabilities in two ways: first, the migration behaviour and necessity for movement of each individual on a population may vary with the nearby presence or absence of suitable habitats. Some individuals may live in high quality and diverse habitats, thus making migration unnecessary, while others may need to migrate long distances to find suitable habitats (Branco et al., 2017). Moreover, the quality of the habitat between populations is also important. Some habitats may pose partial or total barriers to migration due to the tolerance of different species to their characteristics (high slope, high water velocity, low oxygen concentration, high temperatures, presence of predators, etc.). The PCI is able to include these parameters by correcting river segment length by its habitat characteristics, thus weighting the distance (d) between populations by its resistance to the movement of different species. Although that analysis is beyond the scope of this study and habitat characteristics (and their effect in fish species) are difficult to obtain at large scales, it would be advisable to consider them in future studies.

Other challenge is to define separated populations. The area occupied by a population change depending on the scale of study and the

methods used to select the area. Intense field studies are necessary to create accurate maps of populations. However, at large scales, intense fieldwork may be unviable. Here we used habitat suitability models as a proxy for populations and the accuracy of models depend on the quality of presence and absence data used to calibrate them and the set of independent variables selected as predictors (Hortal et al., 2008). Moreover, some species such as generalists or rare species are more difficult to model than others (Gu and Swihart, 2004; Meynard and Quinn, 2007). As there is no ideal modelling method for all circumstances, ensemble models were calibrated (Segurado and Araújo, 2004). We transformed the continuous ensemble model into a binary (suitable/non-suitable) model to simplify the calculation of PCI. However, this may be a source of error as thresholds used to transform the models are not perfect (Freeman and Moisen, 2008). In short, a certain fish species may not be present in the entire suitable habitat estimated by the binary model and may live in habitats deemed non-suitable. In addition to the challenges defining populations to study, we do not know if those populations are the result of past impacts, including the extinction of populations due to the construction of barriers decades or hundreds of years before.

Another problem is the simplicity of most river connectivity methods. Simplicity may be essential to ensure indices are widely used but it does not capture the complexities of barrier cumulative impacts in populations (direct and indirect mortality, invasive species colonization facilitation, etc.) at both small and large scales (Samia et al., 2015). Due to this, it may be difficult to use them in population dynamics models. Indices must accurately reflect reality to predict persistence or extinction of fish populations. Validation of river or fish population connectivity indices with empirical studies is essential if we want to effectively use them in conservation and management plans (Samia et al., 2015).

Lastly, the calculation of all possible prioritization actions would require the analysis of all combinations of dams in a river basin, with different types of solutions (dam removal or fishway construction). This would be the best way to find the most optimal connectivity restoration solution, but requires very powerful computers and is time consuming. Here we have only analysed the impact of single dams to show the capacities of the index. Furthermore, the PCI can also be combined with budget optimization methods to analyse the optimal river connectivity restoration solutions given limited economic resources (McKay et al., 2013).

Although only large totally impassable barriers were analysed as example on this study, the PCI is prepared to analyse the impact of partial barriers and partial river connectivity restoration solutions (e.g. fishways). This can be done by multiplying the partial barrier passabilities, ranging from 0 (impassable) to 1 (completely passable) to create the cumulative barrier passability B as shown in Eq. (2). This study was performed with only large dam data due to the lack of data on small dam presence and passability. If small dams and weirs were added, the connectivity of *meta*-populations may be further reduced.

4.1. Conclusions

During the last two decades river connectivity has gained increasing attention. Numerous theoretical and empirical studies have been published highlighting different aspects of river connectivity and its role in conservation (Clavero and Hermoso, 2015; Erős et al., 2018; Hermoso et al., 2011; Liermann et al., 2012; Maitland et al., 2016; Nilsson et al., 2005). Here we present the basic framework and methodology of a new Population Connectivity Index (PCI) for potamodromous fish species with some examples, we analyse its advantages, shortcomings, applications and further studies to build and improve upon this one. This study is an exercise that analysed occurrence data to showcase a new method to assess the fragmentation of fish populations in rivers, and specific results for these specific fishes populations should not be considered for their management without the revision and updating of data distribution and pieces of evidence about migratory behaviour of

fish populations.

The PCI allows calculating the impact of dams in fish population connectivity and creating dam mitigation plans adjusted to each situation. The index shows that the impact of barriers varies with the dispersal capability of fish species and the distance between populations. The PCI can be used to make species-specific river restoration plans, select locations for new dams and to create ecological corridors connecting important fish populations. However, there is much work to be done if we want to fully understand and mitigate the effects of fragmentation in rivers and their fish communities at different scales. We hope that this study opens the door to assess the impacts of river fragmentation in river organisms and habitats at all scales.

CRediT authorship contribution statement

Amaia A. Rodeles: Conceptualization, Methodology, Formal analysis, Writing - original draft. **David Galicia:** Methodology, Writing - review & editing, Supervision. **Rafael Miranda:** Conceptualization, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was performed with the help of a grant awarded to Amaia A. Rodeles by the Government of Navarra. The authors would like to thank the Iberian Society of Ichthyology (SIBIC) and their collaborating researchers and administrations for providing the fish data necessary for the study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107557>.

References

- Alexandre, C.M., Quintella, B.R., Ferreira, A.F., Romão, F.A., Almeida, P.R., 2014. Swimming performance and ecomorphology of the Iberian barbel *Luciobarbus bocagei* (Steindachner, 1864) on permanent and temporary rivers. *Ecol. Freshw. Fish* 23, 244–258.
- Antunes, C., Cobo, F., Araújo, M.J., 2016. Iberian inland fishes. In: Craig, J.F. (Ed.), *Freshwater Fisheries Ecology*. Wiley & Sons, Singapore, pp. 268–282.
- Baudoin, J.M., Burgun, V., Chanseau, M., Larinier, M., Ovidio, M., Sremski, W., Steinbach, P., Voegtli, B., 2015. Assessing the Passage of Obstacles by Fish. Concepts, Design and Application. Onema, Paris.
- Benitez, J.P., Nzau Matondo, B., Dierckx, A., Ovidio, M., 2015. An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. *Aquat. Ecol.* 49, 481–497.
- Branco, P., Amaral, S.D., Ferreira, M.T., Santos, J.M., 2017. Do small barriers affect the movement of freshwater fish by increasing residency? *Sci. Total Environ.* 581–582, 486–494.
- Bunn, A.G., Urban, D.L., Keitt, T.H., 2000. Landscape connectivity: a conservation application of graph theory. *J. Environ. Manage.* 59, 265–278.
- Campbell Grant, E.H., Lowe, W.H., Fagan, W.F., 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol. Lett.* 10, 165–175.
- Clavero, M., Hermoso, V., 2015. Historical data to plan the recovery of the European eel. *J. Appl. Ecol.* 52, 960–968.
- Corse, E., Tarkan, A.S., Emiroglu, O., Imsiridou, A., Minos, G., Lorenzoni, M., Vilizzi, L., Aboim, M.A., 2015. Covariation of trophic and habitat-related traits in chondrostoms (Cyprinidae): implications for repeated and diversifying evolutionary processes. *J. Zool.* 295, 294–305. <https://doi.org/10.1111/jzo.12212>.
- Cote, D., Kehler, D.G., Bourne, C., Wiersma, Y.F., 2009. A new measure of longitudinal connectivity for stream networks. *Landsc. Ecol.* 24, 101–113.
- Crook, D.A., Lowe, W.H., Allendorf, F.W., Erős, T., Finn, D.S., Gillanders, B.M., Hadwen, W.L., Harrod, C., Hermoso, V., Jennings, S., Kilada, R.W., Nagelkerken, I., Hansen, M.M., Page, T.J., Riginos, C., Fry, B., Hughes, J.M., 2015. Human effects on ecological connectivity in aquatic ecosystems: integrating scientific approaches to

- support management and mitigation. *Sci. Total Environ.* 534, 52–64. <https://doi.org/10.1016/j.scitotenv.2015.04.034>.
- Diebel, M.W., Fedora, M., Cogswell, S., O'Hanley, J.R., 2015. Effects of road crossings on habitat connectivity for stream-resident fish. *River Res. Appl.* 31, 1251–1261. <https://doi.org/10.1002/rra>.
- Doadio, I., 2001. Atlas y libro rojo de los peces continentales de España, second ed. Ministerio de Medio Ambiente, Madrid.
- Doadio, I., Perea, S., Garzón-Heydt, P., González, J.L., 2011. Ictiofauna continental española. Bases para su seguimiento, first ed. Ministerio de Medio Ambiente, Medio Rural y Marino, Madrid.
- Domisch, S., Amatulli, G., Jetz, W., 2015. Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. *Sci. Data* 2, 1–13. <https://doi.org/10.1038/sdata.2015.73>.
- Dunham, J.B., Rieman, B.E., 1999. Metapopulation structure of Bull Trout: influence of physical, biotic and geometrical landscape characteristics. *Ecol. Appl.* 9, 642–655. [https://doi.org/10.1890/1051-0761\(1999\)09\[0642:MSOBTJ\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)09[0642:MSOBTJ]2.0.CO;2).
- Elliott, J.M., Elliott, J.A., 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *J. Fish Biol.* 77, 1793–1817. <https://doi.org/10.1111/j.1095-8649.2010.02762.x>.
- Erős, T., O'Hanley, J.R., Czeglédi, I., 2018. A unified model for optimizing riverscape conservation. *J. Appl. Ecol.* 1871–1883 <https://doi.org/10.1111/1365-2664.13142>.
- Erős, T., Schmera, D., Schick, R.S., 2011. Network thinking in riverscape conservation – a graph-based approach. *Biol. Conserv.* 144, 184–192. <https://doi.org/10.1016/j.biocon.2010.08.013>.
- ESRI, 2011. ArcGIS.
- Ferguson, J.W., Healey, M., Dugan, P., Barlow, C., 2011. Potential effects of dams on migratory fish in the Mekong River: lessons from salmon in the Fraser and Columbia Rivers. *Environ. Manage.* 47, 141–159. <https://doi.org/10.1007/s00267-010-9563-6>.
- Freeman, E.A., Moisen, G.G., 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecol. Modell.* 217, 48–58. <https://doi.org/10.1016/j.ecolmodel.2008.05.015>.
- Galpern, P., Manseau, M., Fall, A., 2011. Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. *Biol. Conserv.* 144, 44–55. <https://doi.org/10.1016/j.biocon.2010.09.002>.
- Gangloff, M.M., 2013. Taxonomic and ecological tradeoffs associated with small dam removals. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 23, 475–480. <https://doi.org/10.1002/aqc.2383>.
- García de Leaniz, C., 2008. Weir removal in salmonid streams: implications, challenges and practicalities. *Hydrobiologia* 609, 83–96. <https://doi.org/10.1007/s10750-008-9397-x>.
- Gido, K.B., Whitnet, J.E., Perkin, J.S., Turner, T.F., 2016. Fragmentation, connectivity and fish species persistence in freshwater ecosystems. In: Closs, G.P., Krkosek, M., Olden, J.D. (Eds.), *Conservation of Freshwater Fishes*. Cambridge University Press, Cambridge, pp. 293–323.
- Grill, G., Lehner, B., Lumsdon, A.E., MacDonald, G.K., Zarfl, C., Reidy Liermann, C., 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environ. Res. Lett.* 10, 015001 <https://doi.org/10.1088/1748-9326/10/1/015001>.
- Grill, G., Ouellet Dallaire, C., Fluet Chouinard, E., Sindorf, N., Lehner, B., 2014. Development of new indicators to evaluate river fragmentation and flow regulation at large scales: a case study for the Mekong River basin. *Ecol. Indic.* 45, 148–159. <https://doi.org/10.1016/j.ecolind.2014.03.026>.
- Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biol. Conserv.* 116, 195–203. [https://doi.org/10.1016/S0006-3207\(03\)00190-3](https://doi.org/10.1016/S0006-3207(03)00190-3).
- Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. *Habitat Suitability and Distribution Models. With Applications in R*, first ed. Cambridge University Press, Cambridge.
- Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.* 42, 3–16.
- Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869. <https://doi.org/10.1111/fwb.12533>.
- Hermoso, V., Linke, S., Prenda, J., Possingham, H.P., 2011. Addressing longitudinal connectivity in the systematic conservation planning of fresh waters. *Freshw. Biol.* 56, 57–70. <https://doi.org/10.1111/j.1365-2427.2009.02390.x>.
- Hijmans, R.J., Cameron, S., Parra, J., Jones, P., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hijmans, R.J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Perminan Lamigueiro, O., Bevan, A., Racine, E.B., Shortridge, A., 2016. Raster: geographic data analysis and modeling [WWW Document]. URL <http://cran.r-project.org/package=raster> (accessed 9.27.16).
- Holthe, E., Lund, E., Finstad, B., Thorstad, E.B., McKinley, R.S., 2005. A fish selective obstacle to prevent dispersion of an unwanted fish species, based on leaping capabilities. *Fish. Manag. Ecol.* 12, 143–147.
- Horreo, J.L., Martínez, J.L., Ayllon, F., Pola, I.G., Monteoliva, J.A., Héland, M., García-Vázquez, E., 2011. Impact of habitat fragmentation on the genetics of populations in dendritic landscapes. *Freshw. Biol.* 56, 2567–2579. <https://doi.org/10.1111/j.1365-2427.2011.02682.x>.
- Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M., Baselga, A., 2008. Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos* 117, 847–858. <https://doi.org/10.1111/j.0030-1299.2008.16434.x>.
- Igraph Core Team, 2015. *igraph: the network analysis package* [WWW Document]. URL <http://igraph.org/> (accessed 9.28.16).
- IUCN, 2019. The IUCN Red List of Threatened Species [WWW Document]. URL <http://www.iucnredlist.org/> (accessed 1.26.19).
- Jonsson, B., Jonsson, N., 2011. *Ecology of Atlantic Salmon and Brown Trout*. Springer, London (UK).
- Kemp, P.S., O'Hanley, J.R., 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fish. Manag. Ecol.* 17, 297–322. <https://doi.org/10.1111/j.1365-2400.2010.00751.x>.
- Knaepkens, G., Maertens, E., Tudorache, C., De Boeck, G., Eens, M., 2007. Evaluation of passive integrated transponder tags for marking the bullhead (*Cottus gobio*), a small benthic freshwater fish: effects on survival, growth and swimming capacity. *Ecol. Freshw. Fish* 16, 404–409.
- Komori, O., Eguchi, S., Saigusa, Y., Kusumoto, B., Kubota, Y., 2020. Sampling bias correction in species distribution models by quasi-linear Poisson point process. *Ecol. Inf.* 55, 101015 <https://doi.org/10.1016/j.ecoinf.2019.101015>.
- Kottelat, M., Freyhof, J., 2007. *Handbook of European Freshwater Fishes*, first ed. Publications Kottelat, Cornol, Switzerland.
- Latorre, D., García-Berthou, E., Rubio-Gracia, F., Galobart, C., Almeida, D., Vila-Gispert, A., 2020. Captive breeding conditions decrease metabolic rates and alter morphological traits in the endangered Spanish toothcarp, *Aphanius iberus*. *Int. Rev. Hydrobiol.* 119–130. <https://doi.org/10.1002/iroh.201902014>.
- Lehner, B., Verdin, K., Jarvis, A., 2008. New global hydrography derived from spaceborne elevation data. *Eos (Washington, DC)* 89, 93–94.
- Levins, R., 1968. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240. <https://doi.org/10.1016/j.inoche.2007.06.005>.
- Liermann, C.R., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam obstruction for global freshwater fish diversity. *Bioscience* 62, 539–548. <https://doi.org/10.1525/bio.2012.62.6.5>.
- Lowe, W.H., McPeck, M.A., 2014. Is dispersal neutral? *Trends Ecol. Evol.* 29, 444–450. <https://doi.org/10.1016/j.tree.2014.05.009>.
- Lucas, M.C., Batley, E., 1996. Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: implications for river management. *J. Appl. Ecol.* 33, 1345–1358.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, USA.
- Maceda-veiga, A., 2013. Towards the conservation of freshwater fish: Iberian Rivers as an example of threats and management practices. *Rev. Fish Biol. Fish.* 23, 1–22. <https://doi.org/10.1007/s11160-012-9275-5>.
- MAGRAMA, 2004. Descargas SIA [WWW Document]. URL <http://servicios2.marm.es/sia/visualizacion/descargas/mapas.jsp> (accessed 2.22.16).
- Maitland, B.M., Poesch, M., Anderson, A.E., 2016. Prioritising culvert removals to restore habitat for at-risk salmonids in the boreal forest. *Fish. Manag. Ecol.* 23, 489–502. <https://doi.org/10.1111/fme.12188>.
- Mameri, D., Sousa-Santos, C., Robalo, J.L., Gil, F., Faria, A.M., 2020. Swimming performance in early life stages of three threatened Iberian Leuciscidae. *Acta Ethol.* 23, 23–29. <https://doi.org/10.1007/s10211-019-00331-9>.
- Mateus, C.S., Quintella, B.R., Almeida, P.R., 2008. The critical swimming speed of Iberian barbel *Barbus bocagei* in relation to size and sex. *J. Fish Biol.* 73, 1783–1789. <https://doi.org/10.1111/j.1095-8649.2008.02023.x>.
- McKay, S.K., Cooper, A.R., Diebel, M.W., Elkins, D., Oldford, G., Roghair, C., Wiefelich, D., 2017. Informing watershed connectivity barrier prioritization decisions: a synthesis. *River Res. Appl.* 33, 847–862.
- McKay, S.K., Schramski, J.R., Conyngham, J.N., Fischenich, J.C., 2013. Assessing upstream fish passage connectivity with network analysis. *Ecol. Appl.* 23, 1396–1409. <https://doi.org/10.1890/12-1564.1>.
- Meynard, C.N., Quinn, J.F., 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *J. Biogeogr.* 34, 1455–1469. <https://doi.org/10.1111/j.1365-2699.2007.01720.x>.
- Milt, A.W., Diebel, M.W., Doran, P.J., Ferris, M.C., Herbert, M., Khoury, M.L., Moody, A.T., Neeson, T.M., Ross, J., Treska, T., O'Hanley, J.R., Walter, L., Wangen, S.R., Yacobson, E., McIntyre, P.B., 2018. Minimizing opportunity costs to aquatic connectivity restoration while controlling an invasive species. *Conserv. Biol.* 32, 894–904. <https://doi.org/10.1111/cobi.13105>.
- Morita, K., Yamamoto, S., 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling Charr populations. *Conserv. Biol.* 16, 1318–1323.
- Nieland, J.L., Sheehan, T.F., Saunders, R., 2015. Assessing demographic effects of dams on diadromous fish: a case study for Atlantic salmon in the Penobscot River, Maine. *ICES J. Mar. Sci.* 72, 2423–2437.
- Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science (80-)* 308, 405–408.
- O'Steen, S., Bennett, A.F., 2003. Thermal acclimation effects differ between voluntary, maximum, and critical swimming velocities in two cyprinid fishes. *Physiol. Biochem. Zool.* 76, 484–496. <https://doi.org/10.1086/376421>.
- Ordeix, M., Pou-Rovira, Q., Sellarés, N., Bardina, M., Casamitjana, A., Solà, C., Munné, A., 2011. Fish pass assessment in the rivers of Catalonia (NE Iberian Peninsula). A case study of weirs associated with hydropower plants and gauging stations. *Limnetica* 30, 405–426.
- Ovidio, M., Philippart, J.C., 2002. The impact of small physical obstacles on upstream movements of six species of fish: synthesis of a 5-year telemetry study in the River Meuse basin. *Hydrobiologia* 483, 55–69. <https://doi.org/10.1023/A:1021398605520>.
- Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-based landscape connectivity indices: towards the prioritization of habitat patches and corridors for conservation. *Landscape Ecol.* 21, 959–967. <https://doi.org/10.1007/s10980-006-0013-z>.

- Pavlov, D.S., 1989. Structures Assisting the Migrations of Non-salmonid Fish. USSR, Rome.
- Pires, D.F., Magalhães, M.F., 2013. First data on the movements of *Iberochondrostoma almakai* (Coelho, Mesquita, Collares-Pereira, 2005) out of dry-season pools in a Mediterranean stream. *An. Biol.* 35, 85–87. <https://doi.org/10.6018/analesbio.0.35.12>.
- R Core Team, 2015. R: a language and environment for statistical computing.
- Rahel, F.J., 2013. Intentional fragmentation as a management strategy in aquatic systems. *Bioscience* 63, 362–372. <https://doi.org/10.1525/bio.2013.63.5.9>.
- Rivas-Martínez, S., 1987. Memoria del mapa de series de vegetación de España, first ed. Ministerio de Agricultura, Pesca y Alimentación, Madrid.
- Rodeles, A.A., Leunda, P.M., Elso, J., Ardaiz, J., Galicia, D., Miranda, R., 2019. Consideration of habitat quality in a river connectivity index for anadromous fishes. *Int. Waters* 9, 278–288. <https://doi.org/10.1080/20442041.2018.1544817>.
- Rubio-Gracia, F., García-Berthou, E., Guasch, H., Zamora, L., Vila-Gispert, A., 2020a. Size-related effects and the influence of metabolic traits and morphology on swimming performance in fish. *Curr. Zool.* 1–11. <https://doi.org/10.1093/cz/zoaa013>.
- Rubio-Gracia, F., García-Berthou, E., Latorre, D., Moreno-Amich, R., Srean, P., Luo, Y., Vila-Gispert, A., 2020b. Differences in swimming performance and energetic costs between an endangered native toothcarp (*Aphanius iberus*) and an invasive mosquitofish (*Gambusia holbrooki*). *Ecol. Freshw. Fish* 29, 230–240. <https://doi.org/10.1111/eff.12509>.
- Samia, Y., Lutscher, F., Hastings, A., 2015. Connectivity, passability and heterogeneity interact to determine fish population persistence in river networks. *J. R. Soc. Interface* 12, 20150435. <https://doi.org/10.1098/rsif.2015.0435>.
- Santos, J.M., Ferreira, M.T., 2008. Microhabitat use by endangered Iberian cyprinids nase *Iberochondrostoma almakai* and chub *Squalius aradensis*. *Aquat. Sci.* 70, 272–281. <https://doi.org/10.1007/s00027-008-8037-x>.
- Sanz-Ronda, F.J., Bravo-Córdoba, F.J., Fuentes-Pérez, J.F., Castro-Santos, T., 2016. Ascent ability of brown trout, *Salmo trutta*, and two Iberian cyprinids – Iberian barbel, *Luciobarbus bocagei*, and northern straight-mouth nase, *Pseudochondrostoma duriense* - in a vertical slot fishway. *Knowl. Manag. Aquat. Ecosyst.* 2016-Janua. <https://doi.org/10.1051/kmae/2015043>.
- Sanz-Ronda, F.J., Ruiz-Legazpi, J., Bravo-Córdoba, F.J., Makrakis, S., Castro-Santos, T., 2015. Sprinting performance of two Iberian fish: *Luciobarbus bocagei* and *Pseudochondrostoma duriense* in an open channel flume. *Ecol. Eng.* 83, 61–70. <https://doi.org/10.1016/j.ecoleng.2015.05.033>.
- Schick, R.S., Lindley, S.T., 2007. Directed connectivity among fish populations in a riverine network. *J. Appl. Ecol.* 44, 1116–1126. <https://doi.org/10.1111/j.1365-2664.2007.01383.x>.
- Segurado, P., Araújo, M.B., 2004. An evaluation of methods for modelling species distributions. *J. Biogeogr.* 31, 1555–1568. <https://doi.org/10.1111/j.1365-2699.2004.01076.x>.
- Seliger, C., Zeiringer, B., 2018. River Connectivity, habitat fragmentation and related restoration measures. In: Schmutz, S., Sendzimir, J. (Eds.), *Riverine Ecosystem Management. Science for Governing towards a Sustainable Future*. Springer, Amsterdam, pp. 171–186. <https://doi.org/10.1007/978-3-319-73250-3>.
- SIBIC, 2015. SIBIC [WWW Document]. URL <http://www.sibic.org/sibic.html> (accessed 1.26.16).
- Silva, A.T., Katopodis, C., Santos, J.M., Ferreira, M.T., Pinheiro, A.N., 2012. Cyprinid swimming behaviour in response to turbulent flow. *Ecol. Eng.* 44, 314–328. <https://doi.org/10.1016/j.ecoleng.2012.04.015>.
- Solà, C., Ordeix, M., Pou-Rovira, Q., Sellarès, N., Queral, A., Bardina, M., Casamitjana, A., Munné, A., 2011. Longitudinal connectivity in hydromorphological quality assessments of rivers. The ICF index: a river connectivity index and its application to Catalan rivers. *Limnetica* 30, 273–292.
- Stahlberg, S., Peckmann, P., 1987. The critical swimming speed of small teleost fish species in a flume. *Arch. für Hydrobiol.* 110, 179–193.
- Stanley, E.H., Doyle, M.W., 2003. Trading off: the ecological effects of dam removal. *Front. Ecol. Environ.* 1, 15–22. [https://doi.org/10.1890/1540-9295\(2003\)001\[0015:TOTEEO\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0015:TOTEEO]2.0.CO;2).
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573. <https://doi.org/10.2307/3544927>.
- Thuiller, W., Georges, D., Engler, R., Breiner, F., 2016. Package BIOMOD2. Ensemble platform for species distribution modeling.
- Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. *Oikos* 90, 7–19.
- Tudorache, C., Viaene, P., Blust, R., Vereecken, H., De Boeck, G., 2008. A comparison of swimming capacity and energy use in seven European freshwater fish species. *Ecol. Freshw. Fish* 17, 284–291. <https://doi.org/10.1111/j.1600-0633.2007.00280.x>.
- Tyers, M., 2017. riverdist: river network distance computation and applications [WWW Document]. URL <https://cran.r-project.org/web/packages/riverdist/index.html> (accessed 12.11.18).
- Veloz, S.D., 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *J. Biogeogr.* 36, 2290–2299.
- Vera-Escalona, I., Senthivasan, S., Habit, E., Ruzzante, D.E., 2018. Past, present, and future of a freshwater fish metapopulation in a threatened landscape. *Conserv. Biol.* 32, 849–859. <https://doi.org/10.1111/cobi.13093>.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. *Nature* 467, 555–561. <https://doi.org/10.1038/nature09549>.
- Wiens, J.A., 2002. Riverine landscapes: taking landscape ecology into the water. *Freshw. Biol.* 47, 501–515.
- Yamamoto, S., Morita, K., Koizumi, I., Maekawa, K., 2004. Genetic differentiation of white-spotted charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial-temporal changes in gene frequencies. *Conserv. Genet.* 5, 529–538. <https://doi.org/10.1023/B:COGE.0000041029.38961.a0>.
- Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2014. A global boom in hydropower dam construction. *Aquat. Sci.* 77, 161–170. <https://doi.org/10.1007/s00027-014-0377-0>.