Limnetica, 39(2): 601-619 (2020). DOI: 10.23818/limn.39.39

Barriers to longitudinal river connectivity: review of impacts, study methods and management for Iberian fish conservation

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Received: 05/07/19 Accepted: 10/09/19

ABSTRACT

Barriers to longitudinal river connectivity: review of impacts, study methods and management for Iberian fish conservation

River connectivity is essential for the correct functioning of freshwater ecosystems at all scales. However, it has not received the necessary attention by researchers, managers and policymakers until recent years. In this review, we recap the state of knowledge in river connectivity and its applications to conservation. We describe the particular characteristics of river connectivity and summarise the effects of its interruption in different freshwater ecosystem elements. We then focus on the effects of the lack of segment connectivity in fish species and review the different methods developed to study it. The application of connectivity in freshwater fish conservation areas is also reviewed, which highlights the lack of studies on this subject. Finally, connectivity restoration is studied. The review addresses these topics in a general way and then focus on the Iberian Peninsula. The Iberian Peninsula is an interesting place to study river connectivity because it has one of the highest numbers of dams per square kilometre and a large number of endemic and endangered freshwater fish species. Despite the high number of fish species affected by water extraction and damming, river connectivity and its effect in Iberian freshwater fish populations have not been well studied. A small number of studies analyse the effect of small dams in nearby fish communities, but large-scale impact assessments are scarce. More connectivity analyses are needed to improve freshwater ecosystem conservation strategies. We conclude addressing some gaps in the knowledge of fragmentation and research opportunities in river connectivity and conservation

Key words: connectivity indices, dam removal, Iberian Peninsula, population isolation, river connectivity, river conservation

RESUMEN

Barreras para la conectividad fluvial longitudinal: revisión de impactos, métodos de estudio y gestión para la conservación de los peces ibéricos

La conectividad de los ríos es esencial para asegurar el correcto funcionamiento de los ecosistemas fluviales a todas las escalas. Sin embargo, no ha recibido la atención necesaria por parte de los investigadores, los gestores y los políticos hasta hace pocos años. En esta revisión recapitulamos el estado del conocimiento de la conectividad fluvial y sus aplicaciones en conservación. Describimos las particularidades de la conectividad de los ríos y resumimos los efectos causados por la fragmentación en diferentes elementos de los ecosistemas fluviales. Después nos centramos en los efectos que la falta de conectividad tiene en las especies de peces y revisamos los distintos métodos desarrollados para estudiar la fragmentación. También exploramos la aplicación de los estudios de conectividad en la selección de áreas para la conservación de ríos. Por último se estudia la restauración de la conectividad fluvial. La revisión analiza estos temas de una forma general para luego centrarse en la península Ibérica. La península Ibérica es un lugar interesante para estudiar la conectividad fluvial ya que contiene uno de los mayores números de presas por kilómetro cuadrado y una gran cantidad de especies de peces dulceacuícolas endémicas y amenazadas. A pesar del gran número de especies de peces amenazadas por la extracción de agua y las presas, la fragmentación fluvial y sus efectos no han sido bien estudiados. Encontramos que se ha realizado un pequeño número de estudios sobre los efectos de presas pequeñas a escala local, pero los análisis a gran escala son escasos. Se necesitan más estudios de conectividad de ríos para mejorar las estrategias de conservación de los ecosistemas fluviales. Concluimos la revisión mostrando algunos huecos en el conocimiento de la fragmentación de ríos y comentando nuevas *oportunidades de investigación en el estudio de la conectividad fluvial y su restauración.*

Palabras clave: *aislamiento de poblaciones, conectividad fluvial, conservación de ríos, derribo de presas, índices de conectividad, península Ibérica*

WHAT IS HYDROLOGICAL CONNECTIVITY?

Connectivity can be defined as the degree to which a landscape facilitates or impedes the movement of organisms among resource patches (Taylor *et al.*, 1993). Landscape connectivity is a fundamental factor in determining the distribution of species and is an essential concept in meta-population biology and landscape ecology (Pringle, 2003).

Although connectivity has been addressed in numerous land studies, hydrological connectivity presents some challenges derived from the peculiar structure of rivers (Fausch *et al.*, 2002; Wiens, 2002). River ecosystems are hierarchically organised dendritic networks, with functional habitats nested across scales. This structure creates isolated populations at smaller spatial scales than in other ecosystems (Fagan, 2002; Campbell Grant *et al.*, 2007; Crook *et al.*, 2015). Movement of organisms inside the river is constrained to following the network branches, and a single barrier can divide a river segment into two totally isolated fragments (Campbell Grant *et al.*, 2007). Moreover, the flow of water is unidirectional, running from the headwaters to the river mouth, transporting sediments, nutrients and organisms. This means that despite the lack of spatial overlap, downstream ecosystems are affected by processes occurring upstream: the flow of water controls hydrologic connectivity (Fullerton *et al.*, 2010).

Hydrological connectivity can be defined as the water-mediated transfer of matter, energy or organisms within or between elements of the hydrologic cycle (Pringle, 2001). Hydrological connectivity is composed of interactive pathways along one temporal and three spatial dimensions: longitudinal (from headwaters to river mouth), lateral (from riverine and riparian habitats to floodplains) and vertical (from riverine to groundwater, Pringle, 2001). There are also two types of connectivity (Branco *et al.*, 2014): structural connectivity refers to the physical relationships between structural elements (Segurado *et al.*, 2013), while functional connectivity is defined as the response of the biological elements (community, populations) to landscape structure (Tischendorf & Fahrig, 2000).

Hydrological connectivity is essential to the ecological integrity of freshwater ecosystems, and reduction or enhancement of this property can have major negative environmental effects (Moss, 2000; Pringle, 2003; Kondolf *et al.*, 2014; Grill *et al.*, 2015; Schmutz & Moog, 2018; Seliger & Zeiringer, 2018). However, until recently, freshwater connectivity and conservation have not received the attention they deserve from scientists and administrators. Less than 20 % of papers published on three important conservation journals between 2011 and 2015 focused on freshwater ecosystems (Di Marco *et al.*, 2017), while only 9 % of connectivity studies applied to conservation between 2000 and 2013 studied fluvial ecosystems (Correa Ayram *et al.*, 2015). Moreover, the research is highly skewed towards developed countries, mainly the United States, and diadromous species such as salmonids (Stanley *et al.*, 2007; Bourne *et al.*, 2011; Keefer *et al.*, 2012; Brown *et al.*, 2013).

In this review we will focus on the Iberian Peninsula. The Iberian Peninsula is a very interesting place to study hydrologic connectivity for two reasons: first, it has one of the highest percentages (> 70 %) of endemic freshwater fish species in Europe (Clavero *et al.*, 2004; Reyjol *et al.*, 2007; Maceda-Veiga, 2013). Second, Spain is one of the countries with the highest dam density per square kilometre in the world (Vidal-Abarca Gutiérrez & Suárez Alonso, 2013), while Portugal also has a large number of dams (Antunes *et al.*, 2016; Fig. 1). According to some estimations there are at least 26 000 river obstacles in Spain

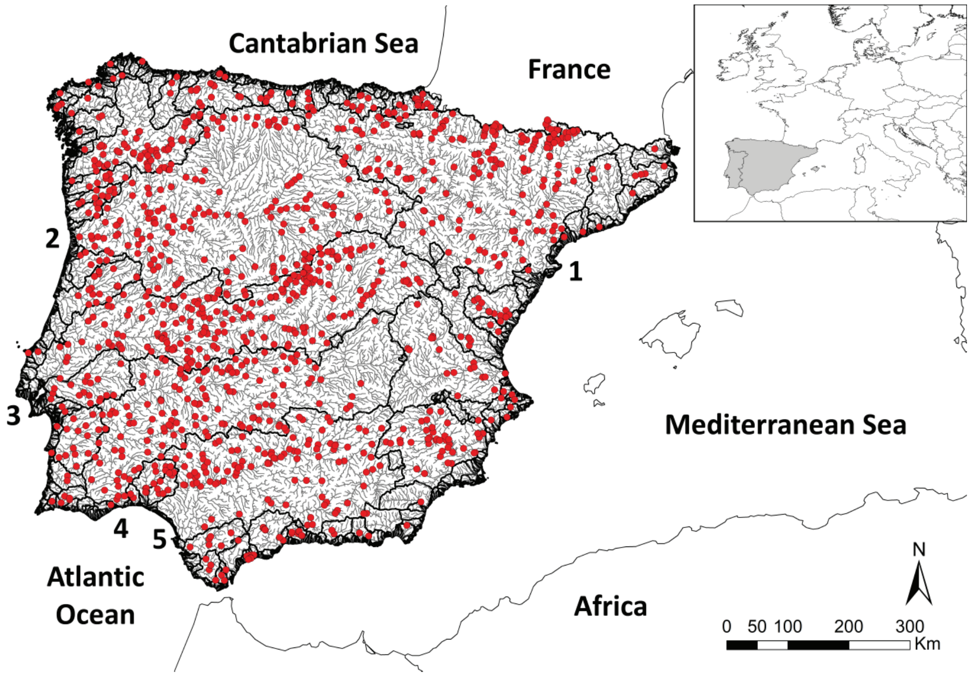

Figure 1. The Iberian Peninsula, its river basins and large dams (> 1 hm^3). Numbers point to the main Iberian river basins by area. 1: Ebro River basin, 2: Duero River basin, 3: Tagus River basin, 4: Guadiana River basin, 5: Guadalquivir River basin. *La península Ibérica, sus cuencas fluviales y sus grandes presas (> 1 hm^3). Los números marcan las principales cuencas de acuerdo con su área. 1: río Ebro, 2: río Duero, 3: río Tajo, 4: río Guadiana, 5: río Guadiana.*

alone (Rincón Sanz & Gortázar Rubial, 2016).

The larger river basins of the Iberian Peninsula are Ebro, Duero, Tagus, Guadiana and Guadalquivir. These basins are heavily fragmented. For example, the Spanish Duero basin (78 900 km^2) has 145 large- and medium-sized dams (22 in the main stem) and more than 3200 small dams and weirs (Confederación Hidrográfica del Duero, 2007). The total river length of the basin is 13 539 km, so, on average, there is a barrier every 4 km. The Ebro basin (85 000 km^2) has 299 large dams and 1818 weirs and small dams (Confederación Hidrográfica del Ebro, 2009) in 12 495 km of rivers and an average of one dam per 6 km. This has profound effects in river ecosystems.

In this review, we will summarize in four sections the state of the knowledge of i) the effects of river fragmentation in freshwater fishes, ii) the methods developed to calculate connectivity, iii) the studies of river conservation and iv) the studies about dam removal and connectivity restoration. Each section will start with a general study and then they will focus on river fragmentation studies on the Iberian Peninsula. Finally, we will comment on understudied areas and research opportunities in freshwater connectivity conservation and management. Longitudinal connectivity (i.e. connectivity along river course) is the most studied form of connectivity, so this review will focus on the effects of the disruption of this dimension of hydrological connectivity (structural and functional) in fish species.

IMPACTS OF LONGITUDINAL CONNECTIVITY FRAGMENTATION IN FRESHWATER FISHES

Large dams, weirs and culverts are the main infrastructures causing river connectivity fragmentation, but their effects on freshwater ecosystems depend on network location, number, passability (i.e. degree of permeation of a barrier measured with different methods), etc. With more than 45 000 large dams and countless small obstacles worldwide, river fragmentation is one of the most important threats facing river ecosystems (Gido *et al.*, 2016; Kemp, 2016). Currently, nearly 50 % of the freshwater ecoregions of the world and 48 % of global river volume are affected by large- and medium-sized dams (Liermann *et al.*, 2012; Grill *et al.*, 2015).

As barriers interrupt the natural downstream flow of matter and energy, they cause numerous different impacts in freshwater fishes, derived from altered hydrological and sediment regimes (Bunn & Arthington, 2002; Kondolf *et al.*, 2014). In addition, the mere loss of connectivity between two adjacent segments could have negative effects on freshwater organisms, especially fishes (Gido *et al.*, 2016). The impossibility of movement through a barrier can affect breeding and feeding migrations and recolonization processes, leading to biodiversity losses. Analysing the effects of one or multiple obstacles on fish species or communities may often be a difficult task due to the masking influence of natural environmental variability or other local and regional impacts (Cumming, 2004; Wang *et al.*, 2011; Gido *et al.*, 2016).

Fishes with different life cycles react differently to the loss of connectivity. Fragmentation of a river basin is more concerning for diadromous fish populations. Diadromous species are the ones that move between the rivers and the ocean to complete their life cycles. The effect of an impassable dam on these species is obvious: the obstacle obstructs the migration of fishes, resulting in the loss of the whole habitat upstream of the barrier. If habitat loss is great enough, the diadromous population affected will decline or even disappear from the river basin (Duncan & Lockwood, 2001; Sheer & Steel, 2006; Fukushima *et al.*, 2007; Limburg & Waldman, 2009; Lucas *et al.*, 2009; Hitt *et al.*, 2012; Nieland *et al.*, 2015; Segurado *et al.*, 2015). Even if the obstacles are partially passable, negative effects remain as migrant fauna spend more time and energy trying to pass the barriers, which leads to lower spawning success, physical damage, easier capture and disease spread (Gregory *et al.*, 2002; March *et al.*, 2003; Garcia de Leaniz, 2008).

The effect of dams in potamodromous species (i.e. fishes constricted to freshwater water that conduct migrations of different spatial scale along the rivers) is more obscure, as they lose migration paths, but stream segments usually have all types of habitat needed by these fishes. Some potamodromous fish species also perform large migrations to spawn, which are affected by dam presence (Lucas & Batley, 1996; Branco *et al.*, 2017).

Fish species are structured in meta-populations (Fagan, 2002; Gido *et al.*, 2016). A meta-population comprises different populations distributed over patches on a heterogeneous landscape connected by dispersal movements. In meta-population theory, local extinctions are offset by recolonizations from other patches, and population genetics depends on the genetic characteristics of the colonizers (Levins, 1968; Hanski & Gilpin, 1991).

In hierarchical dendritic linear systems, such as rivers, there is only one path between sites, and dispersers must pass through all middle points before reaching a destination (Fagan, 2002). When a dam or other barrier is constructed, a path between populations can be completely blocked to dispersers, which can lead to loss of genetic diversity, genetic drift, population decline and eventually, extirpation of the isolated population (Morita & Yamamoto, 2002; Meldgaard *et al.*, 2003; Yamamoto *et al.*, 2004; Wofford *et al.*, 2005; Morita *et al.*, 2009). These effects can be magnified if populations are isolated in smaller areas (MacArthur & Wilson, 1967)

Different studies have shown a positive connection between larger river segments and higher freshwater fish biodiversity (Bain & Wine, 2010; Heino *et al.*, 2015) and a negative relationship between dam presence and species richness upstream (Dodd *et al.*, 2003; Nislow *et al.*, 2011; Wang *et al.*, 2011; Perkin & Gido, 2012; Sá-Oliveira *et al.*, 2015). Other studies do not show differences in fish communities between segments separated by dams (Cumming, 2004; Santos *et al.*, 2006). However, even if population changes have not been noticed yet, species extirpation from an isolated river segment cannot be ruled out as there may be delayed long-term effects (Ewers & Didham, 2006). This is called "extinction debt" and arises from delayed responses of populations to an impact (for example, when mortality slightly exceeds natality). In any case, river network connectivity is one of the main drivers in the distribution and range size of freshwater fish species (Carvajal-Quintero *et al.*, 2019) so river fragmentation has direct consequences on the distribution and persistence of freshwater fish species, according to the degree of connectivity between populations and the size of the habitats affected.

In the Iberian Peninsula, the profound degradation of hydrologic connectivity described in the above has led to the extinction or dramatic decline of migrant fish species (Atlantic sturgeon *Acipenser sturio* L., 1758, Atlantic salmon *Salmo salar* L., 1758, European eel *Anguilla anguilla* (L., 1758), etc.), the isolation of endemic species and the spread of exotic species (Prenda *et al.*, 2006). However, studies of dam impacts and river connectivity loss in fishes are insignificant, despite affecting up to 60 % of Iberian freshwater fish species (Maceda-Veiga, 2013). Atlantic salmon has lost up to 86 % of its historically accessible stream length (Álvarez *et al.*, 2003), completely disappearing from the Duero River basin (Valente & Maia, 2001) and decreasing dramatically in the Cantabrian coast (Álvarez *et al.*, 2001; Sanz Azcárate *et al.*, 2018). Sturgeon was completely extirpated from Iberian river basins (Morais, 2008), the European eel has lost more than 80 % of its historic distribution range (Clavero & Hermoso, 2015), and other migrant species such as the sea lamprey (*Petromyzon marinus* L., 1758) are declining (Nicola *et al.*, 1996).

The majority of endemic Iberian fish species are economically unimportant potamodromous fishes, and the effects of dams in their populations are unknown. The scarcity of information on the biology and conservation status of these species and the absence of river fragmentation studies make it difficult to start adequate conservation and management plans. Due to the strong speciation in the different river basins, fish species are naturally strongly isolated, and some of them only appear in single river basins or sub-basins, which makes them even more vulnerable to additional connectivity alterations and habitat degradation (Aparicio *et al.*, 2000; Clavero *et al.*, 2010).

Studies of dam impacts were conducted in different river basins scattered throughout the territory. A study on the Tagus basin showed that recruitment of brown trout (*Salmo trutta* L., 1758) after the construction of a hydropower dam decreased significantly, showing that dams, even small ones, have effects downstream (Almodóvar & Nicola, 1997). Dams also promote exotic fish invasion and fish community homogenization along the Guadiana River (Clavero & Hermoso, 2011). Cold water discharge from a newly constructed dam caused a shift from a mixed fish community to a salmonid one (Miranda *et al.*, 2012). Another study in Catalonia (north-east of the Iberian Peninsula) indicates that fish extinctions are more likely in small, degraded and regulated stream segments (Aparicio *et al.*, 2000). Impacted stretches on Catalan basins also seem to have poorer habitat structure, lower fish abundance, fish length and total fish weight, and different species composition, with an effect that accumulates downstream (Benejam *et al.*, 2014). Conversely, other studies did not find significant effects of small barriers on fish communities in Spain (Alexandre & Almeida, 2010) or Portugal (Santos *et al.*, 2006).

METHODS TO STUDY LONGITUDINAL RIVER CONNECTIVITY

As hydrological connectivity has received growing attention in the last two decades (Pringle, 2001, 2003; Wiens, 2002), different methods have been developed to assess connectivity and the best solutions to improve it.

To analyse river connectivity, obstacle passability must be assessed first. Passability may be defined as the proportion of fish that are able to pass a barrier or the number of days the barrier is passable. Due to the unique characteristics of each barrier and river reach, assessing passability is usually a difficult task. The simplest methods use a binary passability value (0-1): a barrier is passable or not (Zheng *et al.*, 2009). In numerous cases, barriers are partially passable depending on different factors, such as obstacle height, species, size, swimming ability and flow of water (Kemp & O'Hanley, 2010). There are multiple ways to assess passability, from expert criteria (Kemp &

O'Hanley, 2010) and telemetry and fish surveys (Ovidio & Philippart, 2002) to software simulations such as FishXing (Bourne *et al.*, 2011) and statistical models (Kemp & O'Hanley, 2010).

With the passability values of the obstacles, different indices can be applied to determine the connectivity of a stream or river basin, taking into account the position of each dam in the network. The simplest ones are score-and-ranking type procedures, which rank obstacles according to their passability, but they produce ineffective solutions to improve connectivity as they assess the passability of individual barriers and ignore their cumulative impacts (O'Hanley & Tomberlin, 2005).

Recently, graph theory, a method frequently used in landscape functional connectivity (Pascual-Hortal & Saura, 2006; Galpern *et al.*, 2011), has been adapted to river networks in different connectivity studies (Fullerton *et al.*, 2011). Graph networks commonly represent freshwater systems as edges (river segments) connected by nodes (intersections or barriers). By including obstacle location inside the river network in the analysis, graph theory allows the calculation of cumulative impacts of dams, providing an efficient way to estimate the different sections affected by obstacles (Erös *et al.*, 2011; McKay *et al.*, 2013; Branco *et al.*, 2014; Rincón *et al.*, 2017). Graph theory has not been widely used, but it is gaining more attention and could be used for numerous analyses, such as species connectivity, habitat loss and gain models (Segurado *et al.*, 2015), dam removal selection (McKay *et al.*, 2013; Branco *et al.*, 2014) or colonization and extinction-risk models (Van Looy *et al.*, 2013). Other indices also use dam location inside the river network to analyse cumulative impacts on longitudinal connectivity (Cote *et al.*, 2009; Grill *et al.*, 2014). Some indices are developed to analyse diadromous fish movements, as they migrate from the river mouth upstream (Cote *et al.*, 2009; McKay *et al.*, 2013), while others are used to assess potamodromous movements inside the river (Cote *et al.*, 2009; O'Hanley *et al.*, 2013; Diebel *et al.*, 2015).

In general, connectivity indices use segment length or water volume as a measure of river habitat availability (Cote *et al.*, 2009; McKay *et al.*, 2013; Branco *et al.*, 2014; Grill *et al.*, 2015). However, other segment habitat characteristics may reflect biota needs better than length or water volume: a small segment of high-quality habitat (according to the species requirements) could be more beneficial than a larger segment of poor quality habitat. Different connectivity indices include both river length and habitat quality for both a large variety of fish species (Grill *et al.*, 2014; Diebel *et al.*, 2015; Maitland *et al.*, 2016) or a single species (Rodeles *et al.*, 2019) to adapt their results to fish habitat requirements.

The result of these indices is usually a percentage that represents the connectivity for one obstacle or for the whole river basin (Cote *et al.*, 2009; Kemp & O'Hanley, 2010; McKay *et al.*, 2013).

Connectivity evaluation methods are often used to model potential connectivity improvements (Branco *et al.*, 2014). For example, dam removal is a useful tool to improve river connectivity, but if it is not carefully planned, restoration benefits would be suboptimal (Rodeles *et al.*, 2017). Optimization tools that rank dams by their effects on network connectivity and their removal cost have been developed to maximize river connectivity improvements. O'Hanley & Tomberlin (2005) developed a optimization method using integer programming techniques that produced better results than scoring and ranking procedures, and applied it in Washington State (USA). Afterwards, the optimization method was refined and updated with different techniques (mixed integer linear programming, probability chains, etc.) to include different fish species and spatial scales (O'Hanley & Tomberlin, 2005; O'Hanley, 2011; O'Hanley *et al.*, 2013; Null *et al.*, 2014; King & O´Hanley, 2016; King *et al.*, 2017). Null *et al.* (2014) used another optimization method to analyse trade-offs between hydropower generation, water supply and river connectivity in California (USA). The same tools described above can be used to choose the locations for new dams, analysing the river network to select the least impacting sites for river basin connectivity. However, as far as we know, these studies do not exist yet. For a deep review on the methods selected for connectivity barrier prioritization, read McKay *et al.* (2017).

River connectivity studies in Spain are scarce, although some research has been performed in Catalan basins regarding fishway efficiency and dam passability (Ordeix *et al.*, 2011; Solà *et al.*, 2011; Aparicio *et al.*, 2012). A new connectivity index with asymmetric dam passability was developed and applied to a sub-basin of the Duero River basin (Rincón *et al.*, 2017). In Portugal, longitudinal river connectivity indices have been developed to aid in river connectivity restoration (Branco *et al.*, 2012, 2014; Segurado *et al.*, 2013, 2015). However, major river basin connectivity assessments have not been performed yet. Numerous small dams and weirs in different river basins are not inventoried, which prevents comprehensive longitudinal connectivity analyses (Rincón Sanz & Gortázar Rubial, 2016; Rodeles *et al.*, 2017). We need to know the full extent of Iberian river fragmentation to understand the degree of the threat faced by our freshwater fish species. It will also serve as the starting point for river connectivity restoration, helping to make informed decisions on dam removal.

LONGITUDINAL CONNECTIVITY AND RIVER CONSERVATION

Conservation actions have generally been unsuccessful in the case of freshwater biodiversity due to the special characteristics of freshwater ecosystems and the lack of attention they receive (Dudgeon *et al.*, 2006), with very few studies focusing on fluvial systems (Correa Ayram *et al.*, 2015).

Reserves have been a popular conservation technique for terrestrial ecosystems around the world (Geldmann *et al.*, 2013). Nevertheless, there are few specifically freshwater protected areas (Bower *et al.*, 2015); river segments are protected tangentially by being part of a protected land ecosystem, which does not guarantee effective protection (Saunders *et al.*, 2002; Hermoso *et al.*, 2015; Miranda & Pino-Del-Carpio, 2016).

Numerous studies exist about the selection of terrestrial areas for conservation and the importance of landscape connectivity to reserves (Correa Ayram *et al.*, 2015). However, river structure makes it impossible to extrapolate terrestrial conservation techniques to freshwater ecosystems (Moilanen *et al.*, 2008; Hermoso *et al.*, 2015). The selection of isolated river stretches for protection is not as useful as the selection of land ecosystems because rivers are affected by the upstream and downstream drainage network, the riparian zones and the surrounding land (Pringle, 2001; Bower *et al.*, 2015; Hermoso *et al.*, 2015). River connectivity is essential for the well-being of freshwater ecosystems, and recently, some studies have included river connectivity as a variable in the selection of freshwater reserves (Hermoso *et al.*, 2012, 2017). However, the exclusive conservation of freshwater ecosystems and the design of protected areas have received little effort, and only a small fraction of scientific papers are about freshwater connectivity and its application to fluvial conservation (Galpern *et al.*, 2011; Hermoso *et al.*, 2011, 2017; Correa Ayram *et al.*, 2015; Erös *et al.*, 2018).

Adequate methods are needed for the selection of conservation areas, but because freshwater ecosystems have been less studied, there are no specific tools for the scientific selection of reserves. Software used in terrestrial ecosystems, such as ZONATION and Marxan, is being adapted for the design of river reserves (Moilanen *et al.*, 2008; Hermoso *et al.*, 2011; Hermoso *et al.*, 2017), as well as methods for the analysis of connectivity, such as graph theory (Erös *et al.*, 2011; Fullerton *et al.*, 2011).

Ideally, a freshwater protected area should cover the total length of a river to ensure the adequate conservation of all ecosystems. Rivers are heavily exploited along their courses and may cross different countries in their travel to the oceans, so this approach would find the resistance of governments; therefore, partial solutions are being proposed (Saunders *et al.*, 2002). River connectivity needs to play an essential role in the selection of river reserves as it will determine their conservation efficacies (Hermoso *et al.*, 2015, 2017).

To ensure the conservation of near pristine, non-impacted river stretches, Spain declared 135 Freshwater Natural Reserves (FNR) scattered throughout the country (Fig. 2). The first 82 FNRs were registered in 2015, followed by another batch of 53 reserves in 2017 (Ministerio para la Transición Ecológica, 2017). These

FNRs are a first and very important step in the conservation of freshwater ecosystems in the Iberian Peninsula. However, these reserves do not consider river connectivity between them or even within them, with some FNRs fragmented by dozens of small obstacles (Fig. 3). Due to this, the FNRs are not very efficient for the conservation of fish populations. A connected network of freshwater reserves needs to be protected to achieve effective conservation of river fauna.

Moreover, Iberian Peninsula freshwater ecosystems face new threats, such as climate change, that will further disturb hydrological regimes and imperil fish species (Smith & Darwall, 2006; Hermoso & Clavero, 2011; Schewe *et al.*, 2014). Iberian countries need to seriously engage in plans to protect the water supply while preserving freshwater ecosystems and their connectivity with cohesive national plans and sensible management that allows for conservation. In this way, Spain and Portugal will effectively protect their freshwater resources and species.

EFFECTS OF LONGITUDINAL CONNECTIVITY RESTORATION

Although dam impacts on freshwater fish species are fairly well studied, upstream and downstream dam removal effects are far less analysed (Bednarek, 2001; Hart *et al.*, 2002). The lack of pre- and post-dam removal ecological monitoring is the main reason for the scarcity of dam removal studies (Bednarek, 2001; Doyle *et al.*, 2003, 2005; Rodeles *et al.*, 2017). Dam removal is performed under the assumption that its effects will be positive, but long-term studies (> 5 years) on this topic are usually not found. Long-term monitoring is needed because ecological feedback loops may operate on longer time spans (Bellmore *et al.*, 2019), and some studies suggest that 3-4 years after dam removal, the biota is still in transition (Maloney *et al.*, 2008; Poulos *et al.*, 2014).

Numerous short-term studies show positive effects, such as upstream recolonization and population increase of diadromous fish species (Fjeldstad *et al.*, 2012; Hitt *et al.*, 2012; Pess *et al.*, 2014; Lasne *et al.*, 2015; Birnie-Gauvin *et al.*,

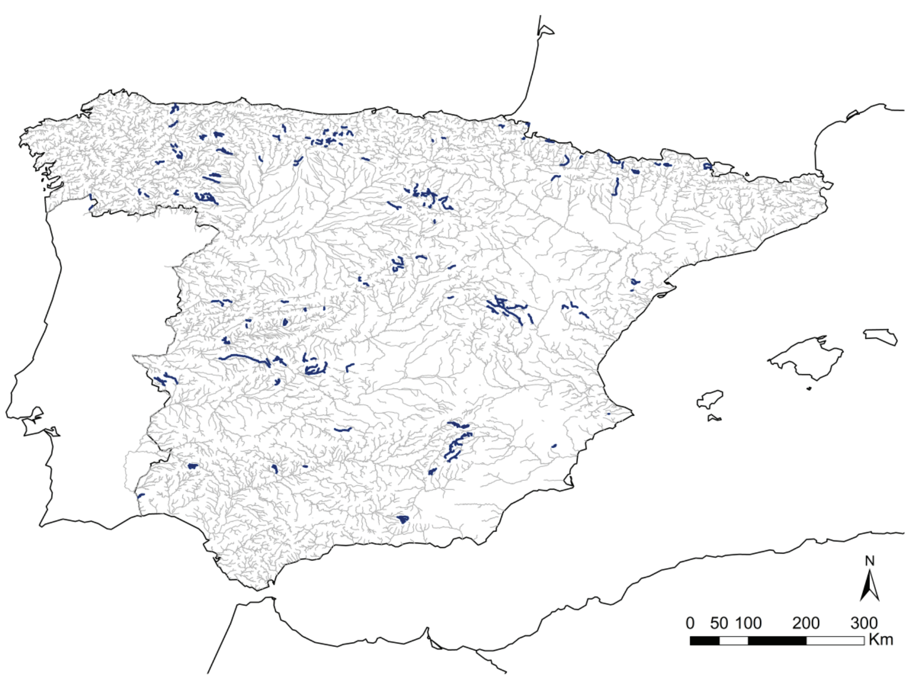

Figure 2. Location of the 135 Freshwater Natural Reserves created in Spain. They are mainly small headwater streams. *Localización de las 135 Reservas Naturales Fluviales creadas en España. La mayoría son pequeños ríos de cabecera.*

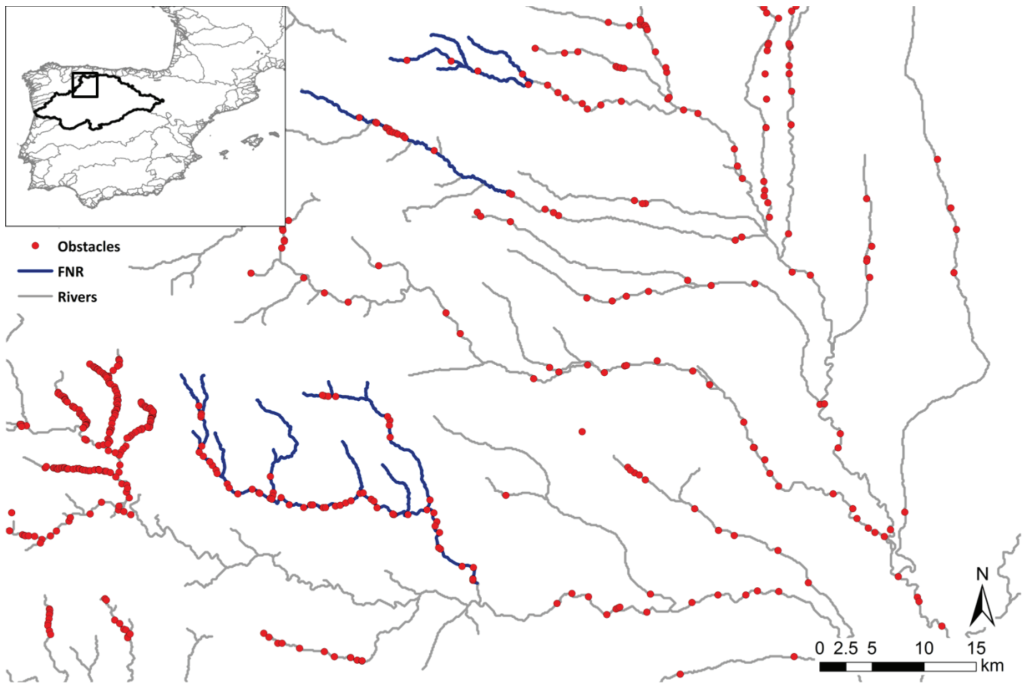

Figure 3. A close look at three Freshwater Natural Reserves (FNR) in the headwaters of the Duero River tributaries (blue lines). The FNRs are fragmented and isolated from one another by numerous small dams and weirs (red dots). *Vista de tres Reservas Naturales Fluviales (FNR) en la cabecera de ríos afluentes del río Duero (líneas azules). Las FNR están fragmentadas y aisladas unas de otras por numerosas pequeñas presas y azudes (puntos rojos).*

2018) and fish community changes (Kanehl *et al.*, 1997; Maloney *et al.*, 2008; Poulos *et al.*, 2014; Kornis *et al.*, 2015). Conversely, some studies do not show significant positive changes (Kareiva *et al.*, 2000; Stanley *et al.*, 2007; Quiñones *et al.*, 2014), while others point to short-term impacts in freshwater ecosystems (Stanley & Doyle, 2003).

Exhaustive pre-removal studies are also essential as connectivity recovery may heighten the risk of exotic species invasion and disease dispersion in some rivers (Rahel, 2007; Stanley *et al.*, 2007; Fausch *et al.*, 2009; Zheng *et al.*, 2009; Jackson & Pringle, 2010).

In short, the results of connectivity restoration may depend on the type of river, dam, timescale and species involved. The new long-term ecosystem equilibrium may not be the same as that of the pre-dam ecosystem (Bellmore *et al.*, 2019). General conclusions of connectivity restoration cannot yet be made as dam removal studies are scarce, short-term and focused on one or few components of the river ecosystem (Hart *et al.*, 2002).

In the Iberian Peninsula, few dams and weirs have fish ladders and, moreover, fish ladders are usually inefficient or are not well evaluated (Nicola *et al.*, 1996; Santos *et al.*, 2006; Ordeix *et al.*, 2011; Aparicio *et al.*, 2012; Rincón Sanz & Gortázar Rubial, 2016). To improve river connectivity in the last two decades, dam removal has become a more prominent restoration technique in Spain, and more than 150 weirs have been removed under the National Strategy for River Restoration (NSRR, MAGRAMA, 2015) and other different projects (LIFE Cipriber, 2015; LIFE Irekibai, 2016). However, there are usually no monitoring studies concerning the effects of the removal of these dams on fish communities, even though the NSRR includes monitoring as a part of each restoration project. In addition, the length of reconnected rivers is very short, so the ecological benefits of NSRR dam removal may be small in comparison to the costs (Rodeles *et al.*, 2017). However, a cost-benefit analysis of 6 dam permeations was conducted to determine their effects in ecosystem services and suggest that permeations are beneficial to human well-being despite their costs (Rincón Sanz & Gortázar Rubial, 2016).

Rivers have not received enough attention from governments in the Iberian Peninsula, but this situation is starting to change. The European Union established the Water Framework Directive (WFD), stating that good quality rivers must be achieved, and restoration of river connectivity is one of its aims. The WFD requires the consideration of fish communities when assessing the ecological quality of rivers (Council of the European Communities, 2000). Although Spain has not yet accomplished this objective and there is much work ahead, some large steps have been taken in this direction. While more organization and restoration monitoring are needed, the NSRR is a good starting point.

FUTURE NEEDS

Freshwater connectivity and conservation have gained attention in the last decades, as the profound impacts humans have on rivers are being acknowledged. However, the special characteristics of rivers (dendritic structure, directionality, etc.) make extrapolation from terrestrial ecosystems a poor method of study and conservation.

Thus, river connectivity conservation is a developing research field. The development of connectivity study methods has not been cohesive (Kemp & O'Hanley, 2010), so the creation of general connectivity frameworks with the ability to adapt to more local circumstances would help spread river fragmentation assessments. Until now, only a few Iberian river basins have complete longitudinal connectivity assessments (Rincón Sanz & Gortázar Rubial, 2016). The first step to achieve the evaluation of all river basins in the Iberian Peninsula and in the world is the development of an inventory of all obstacles (dams, weirs, culverts, etc.) found in streams. In Spain that inventory is incomplete so more effort is needed to improve it. Each barrier has to be located and its passability assessed (height, fisway presence, etc., Rincón Sanz & Gortázar Rubial, 2016). With the complete barrier inventory river connectivity will be able to be assessed for all Iberian river basins. These river connectivity assessments could then be used to detect the most impacting dams, vulnerable river stretches, critical fluvial paths and the best streams for conservation.

To ensure the creation of effective river management and conservation plans, connectivity assessments need to accurately represent reality. However, connectivity indices are typically theoretical models built with as little as three variables (dam passability, dam location and segment length, Kemp & O'Hanley, 2010). Attempts at linking river basin connectivity models to population or community dynamics are almost non-existent due to the difficulty of finding large-scale ecological data (Perkin & Gido, 2012).We need to validate existing connectivity indices with real world ecological data to ensure the benefits of river conservation and restoration actions.

Finally, river connectivity needs to be considered in the selection of river segments for conservation. Spanish FNRs are supposed to be well preserved areas. However, as showed in this review, there are many FNR divided in numerous isolated fragments due to weirs and dams. As stated before, there are different methods in the literature developed to include river connectivity in conservation reserves assessment and new ones could be developed to respond to specific needs.

None of these developed methods for river connectivity assessment are useful if they are not applied in river conservation. There needs to be a better communication between scientists and decision-makers to ensure adequate ecological methods are applied in river management and conservation (Rodeles *et al.*, 2017). This way we would effectively preserve river ecosystem services and biodiversity in a changing and increasingly humanized world.

ACKNOWLEDGEMENTS

This research was performed thanks to the Ph.D. grants received from the Government of Navarra and the Asociación de Amigos de la Universidad de Navarra.

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