UNIVERSIDADE DE LISBOA
INSTITUTO SUPERIOR DE AGRONOMIA

Improving connectivity for river fish

Tese apresentada para obtenção do Grau de Doutor em
Engenharia Florestal e dos Recursos Naturais

Paulo José de Lemos Branco

Orientadora: Doutora Maria Teresa Marques Ferreira da Cunha Cardoso

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Doutor Daniel Hering, Full Professor da University of Duisburg Essen, Germany

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Ana, esta tese é para ti

Abstract

Rivers are severely impacted by barriers that hamper the longitudinal connectivity of the systems, promoting species isolation and affecting the movements of freshwater fish species, which leads to genetic impoverishment and disappearance of populations. This thesis is focused on defining the problems of connectivity infringement as well as on finding solutions to enhance connectivity in barrier fragmented systems. During the studies that are present in this thesis the impact of barriers on the distribution of freshwater fish species, and the reduction of structural and functional connectivity of river basins are accessed. It is also defined a technique to prioritize barriers to intervene in order to enhance connectivity. To augment connectivity, and because barrier removal is often impractical, strategies to retrofit existing pool-type fishways and guidelines for new fishway projects are determined and present in this thesis. It is also demonstrated how flow regime can have an impact on fish fishway negotiation success, moving a step forward towards a holistic technical fishway.

Key-words: Connectivity, Freshwater fish, Connectivity enhancement, Pool-type fishway, Flow regimes

Resumo

Os rios são fortemente afectados pela construção de barreiras que limitam a conectividade longitudinal, levando ao isolamento de espécies ictíicas e limitando os seus movimentos ao longo do sistema. Esta fragmentação diminui a variabilidade genética e leva ao desaparecimento de populações. Esta tese tem como enfoque a definição dos problemas causados pela quebra de conectividade e a determinação de soluções para o aumento de conectividade em sistemas fragmentados. Nesta tese o impacto das barreiras na distribuição de espécies ictíicas de água doce e a redução de conectividade estrutural e funcional de bacias hidrográficas são determinados. É também definida uma técnica de ordenação de barreiras a alterar de modo a aumentar a conectividade. Uma vez que a remoção de barreiras é por vezes impracticável, estratégias para recondicionar passagens para peixes por bacias sucessivas existentes e directrizes para aplicação em novos projectos são determinadas nesta tese. Demonstra-se ainda o impacto que o regime de escoamento tem no sucesso de transposição dos peixes de uma passagem para peixes por bacias sucessivas, aumentando o conhecimento científico em direcção a uma passagem para peixes técnica que seja holística.

Palavras-chave: Conectividade, Peixes de água doce, Aumento da conectividade, Passagem para peixes por bacias sucessivas, Regimes de escoamento

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Section I

Hydrological connectivity: causes and consequences

"To write history without putting any water in it is to leave out a large part of the story. Human experience has not been so dry as that."

Donald Worster, *Rivers of Empire*, 1985

“Rivers flow on every continent and on all but the smallest island. They occur with an almost bewildering variety, ranging from a mere trickle to a mighty surge. As a source of water, rivers have always been objects of wonder and practical concern for people everywhere. They have acted as cradles for civilization and agents of disaster. A river may be a barrier or a highway. It can bear trade or sediment, culture and conflict. A river may inspire or it may terrify.

(…)

A river can cleave a big canyon and twist like a giant snake across its plains; plunge over great cliffs and stretch fingers of earth into the oceans. Rivers dominate landscapes, eroding and creating them. They are, without a doubt, the product of a complex suite of natural processes. But the evolution of many rivers has been driven as much by social systems as by natural ones, surprise though this may at first seem.”

Middleton 2012

Chapter 1

Introduction

Sente-se!
Já está sentado?
Pode-se encostar à vontade!
Quero-o sentado comodamente e descontraído.
Também pode fumar.
O que importa é que me ouça exactamente.
Está a ouvir-me bem?
É que tenho uma coisa a comunicar-lhe que o há-de interessar.
(...)

Bertolt Brecht, Nº9 do suplemento a "Um Livro de Leitura Para Habitantes das Cidades"

1.1. Rivers

Rivers have had a very considerable influence on human history. Rivers were the driving force for the first settlements of human beings. At first, they were a permanent source of water and food, further along the way they provided an ease of transportation. Still to our days, society is dependent of a multitude of freshwater ecosystem services. Some of them are the same since pre-historic times, like clean water provision, but other services have been required from these ecosystems since modern until contemporary times, *e.g.* pollution disposal and leisure (Wilson and Carpenter 1999, Jackson et al. 2001, Postel and Richter 2003). As a result, riverine ecosystems are amongst the most degraded by humans, and are thus some of the most imperiled systems in the world (Naiman and Turner 2000, Sala et al. 2000, Gleick 2003). Nevertheless, healthy river systems provide a river service dependence upon which human life relies (Postel and Richter 2003). To counteract this menace to ecosystems health and to allow these services to be maintained, major restoration efforts in riverine environments are starting to be undertaken (Bernhardt et al. 2005) as humans finally realize the full extent of the impacts forced upon such systems.

In rivers, flow is the overriding force, it is responsible for river geomorphology, it drives sediment transportation, it determines the habitats for fauna and flora, through carbon transport it controls food webs and has a direct impact over behaviour and life histories of animals and plants (Vannote et al. 1980, Frissell et al. 1986, Junk et al. 1989, Calow and Petts 1992, Thorp and Delong 1994, Matthews 1998, Fausch et al. 2002). This overriding force is composed by five elements: magnitude, duration, timing, frequency and rate of change. All five elements are present and act at different temporal and spatial scales which forced biota to evolve in a way to accommodate these variations (Poff et al. 1997, Lake 2003, Richter et al. 2003) (Box 1.1).

1.2. Connectivity

Connectivity can be defined as a functional “exchange pathway of matter, energy and organisms” (Ward and Stanford 1995) or, from a hydrological perspective, as a “water mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle” (Pringle 2003) acting both at regional and global scales. Connectivity comprises four dimensions: longitudinal - along the stream; vertical - between the channel and the hyporheic zone; lateral - between the stream channel and adjacent riparian and upland areas; and temporal - over time (Ward 1989, Brunke and Gonser 1997, Tockner et al. 1998) (Box 1.2). To these, variation at different landscape scale levels should also be added (Pringle 2001). Nevertheless, longitudinal connectivity is regarded as the most important connectivity dimension for freshwater fish species, because it allows upstream and downstream fish migration cycles to occur (Lucas and Baras 2001). The unimpaired longitudinal dimension is of the essence for the maintenance of a multitude of fish species (Fausch et al. 2002). Primarily due to the fact that the variety of habitats that provide vital conditions for fish, substrate for spawning, foraging grounds and seasonal refugia are spatially and temporally separated (Fausch et al. 2002). Longitudinal connectivity research can help to derive new insights about river dynamics and how spatial elements of the riverine landscape influence ecological processes. For that, both classical theories, such as the River Continuum Concept defined by Vannote et al. (1980) and the hierarchical classification of streams (Frissell et al. 1986, Pickett et al. 1989), as well as newer hypotheses on river evolutionary path and structural arrangements (e.g. River Discontinuum (Poole 2002), Network Dynamic Hypothesis (Benda et al. 2004), Riverine Ecosystem Synthesis (Thorp et al. 2006)) should be used (Fullerton et al. 2010).

Although connectivity has proved to be one of the major players in defining riverscapes and on providing for conditions for fish species to endure, it has not been awarded the consideration it deserves (Fullerton et al. 2010). Connectivity can be looked upon two ways, structural and functional, and both of these connectivity components should be analyzed to provide a better understanding of the biodiversity structuring factors at work in a river landscape (Ward et al. 2002). Structural connectivity refers to the topological structure of physically connected elements of the riverine landscape (Keitt et al. 1997). Functional connectivity refers to the relationship established between the fish species of the system and the structural connectivity, this relationship can vary according to fishes' behaviour, ecology, and distribution within the riverine landscape (Tischendorf and Fahrig 2000, Taylor et al. 2006).

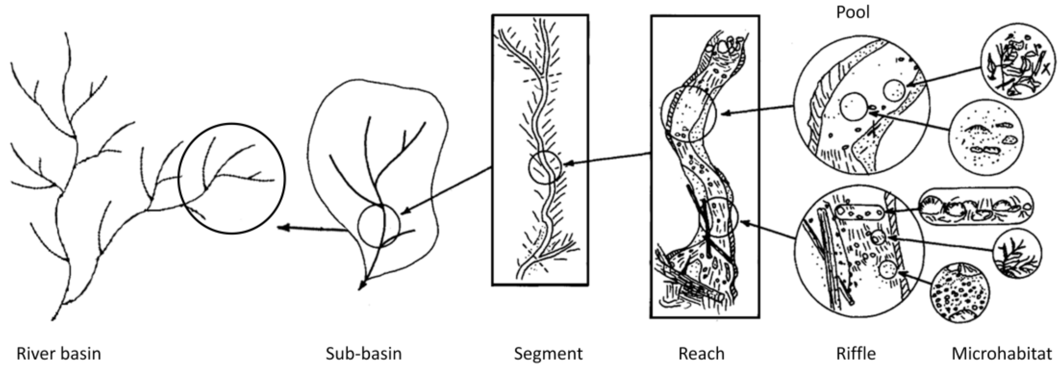
A variety of ecological questions can be encapsulated into the connectivity concept as it defines the connections between spatial elements, both in space and in time (Fullerton et al. 2010). Connectivity awareness has started to increase and became the focus of many ecological studies, including those of freshwater systems where it plays an important role (Wiens 2002). In fact, publications about connectivity (typically impacts of connectivity loss) in ecology journals have increased from 0.5 to 2.5% in the past 10 years (Fullerton et al. 2010). Rivers are complex systems with great spatial and temporal variability, where the connections between the different elements are permanently shaped by large- and small-scale physical processes, altering constantly the structural connectivity and repeatedly affecting its functional component. In spite of the difficulties in studying such systems, connectivity has been the subject of a variety of studies (Ward 1989, 1997, Naiman et al. 1993, Pringle 2001, 2003, Amoros and Bornette 2002), but the relationship between structural and functional connectivity is still open for debate, and has to be addressed thoroughly.

Box 1.1 – River scales

In river systems there is an inherent directionality promoted by the flow of water, which progresses into shaping an important hierarchy, where the conditions present upstream influence the conditions and processes occuring downstream (Allan et al. 1997). Also, geomorphologic and ecologic processes operate differently at different spatial scales (Frissel et al. 1986).

These systems are organised in a way to incorporate successively lower levels. The hierarchy of a river system is spatially nested, meaning that while all levels fall within the river basin, each segment, reach or habitat plays a part in the structure and function of the river systems.

A stream reach comprises multiple pool and riffle structures that are constituted by a variety of micro-habitat units. Reaches are found within stream segments that form sub-basins that contribute as tributaries to the primary stream of the river basin. The image below, adapted from Frissel et al. (1986), represents the scale levels at play in a river system.



Freshwater fish species may be very susceptible to connectivity limitations due to the fact that dispersal and recolonization paths are previously defined and limited to a single dimension, the river channel (Fagan 2002, Campbell et al. 2007, Muneepeerakul et al. 2007), which contrasts with terrestrial or marine organisms that can disperse in two dimensions, making their habitat much more connected.

Box 1.2 - River dimensions

Ward (1989), in a seminal article, describes flowing water systems has having four dimensions.

Longitudinal dimension: Connection along the channel. This is the natural dimension of rivers and the one that was first noted. It is still considered to be the most important dimension for stream fish and is the central point of the present thesis.

Lateral dimension: Connection between the channel and the adjacent riparian/floodplain system. This dimension encompasses active and passive movements of organisms, exchange of nutrients and organic matter (Ward 1988). In addition, lateral connectivity can play a part in influencing successional structure of riparian vegetation that contributes to channel morphology, water temperature and light levels, habitat heterogeneity, quality, quantity and timing of allochtonous inputs.

Vertical dimension: Connection between surface and ground waters. The hyporheic zone is composed by interstice area beneath the stream and stream banks that is saturated with channel water. This is now considered to be an integral component of the river due to the important biogeochemical processes occurring there and because it allows for complex invertebrate communities to be created.

Temporal dimension: There is a hierarchy of time scales in ecological systems. The scale at which one tries to perceive the system depends on one’s object of interest. Rivers can be looked upon short, almost instant, to evolutionary time scales. For instance, when studying the response of a stream to hydropeaking, there is the instant response of the fish community, there is a latter response of the habitat below the dam and there is an even latter response by the species due to habitat alteration. Although expressed at different time scales these responses are intertwined.

Latter, Boon (1992) suggested that conservation actions need to account for a fifth dimension.

Conceptual dimension: Is a theoretic dimension that encompasses philosophy, policy and practice. It questions the motivation for restoration actions, and states that restoration actions should be planned within a broader environmental framework (Boon 1998).

Adding to these five dimensions, variation at different landscape levels should also be considered when studying freshwater systems (Pringle 2001).

1.3. River regulation

Society needs forced rivers to be regulated through the construction of dams and weirs. This regulation is widespread and exists for irrigation demand, hydroelectricity production, flood control, river transport, recreational use, land reclamation in flood plains, among others (Ward and Stanford 1979, Petts 1984, Calow and Petts 1992). The construction of dams and water retention hydraulic structures has increased since the middle of the last century (ICOLD 1998, Ward et al. 1999), and will continue to increase due to increasing water demand and the continuous threat of climatic changes. Estimates point to the existence of more than 16.7 million impoundments worldwide (Lehner et al. 2011). Several works have highlighted the fact that human pressures, especially dams have produced alterations in the abundance and endurance of fish populations (Marmulla 2001). Indeed, over 50% of the world's largest rivers are negatively affected by barrier placement (Nilsson et al. 2005). These barriers severely alter flow velocity, water depth, create vertical outflow drops that modify thermal and hydrology regimes of river systems, promote the loss of original habitat reducing heterogeneity (Berkamp et al. 2000, Pizzuto et al. 2000, De Groot 2002), hamper the movement of river species (Warren and Pardew 1998, Wheeler et al. 2005), and deteriorate water quality through urban, industrial and agricultural waste water. The combined impact of all these alterations has changed dramatically the constitution of river fish communities (Lelek 1987, Bayley and Li 1992, Waidbacher and Haidvogl 1998, De Groot 2002, De Leeuw et al. 2005).

1.4. Connectivity loss

Connectivity, or more correctly its opposing concept - isolation (Moilanen and Nieminen 2002), is considered one of the primary factors influencing species' distribution in riverine environments (MacArthur and Wilson 1967, Levin 1974, Merriam 1984, Fahrig and Merriam 1985), where a single barrier immediately isolates contiguous segments of river (Jager et al. 2001). Dams and weirs promote a breach on the longitudinal connectivity of systems, leading to a significant habitat modification and alterations of the flow regime, with consequences on the existing biotic communities (Larinier 2001). Those impacts have been felt in North America (Quiros 1989, Baum 1994, Meyers 1994, Stolte 1994), Europe (Porcher and Travade 1992), Australia (Barry 1990, Mallen-Cooper and Harris 1990), Africa (Gourène et al. 1999), and Asia (Zhong and Power 1996, Morita and Yamamaoto 2002). These habitat transformations are hazardous, as the alteration of natural flow regimes modifies environmental cues that act as triggers for fish migration (Mallen-Cooper 1995). Migratory fish (Box 1.3) are particularly sensitive to connectivity loss caused by habitat fragmentation (Jungwirth et al. 1998, Lasne et al. 2007) as their ability to reach spawning grounds is seriously affected. Diadromous fish species are obligatory migrants that perform migrations between marine and freshwater environments. For these species, the most downstream barrier completely isolates their access to the rest of the river network. Potamodromous species, although obligatory migrants, only perform migrations within the freshwater environment and are, therefore, able to use habitats found between barriers. Even though this could be seen as granting these species some resilience if suitable spawning habitats are present, the impacts of barriers on potamodromous are widespread (Moyle 1995, Muhar 1996, Dunham et al. 1997, Fagan et al. 2002, Morita and Yamamoto 2002). Such habitat and flow modifications are also usually favorable to generalist species, as so often is the case of exotic species, which are more adapted to the new lentic environments created by barriers (Vila-Gispert et al. 2005).

Although connectivity losses are frequently perceived as main causes of freshwater fish species decline, and its evidence well established for some fish groups such as diadromous species, it is much less clear when and how it affects the distribution of other freshwater fish groups, both potamodromous and sedentary fish. Diadromous fish are amongst the most studied fish species concerning the impacts of man-made structures on the persistence and abundance of their populations, but much less is known on the migratory ecology of potamodromous cyprinids (Lucas and Batley 1997). The establishment of river connectivity is increasingly seen as a basin wide task, and integrating various spatial and temporal scales is essential (Ward et al. 1999, Collares-Pereira and Cowx 2004). This type of information is needed not only to understand overall effects on the targeted populations of river fragmentation by different physical obstacles, but also to develop management guidelines for the connectivity increase to help conservation and management of stream fishes.

The magnitude of connectivity losses and the time period they affect are closely linked to the time of construction, the size and location of the dam, to the characteristics of the river system (Petts 1984, Genhrke and Harris 2001, Gehrke et al. 2002) and to the habitat loss for each particular species and life cycle stage. Therefore, connectivity losses are not linearly related to the number of obstacles, they depend on characteristics such as height, slope and flow alteration. Furthermore, losses are cumulative and dependent on the spatial scale considered (river reach, segment or basin) and on the home range and natural movements of the species affected (sedentary, potamodromous and diadromous). Dams can block or delay fish movements and as a result are responsible for the decline or eradication of many native species throughout Europe (Northcote 1998, Mader and Maier 2008). Even small obstacles can have a significant effect on flow, temperature regime, movement of animals and habitat quality (Larinier 2001), thereby potentially causing change in the composition, structure and distribution of fish assemblages. The fragmentation of the river continuum by such obstacles negatively affects fish populations by increasing loss of genetic variability and risk of extinction through demographic, environmental and genetic stochasticity (Nicola et al. 1996, Peňáz et al. 1999). However, the effects of longitudinal connectivity loss on potamodromous and sedentary Iberian fish species are less well understood, because on one hand, local habitat conditions can mitigate connectivity losses, and on the other hand fish populations are also affected by other human pressures that frequently mask or interfere with connectivity effects.

Connectivity losses should always be viewed within a hierarchical spatiotemporal frame, both for environmental as for biological items (Matthews and Matthews 2003). The direct impacts of dams are more dramatic and immediate. But, and although most studies look at the impact of large hydroelectric developments on fishes (Garcia de Jalon et al. 1994, Chang et al. 1999, Mérona and Albert 1999, Peňáz et al. 1999, Gehrke et al. 2002), the changes in species richness, diversity and community composition (Pusey et al. 1995, Reyes et al. 1996, Gehrke et al. 2002) can also be due to the cumulative impact of small barriers (Nunn et al. 2008, Cote et al. 2009, Lucas et al. 2009).

The Mediterranean systems (Box 1.4) pose an interesting problem regarding the connectivity loss effects. These river systems present large flow variability and tend to naturally present less connectivity during extended parts of the year. The dry summers create extended periods of low to null flow in many parts of the river, naturally fragmenting the systems into a sequence of unconnected habitats (pools) (Gasith and Resh, 1999). As a consequence, fish species become confined in small isolated habitat patches which have the capability to sustain only a reduced number of animals (Pringle 1997, Collares-Pereira et al. 2002). At these temporarily confined habitats, fish face increased predation, competition for resources, water quality degradation (increase of temperature and salinity) and oxygen depletion. Species inhabiting Mediterranean rivers should therefore display adaptations to this natural fragmentation, through higher population resilience and behavioural mechanisms that propels them for a fast colonization of upstream segments when those are reconnected with the remaining river network. Population fragmentation is expected to reduce genetic polymorphism and augment genetic differentiation (Knaepkens et al. 2004). A barrier to fish movement can thus further genetically isolate and deteriorate upstream populations (Knaepkens et al. 2004), leading to a process of genetic erosion that can increase the extinction risk of populations by promoting inbreeding processes and diminish evolutionary flexibility (Meffe and Carroll 1997).

Box 1.3 - Fish migrations

Longitudinal connectivity infringements are of particular concern for species that face the obligation to undertake migrations to complete their life cycle. Different migrations strategies exist enclosing in them different uses of the river network and different degrees of impact from connectivity hindrance (Morita and Yamamoto 2002, Dudley and Platania 2007). Migrations are biologically explained by a rational use of resources recuring to a spatial and temporal displacement according to the specific needs throughout the species life cycle. Population sustainability is closely linked to habitat characteristics, which are the guaranty of successful feeding, locomotion and reproduction (Lucas and Baras 2001).

Migrations can be defined as movements between two or more habitats that take place with a regular periodicity and are undertaken by the majority of the population (Northcote 1978, 1984, Smith 1985). “Migration” has thus far been used to describe movements in marine or freshwater environments and between these two. Here I will only address the migrations in which freshwater environments play a part.

Diadromy refers to obligatory migrants that perform movements between the marine and freshwater environments. Barriers affect the ability of these species to attain nursery habitats essential for successful recruitment (Hall et al. 2011, Hitt et al. 2012). Diadromy can be divided according to the direction of movement:

i) Anadromy refers to species that live, grow and feed on marine environments, but perform migrations inland to freshwater systems where they find suitable grounds to reproduce;

ii) Catadromy refers to species that live, grow and feed on freshwater environments, but perform reproductory migrations to marine systems.

iii) Anfidromy referes to species that reproduce in freshwater systems, their larvae migrate towards the sea where they feed and grow for a short time period after which post-larvae and juveniles migrate back to freshwater systems where they feed and grow.

Potamodromy refers to obligatory migrant species that incur in reproductory movements exclusively within freshwater systems. Barriers affect the ability of species to move within the systems, causing populations extirpation (Winston et al. 1991, Luttrell et al. 1999).

The effects of connectivity loss in regions where rivers experience seasonal flow intermittency have been less studied. Mediterranean rivers are dominated by autochthonous cyprinids, ranging from large benthic potamodromous to small resident water-column species. River fish diversity is accompanied by morphologic and ecologic variations (Ferreira et al. 2007) as species evolved differently to be adapted to different riverine environments. These specializations can be grouped into different morpho-ecological guilds that introduce differences in swimming abilities, behaviour and niche occupancy. To simplify studies, morpho-ecologic similar species can be grouped into guilds - assortment of organisms free of taxonomic strings that use a common array of resources (Fauth et al. 1996) – and a single species can be used as representative (Chan 2001) of one morpho-ecological guild. This method is suitable for multi-specific approaches (Leonard and Orth 1988).

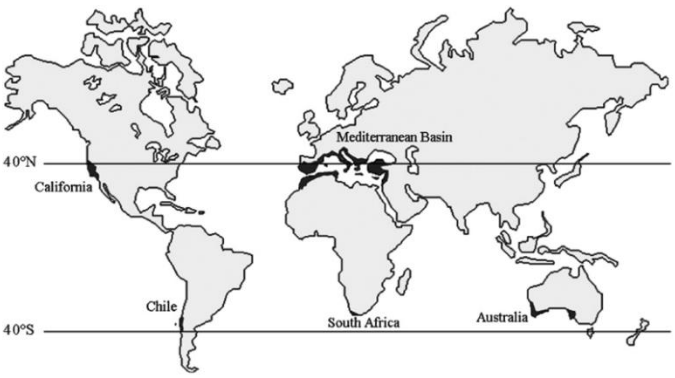
Box 1.4 – What is a Mediterranean river?

Mediterranean rivers are characterised by a predictable annual cycle of flood and drought that varies in intensity according to levels and duration of annual and interannual rainfall (Gasith and Resh 1999). The climate therein has a high degree of seasonality and is characterized by having skewed hydrographs with extended dry summers, which produce seasonal droughts, and by cool rainy winters. This seasonality is coupled with a high hydrologic annual variability.

These systems can be found in five regions where they are influenced by cool off-shore ocean currents: Mediterranean basin (the largest portion and the one from which the epithet was derived), California, central Chile, southern South Africa, southwestern and southern Australia (*vide* map below).

This climatic specificity has created regions of high endemism, and Mediterranean regions are considered biodiversity hot-spots. Nonetheless, Mediterranean regions have foster human societies since their birth. Only 4.3% of the Mediterranean biome is protected and 31% has already been converted into urban areas and high impact agriculture lands, making the Mediterranean biome one of the most unprotected biomes on Earth (The Nature Conservancy 2007). The human dependence on water may aggravate human impacts on rivers in these areas due to irregular water availability. The increasing threat of climate change will limit water availability even further and will facilitate the spread of alien species.

The marked seasonality of these regions has a determinant impact shaping rivers and their fish communities. Mediterranean fish species evolved to be adapted to this seasonality, and are naturally more resilient when faced with connectivity hindrance.



1.5. Connectivity enhancement

There is an increasing concern on today's society over the sustainment of the ecosystems services provided by rivers. To off-set some of the harmful impacts forced upon rivers by human needs and will, river restoration and requalification plans have experienced a boom since the 1980s in number and in allocated resources (Kondolf and Micheli 1995, NRC 1996, Holmes 1998, Bash and Ryan 2002, Henry et al. 2002, Ormerod 2003). Additionally, legislation is starting to be more stringent in relation to impacts enforced on natural ecosystems and species. Recently, the European Water Framework Directive (EWFD – European Commission 2000) was launched by the EU as a tool for adequate management of river basins, the natural geographical and hydrological unit. One of the key objectives of the EWFD is to achieve ‘‘good ecological status’’ of running waters by 2015. The re-establishment of longitudinal connectivity for fish on the basin level is therefore crucial for achieving the main target of the EWFD (Mader and Maier 2008).

Connectivity rehabilitation can be achieved through the installation of fishways, creation of environmental flow regimes suitable for the enhancement of fish movements or the removal of the artificial barrier. The best method to reconnect barrier fragmented systems is undoubtedly the removal of all instream structures that act as barriers (Roni et al. 2002). It is, nonetheless, an endeavour prone to failure due to limiting financial and logistic constraints and to the loss of important services (flood control, irrigation and water supply) provided by these structures. Fishways are a more realistic solution to provide connectivity enhancement as they allow fish to move freely, up and downstream, while working with environmental flow regimes. Nevertheless, both of these options are being used to restore connectivity of river networks (Bednarek 2001, Hart et al. 2002, Calles and Greenberg 2005), because they are preferable over strict habitat enhancement solutions, particularly for isolated populations (Auer 1996).

1.5.1. Prioritization

Restoration objectives are often hampered by budget limitations. There is thus the need to prioritize restoration actions in order to correctly allocate often scarce resources to where they are most needed in order to achieve the restoration goals (Kemp and O'Hanley

2010, O’Hanley 2011, Nunn and Cowx 2012). Methodologies constructed to summarize complex data are extremely helpful and their use is increasing (Spellerberg 1993, Olivier and Beattie 1994, Graça and Coimbra 1998, Harris and Silveira 1999, Ladson et al. 1999). These methods facilitate the decision making process by making the data intelligible to everyone while guarantying scientific accurateness (Karr and Chu 1999, Knapp et al. 2003, Paul 2003). Grant et al. (2007) defined rivers as a unique component of spatially structured networks to which special attention must be granted. Because fluvial landscape ecology is in its infancy and has not fully developed into an integrated field, and river geometry and network makes it difficult to apply terrestrial based landscape metrics, there is the need for concepts and methodologies devised specifically for rivers (Poole 2002, Wiens 2002).

Most of the prioritization tools for connectivity restoration are secluded in grey literature (Kemp and O’Hanley 2010) and are generally unavailable to the decision-makers. Furthermore, the existing scoring-and-ranking systems have a limited scope of action because they only consider the impacts of isolated barriers, ignoring the cumulative non-additive impacts of all barriers in a given network (O’Hanley and Tomberlin 2005, Kemp and O’Hanley 2010). Another limitation of the existing methods is that the prioritizing philosophy aims at increasing connected river length (Mader and Maier 2008, Kocovsky et al. 2009), overlooking the habitat suitability/availability increase. These prioritization schemes favor the structural over the functional connectivity. In fact, Fullerton et al. (2010) defined the development of methodologies to tackle the constrains of riverine structure as one of the most important challenges to understand the consequences of connectivity for river fishes. An understanding of the barriers effect on fish movements, the position of barriers within the river network, the size of the disconnected habitats, suitability of those habitats and hindrance to access to suitable habitats are essential to develop schemes of ranking priority restoration actions (Roni et al. 2002).

Graph theory (Box 1.5) is housed on simple concepts and treats spatial elements of a landscape as nodes and the relationships between those landscape elements as links (Dale and Fortin 2010). Spatial graphs are a special case of Graph theory, where the nodes, besides representing spatial structures, have a location and the relationships between those nodes (links) are defined by the location of nodes (Fall et al. 2007). This method has been applied extensively to landscape studies (Urban and Keitt 2001, Minor and Urban 2008, Dale and Fortin 2010, Galpern et al. 2011), but recently this technique has been applied to river networks (Schick and Lindley 2007, Eros et al. 2011, 2012) and has proved to be an excellent connectivity assessment tool. It allows understanding the connectivity of a riverscape from two distinct perspectives: backwards, perceiving how the network got fragmented (Keitt et al. 1997, Bunn et al. 2000, Urban and Keitt 2001); and forwards, perceiving the impact of projected connectivity restoration actions on the overall network connectivity (Palmer et al. 2005). This theory provides the means to study the non-additive cumulative impacts, on longitudinal connectivity, by considering not only the isolated effect of each barrier but also the joint effect of all artificial barriers present in a system.

1.5.2. Instream structures

Undisturbed rivers sustain fish populations that are naturally adapted to the environment. These rivers can act as benchmarks for restoration projects (Boavida et al. 2011). The Field of Dreams Hypothesis (Palmer et al. 1997) has been applied, as the underlying reasoning, to several restoration plans. The general idea is that if you restore a river stretch, fish will return to colonise it. But, in order to restore degraded sites, the specific factors that limit fish populations must be addressed (Rosenfield and Hatfield 2006, Feld et al. 2011). Fish habitat depletion and fragmentation are commonly compensated through mimicking the natural undisturbed physical structure of the river environment (Shamloo et al. 2001, Katopodis 2002). This mimicking engineering design is often referred to as physiomimesis, a design method useful not only for restoration and habitat improvement, but also for fish passage design (Newbury and Gaboury 1993, Shrubsole 1994, Katopodis 1995, Marsden 1995, Katopodis 1996, Katopodis et al. 2001).

To promote habitat improvement and reduce fragmentation, the installation of instream structures such as submerged weirs, boulders, flow deflectors and logs on degraded river stretches has been extensively used (Reeves et al. 1991, Frissel and Nawa 1992), improving habitat quality and biodiversity (Cowx and Welcome 1998, Roni et al. 2006). These structures develop localized alterations to the channel morphology quite rapidly. If a flood event occurs, habitat changes promoted by the implanted structures will be seen within the first year (Fuller and Lind 1991). Boulder placement is a method for improving fish habitat that is more effective on smaller streams (Stewart et al. 2009) because it changes the physical conditions of the stream by increasing pool habitats and water depth (O'Grady 1995, Vehanen et al. 2003, Roni et al. 2006). These structures also provide fish with cover from visual predators by increasing turbulence and scour, and are known to provide spawning grounds for litophilic fish due to increased gravel retention (Roni et al. 2006) as well as retention of organic matter, contributing for the improvement of food webs (Negishi and Richardson 2003). Boulder placement has been extensively examined for salmonids (O'Grady 1995, Vehanen et al. 2003, Roni et al. 2006), but the effectiveness of boulder placement on the enhancement of habitat for non-salmonid species was only scarcely accessed (Roni et al. 2006).

Box 1.5 – Graph theory

Graph theory is the study of graphs, third lattice mathematical structures that model pairwise relationships between objects (Urban and Keitt 2001). A graph can thus be described as a collection of nodes and of edges that connect pairs of nodes; and can be represented as G = (N,E), where N is a set of *n* nodes linked by a set E of *e* edges (Harary 1969). This has been extensively applied in geography, information technology and computer science (Bunn et al. 2000), mostly concerning efficient flow and connectivity in networks (Gross and Yellen 1999). This theory has been applied to rivers and has shown to adapt well to these constricted networks (Schick and Lindley 2007, Eros et al. 2011, 2012). Below are some definitions of key graph theory terms and vocabulary used throughout the thesis.

Node: Dimensionless point. A set of nodes (elements) compose the graph network. Nodes can exist on a graph without any associated edge, and can be the endpoint of the network.

Edge: Link between two nodes, representing the relationship between the nodes. Edges must have nodes at their ends, each edge needs two nodes. In the present thesis "Edges" are referred to as "Links".

Network: Graph structures in which the nodes are usually weighted by characteristics like abundance, length, area, habitat suitability, etc.; and where edges represent interactions such as physical connections, which can be weighted and have asymmetrical directionalities.

Spatial graph: Graph structure characterized by the spatialization of the nodes. The endpoints of edges are defined by the location of the nodes.

Connectivity: A graph has a high degree of connectivity if node or edge connectedness is high.

Subgraph: Subset of nodes of a graph.

Schematic representation of a graph. Nodes are represented by circles and edges by lines.

1.6. Fishways

Fish ability to recolonise a river stretch depends equally on the existence of suitable habitat as on the ability to navigate there (Hughes 2007). The investment on restoration should be done in an integrated manner, bonding habitat/stretch restoration with connectivity enhancement (Pringle 2003, Kondolf et al. 2006). Otherwise, newly restored habitats will be unconnected and the effort made will be unsuccessful. This is crucial to systems management and conservation (Muhar 1996, Stanford et al. 1996, Cooper and Mangel 1999), as species may need a variety of habitats during their life cycle and may display distinct life histories and behaviours that are evidentiated at different spatial scales.

The construction of fish migration facilities has been one of the most common approaches to mitigate the negative effects associated with the presence of obstacles to fish migration (Larinier 2002, Santos et al. 2005). However, due to their multiple designs and configurations, ranging from conventional ladders to nature-like oriented structures (Box 1.6), the behaviour of fish when facing such devices is virtually unknown and their success is often questionable (Katopodis and Williams 2012). It is rather challenging to ensure that flow and turbulence patterns in each fishway type can provide suitable swimming conditions for multiple fish species.

Pool-type fishways are one of the most widespread types (Larinier and Marmulla 2004). These facilities consist of a rectangular flume with cross-walls arranged in a stepped pattern, forming consecutive pools with water levels increasing in the upstream direction. These pools offer resting areas for fish to recover after cross-wall negotiation and provide an appropriate dissipation of water energy between consecutive pools to ensure that the flow pattern is similar in each pool (Larinier and Marmulla 2004). The cross-walls may be equipped with different openings, such as surface notches and/or submerged orifices at the bottom, which are used by fish to move from pool to pool. The most common pool-type fishway in southwest Europe is the alternate surface notch and submerged orifice design (Larinier 2008) which need a small water flow to operate, a crutial factor in latitudes with extended low flow periods. Such facilities can accommodate moderate upstream water level variations without the need for installing any upstream flow-regulation section. Flow in these facilities depends on the size of the river and can vary from less than 0.1 $m^3.s^{-1}$ in small mountain streams to more than 2 $m^3.s^{-1}$ in large rivers. Head drops between pools can vary between 0.30-0.45 m for salmon and sea-trout, to less than 0.20 m for cyprinids and other species with limited swimming abilities, the length of the pools may vary from 1.2 m to more than 4.5 m, with common fishway slopes of 10 to 12% (Larinier 2008).

The normal flow circulation in a pool-type fishway is the plunging regime. This circulation is created by the jet from the upstream pool plunging towards the fishway floor, moving downstream along the floor, then rising along the face of the next cross-wall and either dropping over the notch or rolling back upstream along the surface of the pool. The streaming flow regime typically occurs at higher flow levels relative to the plunging regime. When streaming flow occurs, a continuous surface jet passes over the crests of the cross-walls and skims along the surface of the pools. Plunging, streaming and other flow regimes that occur in pool-type fishways, depending on slope, discharge, and weir spacing, are presented by Ead et al. (2004) (Box 1.7). Fish selection for either orifices or notches will depend on the species, swimming ability and on the type of flow regime (plunging or streaming) through the fishway (Katopodis 2005).

When working with determined terms one must be certain of their meaning, because they are frequently misused in ecology, promoting communication problems, only solved by correct term determination. Larinier (2008) defined the terms effectiveness and efficiency of fishways. Effectiveness is a qualitative concept that determines if the fishway is negotiable by all target species during the migration period. Efficiency is on the other hand a quantitative concept that refers to the fishway's performance defined by the proportion of the population that successfully navigates the fishway in a suitable time frame. Throughout the thesis these terms are used and applied as defined above. Nevertheless, the terms might be at times misused due to concurrence with cited literature.

Noonan et al. (2012), on a review of passage efficiency in existing fishways, found that although pool-type was the most efficient technical fishway type both for salmonids and non-salmonids, design features of many existing fishways seem to match fish species needs rather poorly. Most of the fish transposition devices of Iberian regions are not suited for native migrants, since they were built based on guidelines created for salmonids (Pinheiro and Ferreira 2001) which have movement and jumping abilities quite different from those of non-salmonid fish. Only the very best designed fishways can approach high performance rates, while even well-designed fishways have variable success due to differences in fish swimming ability, behaviour (Hinch and Bratty 2000, Katopodis 2005, Katopodis and Gervais

2012) and physiologic state (Pon et al. 2009, Hasler et al. 2011), as well as hydraulic (Katopodis and Williams 2012) and turbulence parameters (Silva et al. 2012).

Box 1.6 - Fishways

Fish transposition devices, often termed fish passes, fish ladders or fishways are constructed at barriers to aid fish negotiation of these transversal structures that hinder longitudinal connectivity. Fishways have been regularly built since the 1850's, following the implantation of the first hydroelectric developments during the industrial revolution (Kamula 2001). We can divide fishways into three major groups: technical, nature-like and special (FAO/DVWK 2002).

Technical fishways

Pool-type: Creates a succession of stepped pools that divide the height to be negotiated and provide adequate energy dissipation at each step. Fish negotiation of the cross-walls is done by the orifices that can be placed near the bottom, at the surface or a combination of the two.

Vertical slot: Similar to pool-type fishways, in which the openings are extended from the surface until the bottom creating slots. Each cross-wall can be equipped with one or two slots.

Denil: Linear channel with baffles arranged at regular short intervals and angled against the main direction of flow. The baffles create back flows that dissipate a great deal of energy and cumulatively allow a low flow velocity to be shaped near the bottom of the baffles. This fishway can be built with relatively steep slopes.

Nature-like fishways

Bottom ramp: Occupies the total width of the river channel. It aims at dispersing the hydraulic head (difference in the water level between the impoundements and the water surface downstream) over a determined river length by maintaining a gentle hydraulic gradient of the slope.

Fish ramp: Similar to bottom ramps. Integrated in a portion of the weir, occupies only a part of the river width and concentrates all discharge at low and intermediate water levels.

Bypass channel: Consists on a side-channel that mimics a natural river. These structures can occupy a vast area due to the usually low slopes. Besides helping fish to move past the barrier, bypass channels have the additional advantage of generating new habitat for fish species.

Special fishways

Eel ladders: These can be divided into two types: i) Eel pipes – pipes filled with brush-like structures or gravel, fitted into the base of the barrier. These structures have proved to be not very effective due to cluttering; ii) Eel channels – small shallow channels with brush-like structures or gravel placed at the bottom.

Fish lock: Consists of a lock chamber limited by a lower inlet and an upper outlet structures with closing devices. These devices work by lowering the lock chamber water level to match the inlet water level, then a guiding current is created to attract fish into the lock chamber. The chamber is locked and water level raised to match the outlet level, flow coming from headwaters attracts fish out of the lock chamber.

Fish lift: Fish are attracted to the lift by a guiding current. A trough "captures" the fish by moving upwards until the headwater, where a guiding current guides fish out of the lift. Optimal to be placed at high barriers, and in places were available space is limited, it is also advantageous in locations with presence of low swimming ability species.

Turbulence is a measure of tree-dimensional variation in flow velocity that has direct impact on the fish swimming energy expenditure (Liao et al. 2003), increasing the costs of fishway navigation (Enders et al. 2003). When the turbulence is very high fish might be injured or even die (Cada 2001, Odeh et al. 2002, Neitzel et al. 2004). To reduce navigation costs, fish may exploit the vortices generated by the passage of water around structures, by the motion of other fish (Liao 2007, Przybilla et al. 2010) or even by their own motion (Liao 2003). Recent studies have pointed out the differing effect of turbulence according to its scale in relation to the size of the fish; small scale turbulence can in fact aid fish's locomotion, contrarily larger scale turbulence can disorientate fish and detract its movements (Odeh et al. 2002, Tritico and Cotel 2010). Reynolds shear stress is a force created by the transfer of momentum between adjacent water layers of varying velocities (Tennekes and Lumley 1972) and also infers on fish behaviour. When exercised parallel to a fish it induces alteration in swimming performance and stability (Odeh et al. 2002) causing injuries or death at extreme levels (Cada 2001, Odeh et al. 2002).

1.6.1. Technical holistic fishway

Several authors (Hinch and Rand 2000, Pavlov et al. 2000, FAO/DVWK 2002, Baker and Boubée 2003) state that the inclusion of heterogeneity through the use of structures like logs, boulders or stones at the base of fish passes may potentiate fish negotiation of such devices. Boulder placement at the bottom of fishways presumably potentiates fish passage of pool-type fishways (FAO/DVWK 2002), as the reduction of flow velocity near the bottom promoted by these structures facilitates fishway negotiation particularly by benthic species such as the gudgeon (*Gobio lozanoi*), loach (*Cobitis paludica*) and eel (*Anguilla anguilla*). The boulder substrata increase roughness that allows species with limited swimming capabilities to take advantage of the small velocity refuges, created by each boulder, to migrate upstream, and also to benefit from the velocity breaks and hydraulic shadows that create resting areas. A parameter that should also be regarded as key is the relative depth of flow – relation between the water depth in a pool and the height of the boulder. Shamloo et al. (2001) studied the flow around a hemispherical boulder in a rectangular channel, and found that the relative depth of flow defined the flow regime around an obstacle which influenced the suitability of hydraulic conditions for fish passage. Lower relative depths (low water depth and high boulders) are, in principle, more favourable for fish movements because complex flow conditions and recirculation regions are more prone to occur, enhancing fish movements.

Most of the existing pool-type fishways are designed with a bias because the majority of research on fishways has been focused on large-bodied fishes (Billman and Pyron 2005). Design criteria are better understood for obligatory migrants such as diadromous and some potamodromous species. Conversely, less attention has been given to smaller species (Wang et al. 2010) such as cyprinids (Ovidio and Philippart 2002), which exhibit different behaviour and have limited swimming ability (Santos et al. 2012). This is somewhat regrettable, as these species play an important role on fish assemblages and unrestrained movement is paramount for their survival (Lucas et al. 2000). It is therefore imperative to develop adequate technical and scientific guidelines for these species (Clay 1995, Lucas and Baras 2001, Williams et al. 2012). When developing structures to reduce the impact of hydraulic barriers, the individual features of fish behavior and ecology must be accounted for (Pavlov et al. 2008). The EWFD (European commission 2000) requires effective passage and undisturbed migration for all fish species, even the ones with lower swimming ability, as a key component to restore and manage watersheds. There is thus a need to design more suitable holistic multi-species fishways (Winter and van Densen 2001, Kemp and O'Hanley 2010) with optimum dimensioning values and hydraulic parameters for native freshwater species with different morphological and ecological characteristics. Moreover, several non-salmonid species have recently acquired greater legislative protection (e.g. under the EU Habitats Directive (Council Directive 1992)).

Laboratory trials, where conditions found in the field are easily reproduced while manipulating variables and monitoring confounding factors, are always preferable (Wang et al. 2010), and have been proposed as the starting point of successful fishway designs (Kondratieff and Myrick 2005, Katopodis and Williams 2012). Furthermore, studies on fish passes often lack balanced experimental designs, in which, contrarily to those conducted in the wild, the variables of interest can be manipulated while controlling for confounding effects (Kondratieff and Myrick 2005). The use of full-scale models is encouraged to study fish movements within fishways, because they recreate conditions similar to those found in nature, i.e. complex rather than rectilinear flows, allowing fish to exhibit their natural behaviour, and thus providing more realistic results (Williams et al. 2012). The Field of Dream Hypothesis can easily be applied to fishways, in the sense of – if you built it fish will pass, fish will negotiate a barrier to achieve optimal reproductory or foraging grounds.

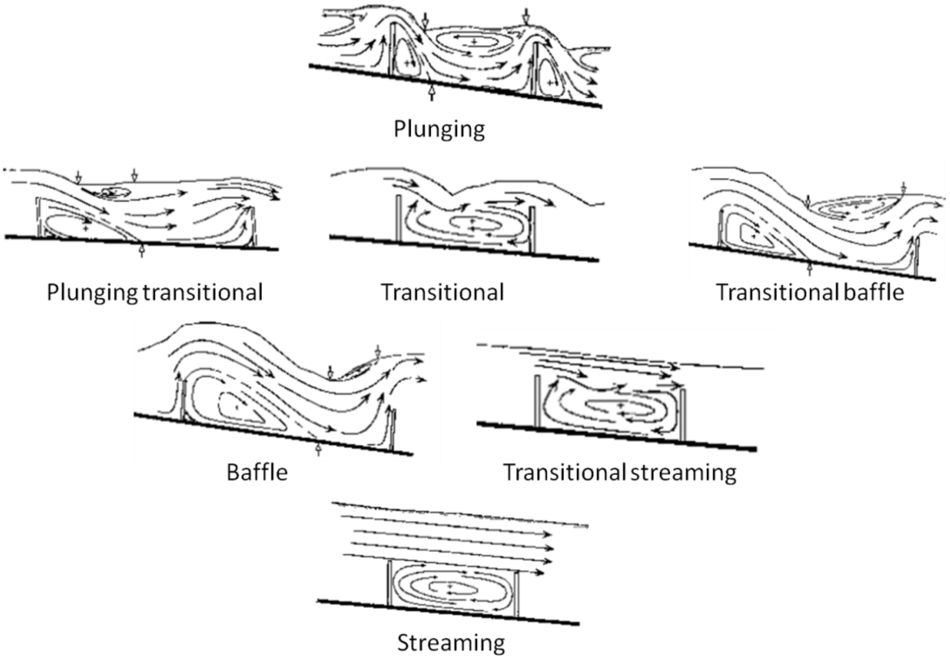
Box 1.7 – Flow regimes in a pool-type fishway

Pool-type fishways are composed by a series of stepped pools divided by cross-walls. Water flows over these cross-walls from one pool to next downstream pool. The flow regime created by the water flow from one pool to the next is determined by flow discharge and by the dimensions of pools and cross-wall openings. Two major flow regimes can be defined:

Plunging flow – is the most common regime found in pool-type fishways and is characterized by a plunge of water towards the fishway floor creating a downstream flow that moves along the floor until the next cross-wall where it rises along the face of the cross-wall and plunges to the next pool. This creates two recirculation regions, one behind the water plunge and other at the surface.

Streaming flow – occurs at higher flow discharges and is characterized by water moving between pools by passing over the crests of the cross-walls and skimming along the surface of the pools. This creates a large recirculation region near the bottom of the pool.

Clay (1961), Rajaratman et al. (1988) and Ead et al. (2004) have all described these regimes, but they have also stated the existence of transition flows between plunging and streaming. Below a figure adapted from Ead et al. (2004) schematizes the two mains flow regimes and the transitional flows.



1.7. Objectives

The study of riverine longitudinal connectivity losses, resultant of man-made obstructions, has been widely focused on long migration fish species. The need to understand the impact of these losses to potamodromous and resident species, and the need to define correct practices for connectivity enhancement framed the aims of this thesis.

1.7.1. General objectives

This thesis aims at two main objectives:

- To determine the impact of connectivity loss for potamodomous and sedentary fish species;
- To develop river connectivity enhancement measures for potamodomous and sedentary fish species.

To pursue and achieve these general objectives, a group of studies were undertaken to respond to seven specific objectives.

1.7.2. Specific objectives:

1 – To assess the impact of connectivity losses in the distribution of Iberian fish species and fish guilds at the basin level;

2 – To assess the influence of barriers on the structural connectivity of a river network;

3 – To assess the influence of barriers on the functional connectivity of a river network for two distinct eco-morphological guilds;

4 – To develop a connectivity enhancement prioritization method for barrier fragmented systems;

5 – To assess the influence of instream boulder placement on the habitat improvement and on poll-type fishway negotiation of Iberian barbel (*Luciobarbus bocagei*);

6 – To assess the influence of different depth of flow in relation to bottom substrata on the movements of Iberian barbel (*Luciobarbus bocagei*) passing through a poll-type fishway;

7 – To assess the performance of fish species from different eco-morphological guilds to move through pool-type fishways, under different flow regimes.

1.8. Thesis structure

The thesis is structured into four distinct sections. Section I – "Hydrological connectivity: causes and consequences" comprises the introduction of the thesis. It is referent to the general framework of the thesis by presenting the state of the art of the subjects approached in the following sections. This section offers the reader the knowledge considered essential to allow for a better understanding of the works presented herein. Additionally, the general and specific objectives of the thesis are presented, as well as, the structure and organization of the thesis.

The following two sections of the thesis (sections II and III) are referent to the studies developed to achieve the objectives of the thesis, and are divided into three chapters each. Each chapter responds to a scientific question and presents the results and conclusions attained, and it is a stand-alone article that has been published, accepted for publication or submitted to a peer-reviewed journal. These articles are presented here in a form identical to the published or submitted version, but have had slight alterations to the formatting in order to create uniformity among works.

Section II – "Barrier impact". In this section, a large scale approach is pursued to understand the connectivity problems affecting freshwater fish species

- Chapter 2– Branco P, Segurado P, Santos JM, Pinheiro P and Ferreira MT (2012) Does longitudinal connectivity loss affect the distribution of freshwater fish? Ecological Engineering 48: 70-78.

- Chapter 3 – Segurado P, Branco P and Ferreira MT (2013) Prioritizing restoration of structural connectivity in rivers: a graph based approach. Landscape Ecology DOI: 10.1007/s10980-013-9883-z.

- Chapter 4 – Branco P, Segurado P, Santos JM and Ferreira MT (2013) Prioritizing connectivity restoration for stream fishes using spatial graphs. Ecological Applications (*Submitted*).

Section III - "Connectivity enhancement". In this section the scale of approach was reduced encompassing here both segment and site scales. This more fine approach allowed the study of connectivity enhancement techniques as solutions for local connectivity problems. These solutions will affect micro scale works that have a combined effect noticeable on the large scale.

- Chapter 5 – Branco P, Boavida I, Santos JM, Pinheiro A and Ferreira MT (2012) Boulders as building blocks: improving habitat and river connectivity for stream fish. Ecohydrology DOI: 10.1002/eco.1290.

- Chapter 6 – Santos JM, Branco P, Silva AS, Katopodis C, Pinheiro A, Viseu T and Ferreira MT (2013) Effect of two flow regimes on the upstream movements of the Iberian barbel (*Luciobarbus bocagei*) in an experimental pool-type fishway. Journal of Applied Ichthyology 29:425-430.

- Chapter 7 – Branco P, Santos JM, Katopodis C, Pinheiro A and Ferreira MT (2013) Pool-type fishways: two different morpho-ecological cyprinid species facing plunging and streaming flows. PLOS ONE DOI: 10.1371/journal.pone.0065089.

Section IV – "General discussion" presents a general discussion of the works presented in the sections II and III, while summarizing the more relevant findings of this thesis. This section also presents a brief reflection on the questions that were left unanswered or that were raised by the findings of this work in which future research should be focused on.

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Section II

Barriers impact

"Water is the driver of Nature"

Leonardo da Vinci

Chapter 2

Does longitudinal connectivity loss affect the distribution of freshwater fish?

Ó Marinheiros pinheiros,
gageiros da tempestade!
Naúfragos arrojados
à duna! Cristos pregados
na areia que vos tem crucificados:
- fazeis-me dor e saudade,
a saudade de mim, a mais cruel,
meus pinheiros de Moel!

Afonso Lopes Vieira, "Onde a terra se acaba e o mar começa" 1940

2.1. Abstract

Loss of natural river network connectivity is presumed to be one of the more generalized and important human-induced alterations in natural environments and is frequently perceived as one of the main causes of the decline of freshwater fish species.

The purpose of the present study was to ascertain the impact of barriers on the distribution of freshwater fish species with distinct life histories. In this study 196 sites in three river basins in Western Iberia were sampled and analyzed for the presence of barriers. Three alternative analytical approaches based on Generalized Linear Models (GLM) were used to test the contribution of connectivity-related variables to species distribution: (1) explore whether connectivity-related variables are included in the best-fitting distribution models; (2) use models calibrated at non-disturbed sites to compute deviations from model predictions made at sites with connectivity-related disturbances; and (3) use a hierarchical partitioning approach, in which the improvement of model fit due to the inclusion of connectivity as a predictor variable is assessed using all possible variable combinations.

The results indicate a general lack of influence of barriers on freshwater fish species distributions. The effects of environment and human pressures exceeded the isolated effect of connectivity losses. Further studies based on experimental designs that are more specifically directed at this specific issue are needed in order to fully understand the effects of barriers on species and communities. A more thorough assessment of the effects of connectivity on fish is crucial to the implementation of adequate restoration actions that are in turn needed to achieve the goals of the European Water Framework Directive.

Keywords: Longitudinal connectivity, freshwater fish, potamodromous fish, barriers, GLM, Western Iberia

2.2. Introduction

Connectivity – or more precisely, isolation (Moilanen and Nieminen 2002) – is considered to be one of the primary factors that influence the distribution of species (MacArthur and Wilson 1967, Levin 1974, Merriam 1984, Fahrig and Merriam, 1985). In riverine environments a single barrier immediately isolates contiguous river segments (Jager et al.

2001). The increasing demand for water supplies and the lurking threat of climatic changes are driving the construction of hydraulic structures for water retention, such as dams and weirs. This construction has accelerated over the last 50 years (ICOLD 1998, Ward et al. 1999), resulting in reduced connectivity and the loss of successional trajectories in watercourses (Ward and Stanford 1995, Ward et al. 1999). Such habitat alteration is hazardous, as the associated modification of the natural flow alters the environmental triggers for fish migration (Mallen-Cooper 1995). These habitat transformations frequently favor generalist species, such as the exotic species in Mediterranean rivers, which are more adapted to the lentic environments (Vila-Gispert et al. 2005) created by barriers.

The concept of longitudinal connectivity is based on the *river continuum* concept postulated by Vannote et al. (1980), and is related to the habitat fragmentation theory (Andrèn et al. 1985, Wilcove et al. 1986, Dickman 1987, Noss and Csuti 1997) and the concept of ecological corridors (Forman and Godron, 1986). Connectivity can be defined as a functional “exchange pathway of matter, energy and organisms” (Ward and Stanford 1995) or, from a hydrological perspective, as a “water mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle” (Pringle 2003) that acts at both regional and global scales. Connectivity is comprising of four dimensions: longitudinal, vertical, lateral, and temporal (Ward 1989, Brunke and Gonser 1997, Tockner et al. 1998). However, longitudinal connectivity is regarded as the most important connectivity dimension for freshwater fish species, because it allows upstream and downstream fish migration cycles to occur (Lucas and Baras 2001).

Barriers such as weirs and dams interrupt longitudinal connectivity and promote species isolation (Falke and Gido 2006), presumably thus affecting fish movements for reproduction, feeding and habitat colonization purposes, with potential genetic impoverishment and loss of population fractions, while possibly promoting the spread of alien fauna. Even small obstacles can have a significant effect on flow, temperature regime, movement of animals and habitat quality (Larinier 2001), thereby potentially altering the natural distributions of fish species.

For the species with an ecological obligation to undertake reproductive migrations, the maintenance of longitudinal connectivity in riverine systems is reported to be of paramount importance (Jungwirth et al. 1998, Lasne et al. 2007), especially for the long-distance migratory species that migrate between the marine and freshwater environments. The effect of barriers on the decline of populations of these groups is well documented (Jungwirth et al. 1998, Lasne et al. 2007). However, evidence for barrier effects in non-diadromous species is much harder to understand and less well documented (Lucas and Batley 1997), especially in cases in which other human pressures are also affecting fish populations.

The Iberian region poses another interesting problem with regard to the effects of connectivity loss. River systems present a large flow variability and tend to naturally present less connectivity for extended parts of the year. Mediterranean species ought therefore to display adaptations to this natural variability, through higher population resilience and behavioral mechanisms – for example, the urge for a rapid colonization of upstream segments when temporal windows enable the river to be connected. Still, the most common and abundant native species in Iberian freshwater systems – the potamodromous cyprinids that perform reproductive migrations within rivers – ought nonetheless to be affected by the multiple barriers built along the systems. These species have been the object of much less study, and knowledge of their migration ecology and their ability to negotiate obstacles is scarce (Lucas and Batley 1997).

The Water Framework Directive (WFD 2000) was launched by the EU with the basic goal of ensuring that all the various types of body of water attain a good ecological status. Ecological status before and after restoration is primarily classified in terms of biological quality elements, complemented by abiotic and hydrogeomorphological elements that include river connectivity (Mader and Maier 2008), which is often viewed as a priority (Roni et al. 2002, Mader and Maier 2008). However, it is necessary to incorporate statistical uncertainty into the ecological classifications and this requires reliable responses of species and communities to specific pressures. One important question is whether we are able to describe sufficiently robust responses in order to use them as guidelines for the restoration of river connectivity.

The present study used empirical data on species presence and absence to look at the distribution of fish species in three Portuguese river basins. The effects of barriers were quantified and the influence of covariables controlled by applying several Generalized Linear Modeling (GLM) techniques. The following questions were asked: i) Are distributions of potamodromous species negatively associated with the number of upstream or downstream barriers?; ii) Are distributions of exotic species positively associated with the number of upstream or downstream barriers?; and iii) Are distributions of resident species associated with the number of upstream or downstream barriers?

2.3. Methods

The present study assumes an underlying premise that species with different life histories are affected in different ways by connectivity losses. In theory, species that are more adapted to lotic environments are negatively affected by transversal obstacles, while conversely lentic fish species are promoted by such alterations. The seven studied species were ubiquitous to the three sampled basins and present in at least 15 of the 196 considered sites. Two of the species are potamodromous (the Iberian barbel *Luciobarbus bocagei*, and the Iberian straight-mouth nase *Pseudochondrostoma polylepis*), two are resident (the Calandino *Squalius alburnoides*, and the Southern Iberian spined-loach *Cobitis paludica*), and three are exotic (the mosquito fish *Gambusia holbrooki*, the pumpkinseed sunfish *Lepomis gibbosus*, and the Pyrenean gudgeon *Gobio lozanoi*).

2.3.1. *Study area*

The study area is comprising of three river basins – the Tagus, Mondego, and Vouga – in central Portugal (Fig. 2.1), all of which flow westwards to the Atlantic Ocean. This area includes a large assortment of landscapes, ranging from mountains to coastal lowlands. The Tagus is the longest Iberian river (700 km), originates in Central Spain, and its basin covers an area of 24,800 km^2 in Portuguese territory. The Mondego (227 km), which lies to the north of the Tagus, is the largest river that runs exclusively in Portuguese territory, where its basin covers an area of 6,670 km^2. The Vouga catchment (136 km) is the smallest and northernmost of the three sampled river basins, with an area of 3,600 km^2 (INAG I.P.).

2.3.2. *Fish sampling*

A total of 196 sites in the three studied basins were sampled between 1996 and 2006. The sampling was performed using electrofishing, which is the least biased method for sampling stream fish (Cowx 1989) and is similar to the ones defined by the protocol adopted by the European Committee for Standardization (CEN norm 14011, March 2003). The field sampling team moved upstream in a zigzag pattern, thus ensuring that all habitats were covered by the sampling procedure. Fish were collected using a dip net and were promptly placed in a container filled with river water. After the sampling all the fish were counted, identified to the species level and returned to the river alive.

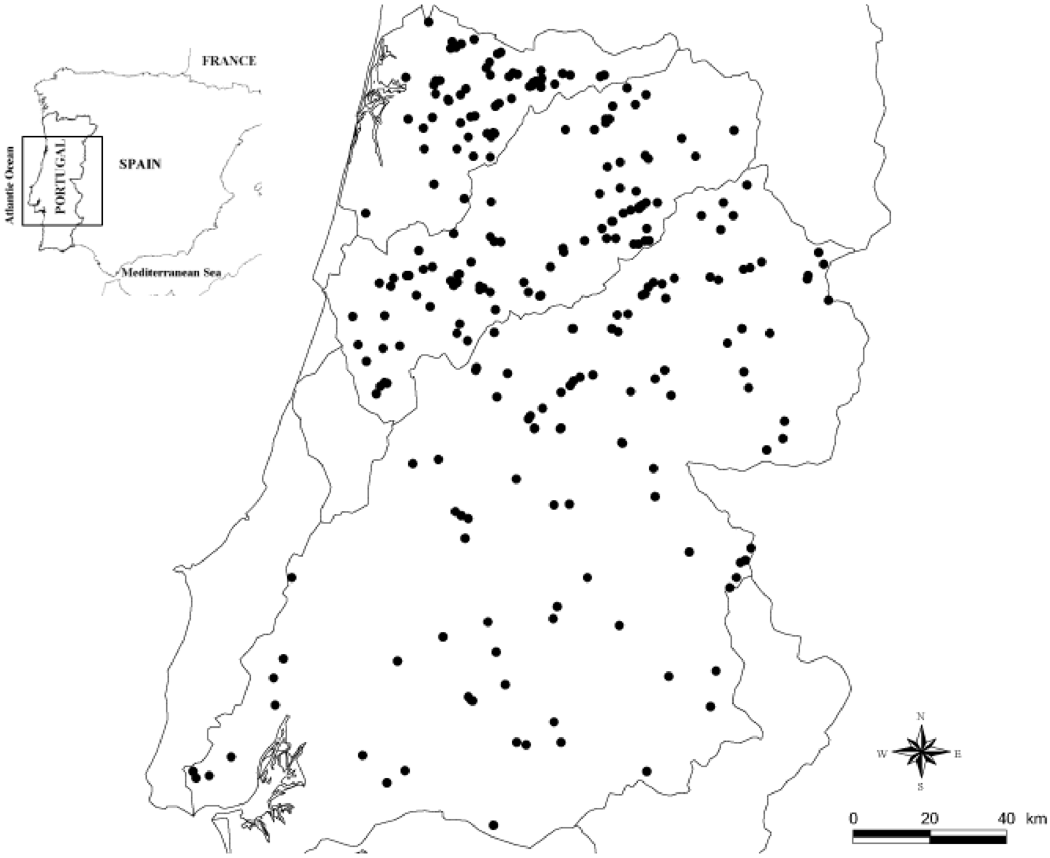

Figure 2.1 – Location of the 196 sampling points in the three river basins (Tagus, Mondego, and Vouga) in central Portugal.

2.3.3. *Environmental and pressure variables*

Twelve variables describing the natural environmental gradient were compiled for each site (EU project EFI+, see documentation at: http://efi-plus.boku.ac.at/download.htm). They were comprised of three climatic (mean total annual precipitation on the catchment, local mean temperature in July, local difference between mean January and July temperature), three topographical (mean catchment altitude, local altitude, river slope), and one geological (natural sediment) variable, and five variables directly or indirectly related to river geomorphology (geomorphologic river type, valley form, floodplain extent, distance to source, catchment area). The climatic, topographical and geological variables were derived from the CCM2 European River Network (Vogt et al. 2007) using the ArcGis 9.3 software (ESRI). Geomorphologic river type, floodplain extent, and valley form were recorded during the field work (EU project EFI+, see documentation at: http://efi-plus.boku.ac.at/download.htm). Some of this information was complemented by a visual analysis of sites on Google Earth (Google Inc.). River slope, distance to source, and catchment area were log-transformed.

Each set of variables except natural sediment, river slope, and mean total annual precipitation on the catchment was summarized into a reduced number of dimensions using the axis scores of a Principal Component Analysis (PCA). For climatic and topographical variables only the scores of the first axis were used, because this axis explained a large percentage of total variance (86% for both variables). In the case of geomorphology, a special kind of PCA – the Hill-Smith ordination (Hill and Smith 1976) – was used because it permits the inclusion of mixed-type variables (quantitative, factor, and ordered) in the analysis. In this case, the scores of the two first axes were used. This ordination was computed with the dudi.mix function (Dray and Dufour 2007) from the Ade4 package (Thioulouse et al. 1997) for R version 2.9.1 (R Development Core Team 2007).

Connectivity-related variables were derived from aerial imagery (Google Earth, Google Inc.) through visual assessment of river stretches up and downstream from the sampling sites, by registering all the apparently insurmountable barriers in the river channel (Table 2.1). The length of each inspected river segment varied according to the catchment size upstream of the sampling site. Segments of 1, 5, and 10 km were considered when catchment sites were respectively less than 100 km^2, from 100 to 1,000 km^2, and greater than 1,000 km^2. Connectivity reference sites were considered to be those without any influence from barriers, up or downstream, in the selected segment.

In addition to connectivity-related variables, seventeen human-induced pressure variables related to alterations in hydrology, morphology, and water quality (EFI+, see documentation at: http://efi-plus.boku.ac.at/download.htm) were also considered and assigned to different categories (Table 2.1). These variables were assessed using on-site measurements, expert judgment and satellite imagery from Google Earth (Google Inc.). Each set of human pressure variables except connectivity-related variables was then summarized into one dimension using the first axis scores of a Multivariate Correspondence Analysis (MCA).

Table 2.1 – Pressure variables and classification scheme. “No” means that no pressure of that kind was recorded. Parenthesised values state the score given to each of the pressure variable’s classification class.

Pressure type	Single pressure variables	Score
Connectivity	Number of barriers upstream or downstream in the river segment (2 separate variables) (Barriers_Up and Barriers_Down)	No barrier (1) 1km segments =1 (3), >1 (4) 5 km segments <=2 (3), >2 (4) 10 km segments <=3 (3), >3 (4)
Hydrology	Impoundment	No (1), weak (3), strong (5)
	Hydropeaking	No (1), partial (3), yes (4)
	Water abstraction	No (1), weak (3), strong (5)
	Hydrological modifications	No (1), yes (3)
Morphology	Channelization	No (1), intermediate (3), straightened (5)
	U-shaped cross section	No (1), intermediate (3), yes (5)
	Instream habitat alterations	No (1), slight (2), high (5)
	Riparian vegetation alteration	No (1), local (2), intermediate (3), high (5)
	Embankment	No (1), continuous permeable (3), continuous impermeable (5)
	Flood protection	No (1), yes (3)
	Former floodplain	No (1), yes (3)
	Sedimentation	No (1), low (3), intermediate (4), strong (5)
Water Quality	Toxic substances	No (1), intermediate (3), high (5)
	Eutrophication	No (1), low (3), intermediate (4), extreme (5)
	Organic pollution	No (1), weak (3), strong (5)
	Organic siltation	No (1), yes (3)
	Water Quality Index Score	1 (good quality) – 5 (poor quality)

2.3.4. *Data analysis*

Analyses were based on species presence-absence data because abundance is more susceptible to seasonal and annual variations, especially in the case of Mediterranean rivers (Magalhães et al. 2007, Hermoso et al. 2009). Furthermore, the sampling effort was not constant among sites and this could introduce additional bias into some statistical analyses. Three alternative approaches based on Generalized Linear Models (GLM), assuming a binomial distribution of errors and a logit link function (logistic regression), were used to quantify the contribution of connectivity-related variables to each species occurrence. In a first approach the effect of the number of upstream and downstream barriers was tested in conjunction with the available environmental and pressure variables using two alternative model selection procedures based on Akaike's information criterion (AIC; Akaike 1973): a stepwise variable selection and an information-theoretical approach based on the computation of AIC weights (Burnham and Anderson 2002). The stepwise selection procedure was comprised of two steps: (1) a first model selection based exclusively on environmental variables; and (2) a second model selection based on pressure variables (including connectivity-related variables), in which the environmental variables selected in the first step were retained in the second step. The information-theoretical procedure was based on 66 candidate models that were selected following the criteria of both biological significance and non-redundancy of variables. In a second step, candidate models were compared using AIC weights and the final model was selected. The AIC weights sum to 1 for all candidate models and can be defined as the probability that the model would be selected as the best-fitting model if the data were collected again under identical circumstances (Burnham and Anderson 2002). For both model selection procedures, if the connectivity-related variables were retained in the final model, it was assumed that they affected fish occurrence.

A second approach was based on deviations from expected occurrences at sites affected by upstream or/and downstream barriers, using predictive models. This approach was comprised of two steps: (1) adjustment of a GLM for connectivity reference sites using environmental and pressure variables, excluding those related to connectivity; (2) computation of the observed minus the expected values (residuals) for the whole set of sites; and (3) assessment and testing for differences in the residuals between reference and non-reference sites. Model selection was based on the same procedures as those used in the first approach (see previous paragraph), except that only 33 candidate models were considered for the information-theoretical procedure. If the residuals from non-reference sites were significantly more negative than those from reference sites, this would indicate that species tended to be absent from sites affected by upstream or/and downstream barriers, when the model predicted their presence.

A third approach was based on partition techniques and involved estimating the independent contribution of pressure variables to statistical models for species distribution. With this approach it was assumed that the effects of connectivity loss were proportional to the percentage of variation in species data explained exclusively by the number of upstream and/or downstream barriers. A hierarchical partitioning approach was used to quantify the independent (i.e. controlling for natural environmental and other pressure co-variability) contribution of the connectivity-related variables to the occurrence of each species. Hierarchical partitioning involved the computation of the increase in the fit of GLM with a particular predictor compared to the equivalent model without that variable, and averaging the improvement in the fit across all possible models (i.e. considering all possible variable combinations) with that predictor (for more details see MacNally 2002, Quinn and Keough 2002). As a result, for each independent variable, hierarchical partitioning provided an estimate of both the independent contribution and the contribution that was shared with all remaining variables (Chevan and Sutherland 1991).

All statistical analyses were performed with R software version 2.9.1 (R Development Core Team 2009).

2.4. Results

2.4.1. *Potamodromous species*

Variable stepwise selection through AIC did not select any connectivity-related variable for *L. bocagei* but, with a positive contribution, it did select the presence of barriers downstream (Barriers_Down) for *P. polylepis* (Table 2.2). Model selection through AIC weights gave similar results, but the model selected for the nase included the variables for both barriers (Barriers_Up and Barriers_Down) with a positive relationship with the distribution of the species (Table 2.3). The analysis based on residuals showed that there were no significant differences (Mann-Whitney U tests, p>0.05) among reference and non-reference sites (connectivity wise) in the residual values for either *L. bocagei* or *P. polylepis* (Table 2.4 and 2.5). The results of the analysis based on hierarchical variation partitioning (Figure 2.2) showed that the most important variables when it came to explaining the variation for these two species did not include the connectivity variables.

2.4.2. *Resident species*

For *C. paludica*, no connectivity-related variables were chosen with the AIC criteria (Table 2.2), nor was any present in the best (i.e. the most parsimonious) model found through AIC weights (Table 2.3). Conversely, the presence of barriers downstream (Barriers_Down) was chosen by the AIC stepwise selection for inclusion in the model for the distribution of *S.*

alburnoides, with a positive contribution in the model. The most parsimonious model for this species, which was chosen by AIC weights, not only included the variable Barriers_Down with a positive contribution, but also the Barriers_Up variable, in this case with a negative contribution. When the residuals of connectivity reference sites were compared with connectivity-impacted sites, no differences were detected for *S. alburnoides* (Table 2.4 and 2.5), but a significant difference among the model residuals of the two site types (Table 2.4 and 2.5) was found for *C. paludica*. This difference among sites was corroborated by the box and whiskers plots, where some differences are visible (Figure 2.3). The hierarchical partitioning of variation for the resident species showed that the connectivity-related variables are among the least important variables when it comes to explaining the variation in the distribution of the species (Figure 2.2).

Table 2.2 – Species' best model chosen through stepwise AIC variable selection. Each variable is represented with its contribution to the model.

Species	Variables selected in the model (with each variable's contribution)
Potamodromous species	
Luciobarbus bocagei	Slope (-), Precipitation (+), Hidrology (+), Water_Quality (-)
Pseudochondrostoma polylepis	Geomorphology1 (-), Slope (-), Temperature (+), Natural_Sediment (+), Precipitation (+), Hidrology (+), Water_Quality (-), Barriers_Down (+)
Resident species	
Cobitis paludica	Slope (-), Precipitation (-), Temperature (-), Morphology (+), Water_Quality (-)
Squalius alburnoides	Slope (-), Natural_Sediment (+), Temperature (+), Water_Quality (-), Barriers_Down (+)
Exotic species	
Gambusia holbrooki	Geomorphology1 (-), Geomorphology2 (-), Slope (-), Altitude (-), Temperature (+), Morphology (+)
Lepomis gibbosus	Geomorph1 (-), Geomorph2 (-), Slope (-), Precipitation (+)
Gobio lozanoi	Geomorph1 (-), Geomorph2 (-), Altitude (-), Precipitation (+)

Note: Temperature variable corresponds to the scores of the first axis of a PCA using local mean temperature in July and local difference between mean January and July temperature. Altitude variable corresponds to the scores of the first axis of a PCA using mean catchment altitude and local altitude. Geomorphology1 and Geomorphology2 variables correspond to the two first axis of and Hill-Smith ordination PCA using geomorphologic river type, valley form, floodplain extent, distance to source and catchment area. Hydrology, Morphology and Water_Quality each represents the first axis of a MCA using human induced pressure variables present in Table 2.1.

2.4.3. *Exotic species*

In accordance with the results of the stepwise AIC method (Table 2.2), no variables related with connectivity were selected in the models for the three exotic species (*G. holbrooki*, *L. gibbosus*, and *G. lozanoi*). Only the model for the *L. gibbosus* that was most parsimonious by AIC weights included the presence of both barriers upstream (Barriers_Up) and barriers downstream (Barriers_Down), with a negative and a positive contribution respectively (Table 2.3).

Table 2.3 **–** Species' most parsimonious model chosen through AIC Weights criterion, from an *a priori* 66 model batch. Each variable is represented with its contribution to the model.

Species	Variables selected in the model (with each variable's contribution)
Potamodromous species	
Luciobarbus bocagei	Slope (-), Natural Sediment (+), Temperature (+), Hidrology (+), Morphology (+)
Pseudochondrostoma polylepis	Slope (-), Natural Sediment (+), Temperature (+), Hidrology (+), Water_Quality (-), Barriers_Up (+), Barriers_Down (+)
Resident species	
Cobitis paludica	Geomorphology1 (+), Geomorphology2 (+), Precipitation (-), Temperature (-), Morphology (+)
Squalius alburnoides	Geomorphology1 (-), Geomorphology2 (-), Natural_Sediment (+), Precipitation (-), Temperature (+), Water_Quality (-), Barriers_Up (-), Barriers_Down (+)
Exotic species	
Gambusia holbrooki	Geomorphology1 (-), Geomorphology2 (-), Natural_Sediment (-), Precipitation (-), Temperature (+), Morphology (+), Water_Quality (+), Barriers_Up (-), Barriers_Down (+)
Lepomis gibbosus	Geomorphology1 (-), Geomorphology2 (-), Precipitation (-), Temperature (+), Morphology (+), Hidrology (+)
Gobio lozanoi	Altitude (-), Natural_Sediment (-), Hidrology (+), Water_Quality (-)

Note: Temperature variable corresponds to the scores of the first axis of a PCA using local mean temperature in July and local difference between mean January and July temperature. Geomorphology1 and Geomorphology2 variables correspond to the two first axis of and Hill-Smith ordination PCA using geomorphologic river type, valley form, floodplain extent, distance to source and catchment area. Hydrology, Morphology and Water_Quality each represents the first axis of a MCA using human induced pressure variables present in Table 2.1.

The analysis of residuals with variables selected through stepwise AIC showed that there were no differences among the model residuals of the reference and the impacted sites (Mann-Whitney U test; Table 2.4). The residual analysis with the model selected using the AIC Weights criterion detected differences among the model residuals of the reference and the impacted sites for both *L. gibbosus* and *G. lozanoi* (Mann-Whitney U test; Table 2.5; Figure 2.3). Finally, the hierarchical variation partitioning indicated that the connectivity variables were the least important when it came to explaining the distribution of the exotic fish species (Figure 2.2).

Table 2.4 **-** Mann-Whitney U Test between the residuals, reference and non-reference sites, of each species' model, with variables selected through stepwise AIC.

Species	Reference	Non-Reference	U	p-level
Luciobarbus bocagei	9693.5	9612.5	4440.5	0.372924
Pseudochondrostoma polylepis	9499.0	9807.0	4246.0	0.167201
Cobitis paludica	10865.0	8441.0	3976.0	0.039227
Squalius alburnoides	9536.0	9770.0	4283.0	0.197748
Gambusia holbrooki	10025.0	9281.0	4772.0	0.955779
Lepomis gibbosus	10167.0	9139.0	4674.0	0.762298
Gobio lozanoi	10402.0	8904.0	4439.0	0.370899

Table 2.5 **-** Mann-Whitney U Test between the residuals, reference and non-reference sites, of each species' model selected through AIC Weights criterion.

Species	Reference	Non-Reference	U	p-level
Luciobarbus bocagei	9805.0	9501.0	4552.0	0.541882
Pseudochondrostoma polylepis	9453.0	9853.0	4200.0	0.134342
Cobitis paludica	11100.0	8206.0	3741.0	0.007952
Squalius alburnoides	9536.0	9770.0	4283.0	0.197748
Gambusia holbrooki	10729.0	8577.0	4112.0	0.085614
Lepomis gibbosus	11075.0	8231.0	3766.0	0.009567
Gobio lozanoi	10916.0	8390.0	3925.0	0.028500

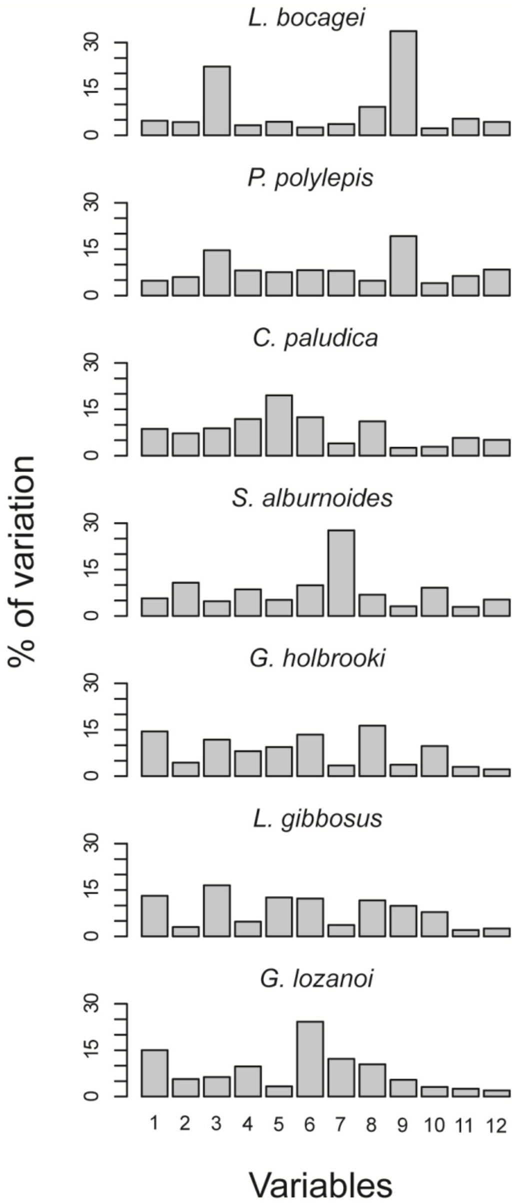

Figure 2.2 – Pure contribution of each environmental variable to the percentage of explained variation of each species distribution using a Hierarchical Variation Partitioning technique. 1 - Geomorphology1, 2 - Geomorphology2, 3 - Slope, 4 - Natural Sediment, 5 - Precipitation, 6 - Altitude, 7 - Temperature, 8 - Morphology, 9 - Hydrology, 10 - Water_Quality, 11 - Barriers_Up, 12 - Barriers_Down.

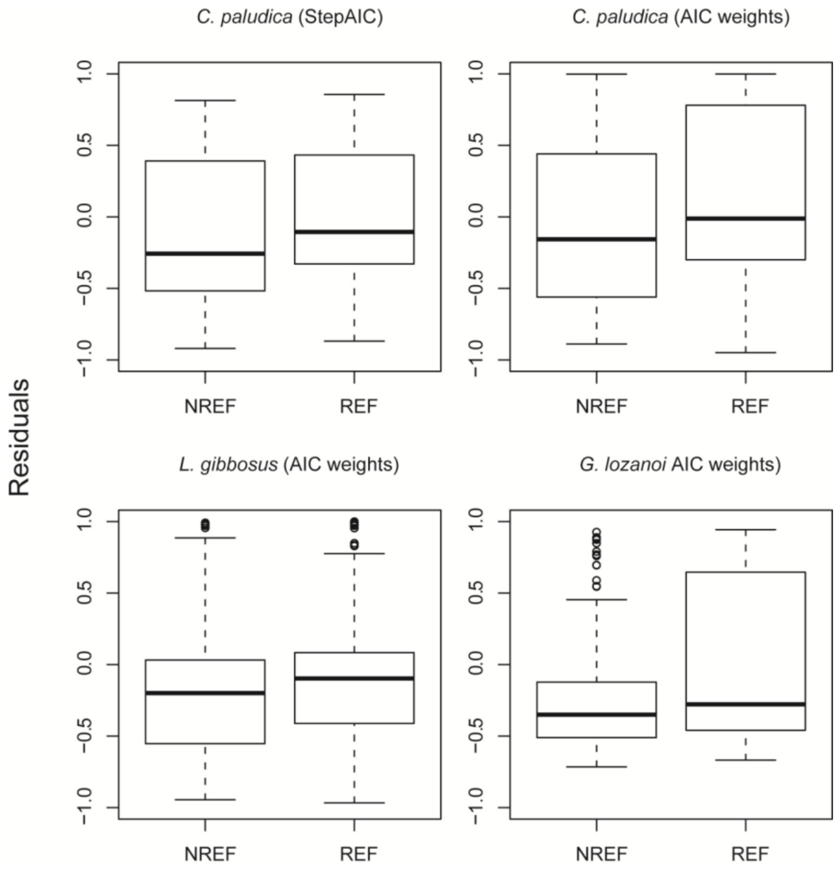

Figure 2.3 – Box and Whiskers plots of the residual analysis. NREF – Non-reference site, i.e. impacted by barriers; REF – Reference site, i.e. not impacted by barriers. On the y-axis zero (0) means no deviation from predicted occurrences, negative (-) values mean that a given species was absent from a site where it was predicted to be present, positive values mean that a given species is present at a site where it was predicted to be absent.

2.5. Discussion

River connectivity is commonly referred to in the literature as being one of, if not the, most important variable for consideration when studying freshwater systems (e.g. Cowx and Welcomme 1998, Roni et al. 2002, Kondolf et al. 2006, Rahel 2007). The connectivity of rivers is based on four dimensions (Ward 1989), but in many parts of the river system the longitudinal component is the most important for freshwater fish species. Unlike other studies, ours particularly attempts to quantify the importance of longitudinal connectivity, based on distinct analytical techniques. Models are simplifications of the ecological reality, and as such, inevitably suffer from limitations. Using more than one model can crosscorroborate or question the results obtained – something that does not happen in the usual approach involving a single data treatment (Segurado and Araújo 2004). The extensive sampling period, the seasonal and annual fluctuations in the numbers of the different species in Mediterranean rivers and the different sampling efforts among sites required the use of presence-absence data (Magalhães et al. 2007, Hermoso et al. 2009) to minimize statistical errors and unweighted sampling.

Results show that tracing the effects of longitudinal connectivity losses in Mediterranean freshwater fish species is a difficult endeavor. None of the methodologies used to determine the distribution of the Iberian barbel – a species with a potamodromous life history, which ought supposedly to be negatively affected by connectivity loss – present a traceable impact caused by transversal barriers. The influence of the barrier variables was only detected for the nase. They were selected as part of the most parsimonious model for this species' distribution. Furthermore, hierarchical variation partitioning showed that the most important variables when it comes to explaining the distribution of both these potamodromous species do not include connectivity variables. The results of the residual analysis show that the influence of barriers was not significant, which means that deviations from the expected probabilities of occurrence did not differ among reference and non-reference sites. These findings contradict the general postulations made for potamodromous species (e.g. Cote et al. 2009, Fullerton et al. 2010).

Due to the fragmentation of their populations, it is also expected that resident native species will be negatively influenced by connectivity losses, albeit to a lesser extent than potamodromous species. In general, the distinct techniques used yielded results that were similar to those of earlier studies, though the residual analysis (Mann-Whitney) of the *Cobitis paludica* showed significant differences, which are noticeable on the box plots comparing the residuals of reference and impacted sites. However, the other methodologies adopted showed opposite trends. The composition of *S. alburnoides* distribution models included barrier variables, but the residual analysis and the variation partitioning demonstrated that these variables are not important to an explanation of the species distribution, or to altering the predictability of the models. For species with a limited home range, connectivity loss should have less effect on species occurrence than local habitat conditions.

Exotic species were expected to be positively impacted by lack of connectivity because the new lentic habitats created along the river act as population sources (Adams et al. 2001, Fukushima et al. 2007, Spens et al. 2007) and flow regulation associated with barriers usually prevents the winter flashing flows that are typical of Mediterranean areas and are assumed to be deleterious to these species. However, the results show that the distribution of the three exotic species studied is not amplified by barriers. Barrier variables were present in the most parsimonious model for *G. holbrooki* distribution, and the residual analysis with model selection through the AIC Weights criterion pointed to the influence of barriers on the distribution of *L. gibbosus* and *G. lozanoi*. However, hierarchical variation partitioning and residual analysis with variable selection through stepwise selection did not reveal any influence of connectivity on fish distributions. In fact, these were the least important variables when it came to explaining exotic fish distribution. *G. lozanoi* is a translocated Iberian species and may be well adapted to summer disconnectivity, while *L. gibbosus* is highly dependent on local habitat conditions and a certain degree of organic pollution (Fox et al. 2007) and is known to prefer lentic-like conditions. This is a highly tolerant and opportunistic species with regard to both feeding and habitat preferences, and is likely to be able to survive most conditions, particularly as a result of the development of population ecomorphs (Vila-Gispert et al. 2007).

In the present study the effect of environment and of other pressures exceeded the isolated effect of connectivity. Most of the barriers we analyzed produce low-depth lentic environments, which make it possible to maintain a certain degree of habitat heterogeneity. This may reflect or mimic natural variability in habitat and/or food availability, thereby explaining the resilience of the studied sites (Santos et al. 2006) in terms of non-significant differences in fish species distributions.

Nevertheless, these results could have been limited/hampered to some extent by a number of factors. The lack of historical data on the species distribution prior to barrier construction precluded a temporal analysis of the data and obliged us to adopt a spatial treatment. Even if it is systematic and always conducted by the same operator, the detection of barriers through airborne imagery is in itself liable to produce errors due to image resolution and to a variable shade effect resulting from different times of day, seasons and angles of view. The present study did not include a field habitat survey extensive enough to evaluate the existence of suitable habitats – namely for the reproduction of potamodromous fish species between barriers – that might limit their need to migrate further upstream to conclude their life cycle (Santos et al., 2006). Remote imagery may be used to map riffle habitats for spawning in the future, but this technology is not readily available at the moment.

Barriers of different sizes were pooled together in the present study. It is reasonable to expect that big barriers, such as dams and small hydropower plants, will be completely insurmountable, but the same cannot be assumed for smaller barriers like small weirs (<2m). When water rises to uncommon levels weirs may be submerged, becoming partly surmountable and ceasing to act as barriers to fish movements (Ovidio and Phillipart 2002). Fish movements are mostly active, but they can also be passive, especially in the larval and juvenile phases, with drifting movements able to recolonize downstream segments. This is especially true during autumn, when river connectivity increases in relation to small obstacles and flashy flows may occur. In fact, connectivity studies focused on potamodromous species ought to incorporate discharge variability, because it governs the extent to which obstacles are transposable (Fullerton et al. 2010). Connectivity studies in Mediterranean rivers also need to incorporate the temporal dimension. Human translocation of fish species has been considered to be an important factor in some cases (Maitland 1987). Indeed, the potamodromous species considered in the present study are appreciated by anglers, as there is no practice of stocking these species in Portugal.

In the last ten years the percentage of publications evaluating connectivity (mostly the impacts of its losses) in ecology-oriented journals increased from 0.5 to 2.5% (Fullerton et al. 2010). Studies focused on connectivity disruption assume that the construction of barriers may cause some populations to be lost, while others become more fragmented, with less movement of individuals between them. In addition to direct impacts on connectivity caused by physical barriers, hydromodification can also disrupt connectivity by dewatering habitats or altering thermal regimes (Fullerton et al. 2010). Many of these studies do not consider connectivity as a measurable effect, but rather as a condition of testing (e. g. Navarro et al. 2007, Benejam et al. 2010). Fullerton et al. (2010) propose that if we are to improve the understanding of hydrologic connectivity for wide-ranging riverine fish, we need to address the river structure dimension (type of river network, type of flow regime, and scale-dependence of the natural connectivity), the temporal dimension (how boundaries change, how individual species react to change, how complex and wide-ranging life cycles are), and the human dimension (intertwined anthropogenic factors and alignment of management goals).

Barriers have an effect on the availability to species of suitable habitats, and many of them also promote flow-regime alteration. The re-establishment of longitudinal connectivity in river systems is therefore one of the goals which the WFD (WFD 2000) proposes in order to obtain a good ecological status (Mader and Maier 2008). In the present study we found that obstacles do not significantly alter species distribution. Other potential effects, such as those on community structure, recruitment and abundance, have to be looked at attentively. In general, these effects may be detected by the biotic or multimetric indices that are being used in the ongoing Europe-wide monitoring of ecological quality, at the community level (see http://www.wiser.eu/). However, it is apparent from the present study that more effort should be put into understanding the effects of connectivity and connectivity loss on freshwater fish species and communities. There are indicators which suggest that a great deal of planning and financial effort will be put into river restoration in the coming decades. It is therefore important to ensure a maximum cost/benefit ratio as ecosystems move towards an ecologically healthier status.

Our general results point towards a shift in the way in which connectivity is seen in large-scale approaches. At this macro-scale barriers may alter community structure, recruitment and abundance, but given that for some of them the blockage may be only intermittent, they do not alter the distribution of fish species.

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Chapter 3

Prioritizing restoration of structural connectivity in rivers: A graph based approach

Aquela senhora tem um piano
Que é agradável mas não é o correr dos rios
Nem o murmúrio que as árvores fazem…
(…)
Alberto Caeiro, XI – "O Guardador de Rebanhos"

3.1. Abstract

Longitudinal connectivity is considered a key issue in river management, as it shapes ecological processes from single organisms to populations and ecosystems. Recently, it was shown that network analysis based on spatial graphs has promising applications as a tool for the assessment of connectivity in riverine systems. In this study we used a graph theory approach to identify which barriers most impacted the structural connectivity of a river basin and which connections should preferably be restored or enhanced in order to effectively improve the overall connectivity. An innovative aspect of the proposed methodology is the consideration of the cumulative non-additive impacts produced by barriers, which are especially relevant to organisms of high mobility such as fish. The portuguese River Tagus basin was used as a case study. The cumulative effect of barriers was studied using two approaches: (1) an historical approach in which the impact of barriers was assessed sequentially following the historical succession of construction; and (2) a "backward" approach in which barriers were sequentially removed according to their impact. The overall structural connectivity of the river basin decreased to about 50% of its original value after the major dams were constructed. Results show that it would be necessary to rehabilitate 11 connections in order to increase the overall structural connectivity to 90% of its original value. This work proposes a novel and straightforward approach to prioritize rehabilitation actions in river systems, providing a promising tool for decision-makers.

Keywords: connectivity, conservation planning, fishes, graph theory, Portugal, restoration, river

3.2. Introduction

Connectivity among landscape elements has long been recognised as a major issue in landscape planning and management for conservation (MacArthur and Wilson 1967, Levin 1974, Merriam 1984, Fahrig and Merriam 1985). The relevance of connectivity, especially longitudinal connectivity, to the ecological processes in rivers has grown in the last decade, since landscape concepts as well as models of metatapopulation dynamics have been extended to accommodate the dendritic nature of river networks (Fagan 2002, Fausch et al.

2002, Ward et al. 2002, Wiens 2002, Grant 2011). Fish communities are affected by longitudinal connectivity not only in ecological processes occurring at the population level, such as gene flow, flux of dispersing individuals and metapopulation dynamics (Minor and Urban 2007), but also at the individuals level, since many fish depend on upstream or downstream migrations to feed, reproduce and find shelter from predators and extreme events (Lucas and Baras 2001, Liermann et al. 2012). The disruption of longitudinal connectivity caused by artificial barriers in rivers is currently thought to be a major threat to freshwater fish communities at the global scale (Humphries and Winemiller 2009). Despite this, approaches to freshwater conservation planning have often disregarded the connected nature of rivers (but see Erös et al. 2011, Hermoso et al. 2011).

The rehabilitation of longitudinal connectivity in rivers was considered a key action for achieving the main ecological goals of the EU Water Framework Directive (WFD 2000/60/CE) (Mader and Maier 2008). Connectivity rehabilitation measures may include actions such as the installation of fishways, the reposition of environmental flow regimes suitable for fish movements or even the removal of insurmountable obstacles. However, because it is not possible to rehabilitate all connectivity barriers due to obvious logistic and financial limitations, it is crucial to find objective scoring and ranking schemes to prioritize restoration targets (O'Hanley and Tomberlin 2005, Kemp and O'Hanley 2010). These simplifications aim at easing the decision-making process while maintaining scientific accuracy (Paul 2003). However, most of the available prioritisation tools for connectivity restoration targets have been restricted to grey literature (Kemp and O'Hanley 2010), or have been proposed for single species at very restricted areas (e.g. Steel 2004). Additionally, the scoring-and-ranking systems that have been proposed only consider the isolated effect of individual barriers, thereby ignoring the cumulative non-additive impacts produced by spatially interconnected structures (O'Hanley and Tomberlin 2005, Kemp and O'Hanley 2010).

The development of methodological frameworks that tackle the specific constraints of riverine structure is one of the most important challenges for understanding the ecological consequences of connectivity for riverine fish (Fullerton et al. 2010). Recently, it was shown that network analysis based on spatial graphs (Urban and Keitt 2001, Minor and Urban 2008, Dale and Fortin 2010, Galpern et al. 2011) has promising applications as a framework for the assessment of connectivity in riverine systems (Schick and Lindley 2007, Erös et al. 2011, 2012). One potential application is the quantitative examination of cumulative effects of barriers, i.e assuming that the effect of one barrier is not independent from the effect of the remaining barriers, an issue that has seldom been addressed at the scale of river networks.

Here we analyse the historical changes on the overall structural connectivity of the Tagus river basin in Portugal, from the first (1928) to the last (2004) major dam to be constructed. Based on this analysis we propose a general methodology using patch-based spatial graphs, which allows to prioritize the targets of connectivity restoration actions taking into account the inter-dependencies among the effects of individual barriers. The main objective is to produce a tool that, along with other tools that deal with river hydrological and morphological alterations, biological effects on populations and community parameters, and socio-economic impacts, will help decision-makers to set management and planning targets.

3.3. Methods

3.3.1. *Study area*

As a case study, we analysed the Tagus river network in Portugal, limited upstream by the Cedillo dam in the Spanish border (Fig. 3.1). The Tagus is the longest Iberian river (700 km), flowing westwards from Central Spain to the Portuguese West coast. Its basin covers an area of 24,800 km2 in Portuguese territory (INAG I.P. 1999). In the period ranging from 1928 to 2004, twenty nine major dams were built in the study area. These structures affected, either directly (connectivity loss, flow alterations) or indirectly (land use changes), the fish fauna (Assis 1990, Godinho and Ferreira 2000).

3.3.2. *Model of the river network topology*

We used a patch-based spatial graph approach (Erös et al. 2012) to model the effects of the major existing dams, following a similar procedure to the one described in Erös et al. (2011). A graph network is represented by *G = (N,L)*, where *N* is a set of *n* nodes connected by *l* links (*L*). Here we defined river segments as habitat patches (nodes), and confluences as links between patches. We considered dams as total barriers to up and downstream movements, therefore splitting the original graph into several components. Dams were located at river segments and therefore corresponded to node deletion. Links among nodes were defined as undirected, i.e., nodes are linked at both upstream and downstream directions, and binary (linked/not linked). Definition of stream segments was based on the GIS riverscape theme CCM2 (Vogt et al. 2007).

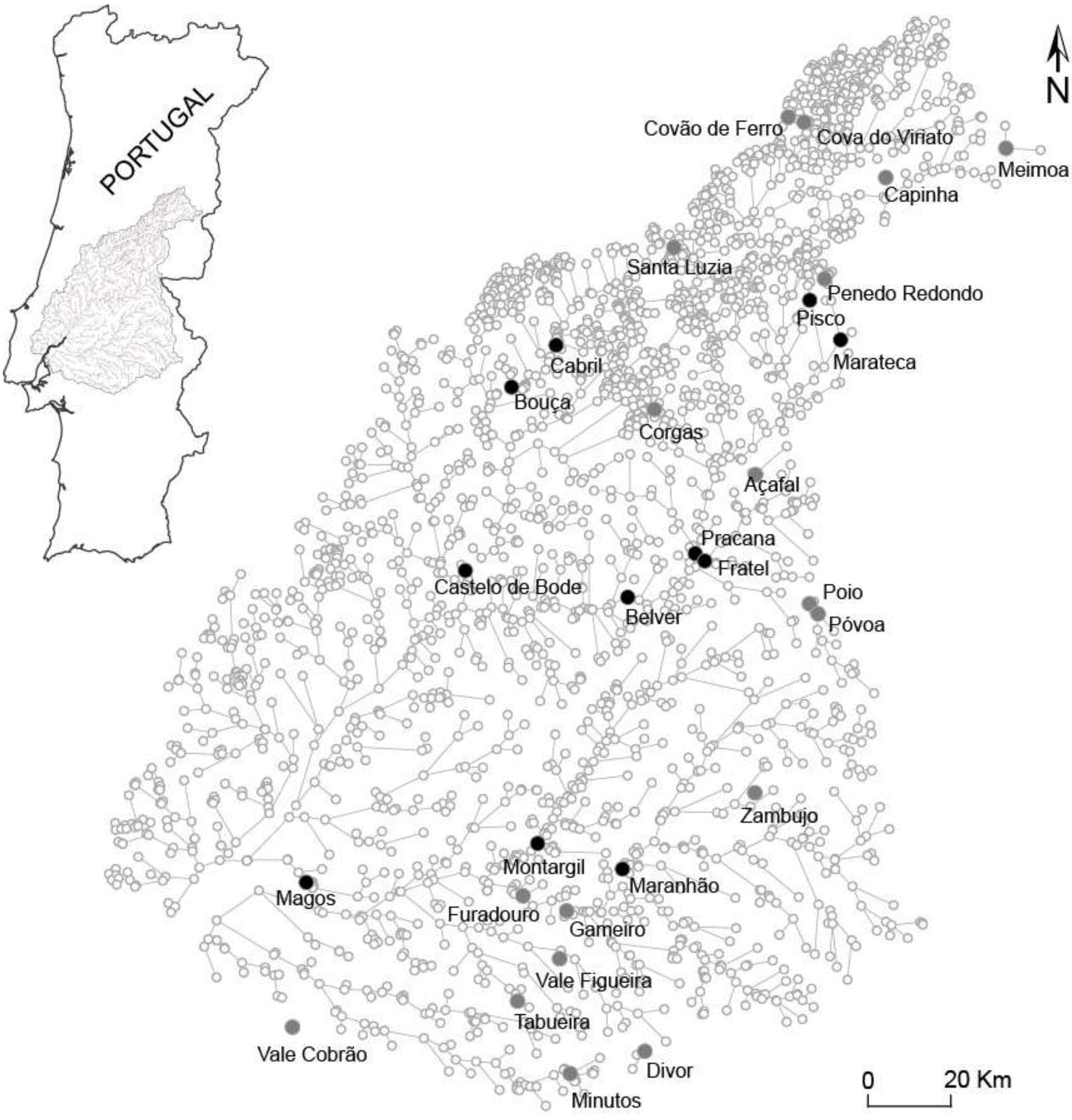

Figure 3.1 - Study area and graph model of the target river basin with the location of the major dams considered in this study (filled circles). Black circles represent the set of eleven dams whose removal would re-establish 90% of the overall connectivity as given by IIC (see results for further details).

3.3.3. *Data analysis*

We used both the Betweeness Centrality (BC) and the Integral Connectivity Index (IIC) as the overall connectivity metrics, which were shown to be among the metrics that capture most of the variability in patch rankings (Baranyi et al. 2011). BC measures the frequency with which a node falls within the shortest path between pairs of other nodes in the network, thereby quantifying the role of patches as “stepping stones” (Minor and Urban 2007). IIC ranges from 0 to 1 and increases with improved connectivity. IIC equals 1 in the case all the landscape is connected and 0 when no connections exist among patches (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007). This index has the advantage of quantifying the importance of habitat patches for maintaining overall landscape connectivity, both through graph structures and habitat availability. It also allows to evaluate the importance of any landscape element or combination of landscape elements for maintaining overall connectivity, which is an aspect that is not accomplished by several of other available connectivity indices (Pascual-Hortal and Saura 2006). In both metrics, the importance of nodes is greatly determined by their positions in the graph. Node importance tends to decrease from central to peripheral sectors in the graph. The connectivity metrics were computed using Conefor Sensinode v2.6 (Saura and Torné 2009, Saura and Rubio 2010).

We used the segment length as a measure of habitat availability, based on the assumption that large habitats usually contain more species with larger and more stable populations (Erös et al. 2011). An important feature of IIC is that it integrates the habitat area existing within patches with the area made available by the interpatch connections into a single measure (Laita et al. 2011). The impact of each barrier on overall connectivity was assessed with two approaches: either considering the isolated effect of each barrier or considering its join effect with the remaining barriers. The isolated effect of each barrier was assessed by computing their specific effect on decreasing the overall connectivity (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007). This was performed in a stepwise fashion by removing one-by-one each node, which we assume to be equivalent to placing barriers, following reposition of the node after each removal step, and computing the percentage of change in the IIC (dIIC) at each step. The joint effect was studied using two approaches. The joint effect was studied using two approaches. First, beginning from the original river graph with no dams we assessed the impact of barriers by removing the nodes neutralized by dams following their temporal sequence of construction. With this approach we were able to assess the historical evolution of the cumulative impact of dams. Then, beginning from the actual fragmented graph containing all the dams, we sequentially removed dams and replaced them with nodes (integral river tracts), with no reposition after each step. This approach followed a descending order of dam restoration impact in connectivity: after each step, the node with the strongest impact in the newly formed graph, as measured by the percentage of IIC increase, was selected to be restored. We stopped the procedure when reached 90% of the original connectivity, that is, the connectivity of the river in absence of dams.

3.4. Results

Since the two measures of connectivity resulted to be highly correlated (Pearson correlation, $r=0.94$, $p<0.001$), we only used IIC to rank the river barriers. The isolated effect of each dam on the overall structural connectivity varied from less than 0.1% to about 20% of the original IIC (i.e., before any artificial barriers were present) (Fig. 3.2a). According to the analysis of the historical impacts of major dams, the overall structural connectivity of the river basin, as measured by IIC, decreased to about 50% of its original value from 1928 to 2004 (Fig. 3.2a). The earliest five big dams (1929 to 1942) contributed only to a decrease of approximately 3% of the overall connectivity. Among the barriers with the strongest impact on the connectivity metrics, two barriers implemented in 1950-1951 contributed to a decrease of approximately 23% of the overall connectivity. The latest fifteen barriers, built from 1959 to 2004, contributed only to a decrease of approximately 2% of the overall connectivity.

There is no direct relationship between the isolated effect and the joint effect of dams, i.e., when considering the dams that already existed in the year of construction (Fig. 3.2a). Nevertheless, the dam that showed the strongest isolated effect (Castelo de Bode), also showed the strongest historical impact and was also the top ranked dam according to the backward procedure for dam rehabilitation prioritization (Fig. 3.2b). However, the barrier with the second strongest isolated effect (Bouça; Fig. 3.2a) showed a very low historical impact (Fig. 3.2b) and was scored in the 7th position according to the prioritization procedure.

The results of the dam ranking procedure based on the backward elimination of barriers indicate that it would be necessary to rehabilitate 11 connections, out of 29, in order to increase the overall structural connectivity to 90% of its original value (Fig. 3.1, 3.2b).

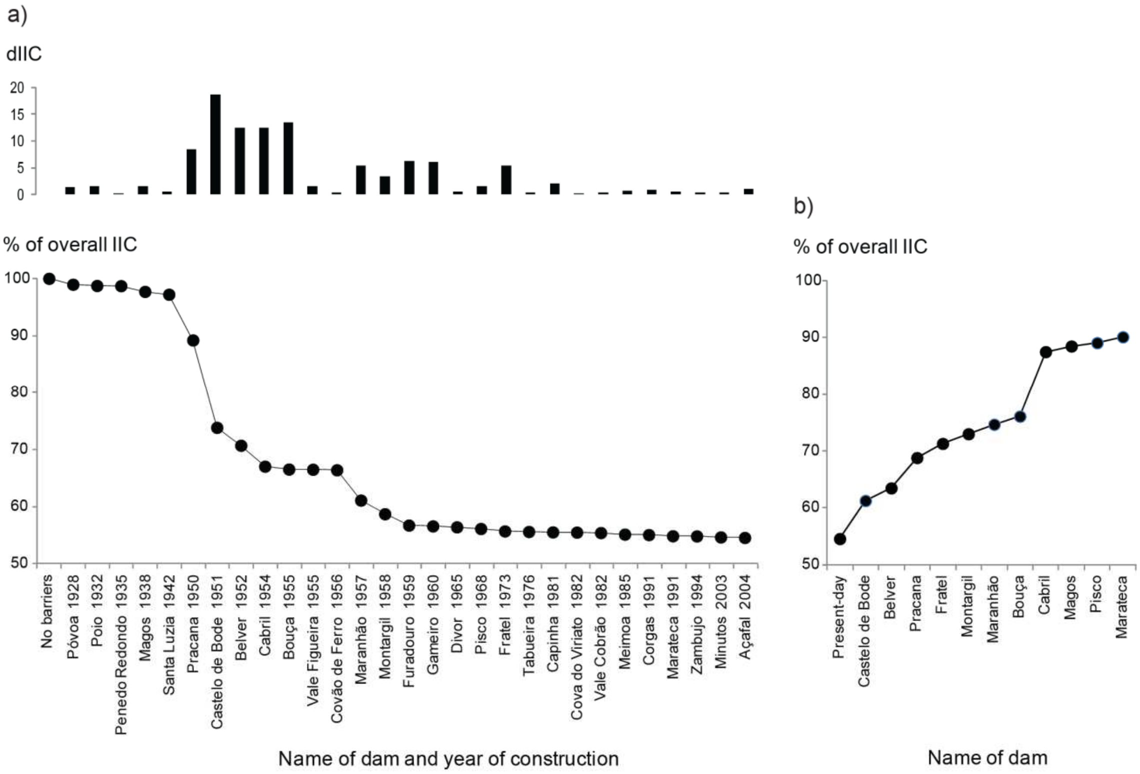

Figure 3.2 – Percentage of change in the overall connectivity (IIC) based on the historical sequence of dam construction, with the isolated effects of each dam shown in the upper barplot (a), and change in the overall connectivity (IIC) based on the "backward" barrier removal procedure (b).

3.5. Discussion

This study provides a general framework for ranking river barriers with the purpose of prioritizing connectivity rehabilitation actions, based in objective and quantitative measures of connectivity. For this purpose we propose the use of a patch-based spatial graph approach, for five main reasons: (1) it possess a large benefit to effort ratio for conservation issues that involve the characterization of connectivity at large geographical extents (Calabrese and Fagan 2004); (2) it is a straightforward approach with an increasing number of freeware computer packages available (e.g. Saura and Torné 2009); (3) it has been increasingly and successfully applied on landscape management and planning for conservation, including aquatic ecosystems (e.g. Schick and Lindley 2007, Erös et al. 2011, Pereira et al. 2011); (4) it allows to prioritize habitat patches in terms of their importance to the overall connectivity (Pascual-Hortal and Saura 2006), and (5), as shown in this study, it allows a direct consideration of the cumulative effect of all existing barriers, which has been pointed out as the main limitation of the existing scoring and ranking schemes for connectivity restoration (O'Hanley and Tomberlin 2005, Kemp and O'Hanley 2010).

In addition, some problems that have been identified concerning inconsistencies among patch prioritizations based on different graph-based measures (Laita et al. 2011) may largely be attenuated in the case of river networks. For example Laita et al. (2011) argue that measures based on the shortest paths (e.g. BC and IIC) may react unpredictably to patch loss since the measures also rate the possible new shortest paths formed in a network. This is not the case of river networks in which, most often, there is only one possible path between pairs of nodes. This property possibly explains the high correlation we found between BC and IIC in the studied riverscape compared to results from other studies focused on 2D landscapes (Bodin and Saura 2010).

In this study the impact of each dam, as measured by IIC, corresponds to its effect on the remaining overall connectivity following its implantation. An important advantage of the proposed methodology, based on variations in IIC, is that it relies on single measures that are quantified in relation to the original (reference) conditions of nonexistent artificial barriers. This feature allows the decision maker to establish restoration goals in terms of the proportion of connectivity gains relatively to the original situation or a desired conservation state. Taking the example of our case study, if the restoration goal would be to achieve 90% of the original connectivity value, it would be necessary to intervene only on 11 of the 29 existing dams. On the other hand, since the proposed procedure allows to quantify the contribution of all stream segments of the river network to the overall connectivity, it can be applied in other decision-making situations such as the selection of sites for the implementation of new structures that may hinder the longitudinal connectivity of rivers (dams, weirs, bridges, roads, etc).

An additional feature of the methodology is that it easily allows to measure the historical impacts of barrier construction on the connectivity of river networks. It may help to improve knowledge about the impacts of dam construction on fish communities by crossing the historical variation of overall connectivity measures with historical data on fish (e.g. fishery data).

In general, due to the ability of IIC to take into account the topological position of nodes, removal of dams located on central sectors of the river network will re-establish a greater amount of connectivity than the removal of dams located in a peripheral position. However, an important result of this study is that no direct relationship was shown to exist between the individual and the joint contributions of barriers to the overall connectivity metrics. This is because the impact of a barrier on connectivity is also very dependent on the location of the barriers that have already been implemented. However, the magnitude of the individual effect of dams is more influential in the first barriers to be implemented. Using simulated dendritic ecological networks, Cote et al. (2009) showed that the biggest losses to connectivity occurred with the addition of the first few barriers in the system. This was true either assuming or not the existence of interference among barriers. According to our results the historical impact of the earliest first few dams was not very strong. This is because their individual effect was low, given their position in the river network. In fact, the first dams to be installed, possibly due to technical and financial limitations, tended to be located in rivers of lower order (upstream) and hence with lower importance in terms of the overall connectivity. The strongest historical impact on connectivity was after the implementation of the first barriers with high individual effect. Similarly to the simulations of Cote et al. (2009), we found that beyond a certain point, subsequent barrier additions have increasingly smaller effects on the connectivity.

There are some caveats when assuming that segment length is proportional to habitat availability. Each river basin and target organism has its own particularities that practitioners should be aware of when applying prioritization schemes such as the one described in this study. For example, segment length naturally decreases from lower to upstream reaches, which may result in the overestimation of the importance of segments located in the mainstream rivers. Typically these sections of rivers are more altered and disturbed than upstream reaches, with nonindigenous species representing a large proportion of species diversity. The use of segment length also does not capture the succession of different guilds of species that occur along the longitudinal environmental gradient.

Nevertheless, the framework proposed may easily be extended to more realistic fish-specific functional connectivity attributes. Instead of considering the segment length in the

IIC computation it is possible to use the outputs of habitat suitability models for a specific species or functional guild, to compute the connectivity index (e.g. Pereira et al. 2011). Different weights can be given to segments, based on different habitat attributes such as suitability for fish spawning, reproduction, feeding activities, etc. Other habitat quality criteria, e.g. based on relationships with biodiversity attributes, may also be used.

In this study, for the sake of simplicity, we only considered hydroelectric dams and other large hydro-modifications which largely represent full barriers to fish passage. However, the implementation of different barrier permeabilities to fish movements within graph-based connectivity metrics is also possible, using connectivity metrics such as the Probability of Connectivity (PC) (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007). This allows extending the proposed framework to smaller barriers that do not totally hamper fish movements. There is also the possibility of considering asymmetrical permeabilities to movement associated to the links among pairs of nodes (Urban et al. 2009, Schick and Lindley 2007), which is the case when small longitudinal barriers are present, often showing a higher permeability in the downstream direction. Asymmetrical links among segments are also important to consider for species or functional guilds with reduced mobility, for example benthic species that are unable to surmount riffle zones in the upstream direction.

Most existing proposed decision-making procedures to prioritise connectivity rehabilitation of barriers, from simple benefit-cost ratio for each individual barrier to more complex optimization models such as the one proposed by O'Hanley and Tomberlin (2005), have been essentially based on three measures (O'Hanley and Tomberlin 2005): (1) the net increase in accessible habitat after barrier removal, in terms of quality-weighted area or river length, (2) degree to which a barrier impairs movement, and (3) cost of repair. However the proposed schemes have neglected the contribution of disrupted links to the overall connectivity of the river network. Barriers that are located at key river reaches, in terms of their contribution to the overall integrity of the river network should also be favoured in prioritization schemes. This study provides an innovative approach to accommodate this parameter within a methodological framework aiming to prioritize connectivity enhancement/rehabilitation actions in river networks.

In order to allow a more fine approach to connectivity enhancement, future works should consider the integration of the proposed methodology with a cost benefit analysis, incorporating thus the balance between environmental and socioeconomic goals, allowing a tangible implementation of concrete rehabilitation actions.

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Chapter 4

Dam selection to enhance functional connectivity of river networks for fishes

"The saddest aspect of life right now is that science gathers knowledge faster than society gathers wisdom."

Isaac Asimov

4.1. Abstract

Freshwater systems are severely impacted by connectivity reduction due to the construction of dams and weirs. The breach of this longitudinal connectivity imperils freshwater fish species worldwide. There is thus an increasing need for numerical tools that help decision-makers to correctly allocate resources to priority restoration actions. This study provides a methodology for prioritizing the removal of barriers. It is based on spatial graphs, which represent structural units as nodes and relationships between them as links, and uses habitat suitability modeling (Boosted Regression Trees) to weight nodes. To exemplify the application of this procedure we used the Tagus river network and evaluated the impact of the dams in it (29 built between 1928 and 2004) on the occurrence of each of two fish species (Iberian barbel *Luciobarbus bocagei* – representing large potamodromous fish; and Iberian chub *Squalius pyrenaicus* – representing small water-column residents) and on the combination of both. Results show that dam construction on the Tagus was responsible for a 49.8 – 54.3% reduction in connectivity. Actions to promote connectivity in 7 of the implanted dams would increase connectivity by 37.1 – 40.1%. This prioritization method makes it possible to model the impact of the removal or placement of an insurmountable barrier in a river network, facilitating resource allocation and minimizing the impact of new barrier implantation.

Keywords: longitudinal connectivity, stream fish, connectivity enhancement, dam removal, prioritization method, river restoration, spatial graph, habitat suitability, boosted regression trees

4.2. Introduction

Riverine environments are among the most endangered environments on Earth (Naiman and Turner 2000, Sala et al. 2000, Gleick 2003). Connectivity can be understood as the functional “exchange pathway of matter, energy and organisms” (Ward and Stanford 1995). Its most important role for freshwater fish species lies in its longitudinal dimension. The origins of the longitudinal connectivity concept are to be found in the river continuum concept (Vannote et al. 1980). It is interrelated with the theory of habitat fragmentation (Andrèn et al. 1985, Wilcove et al. 1986, Dickman 1987, Noss and Csuti 1997) and the notion of ecological corridors (Forman and Godron 1986). A breach of this longitudinal connectivity leads to isolation (Moilanen and Nieminen 2002), which is one of the most pressing factors influencing species distributions (MacArthur and Wilson 1967, Levin 1974, Merriam 1984, Fahrig and Merriam 1985). Connectivity interruption has led to declines in the populations of half of the threatened European fish species (Northcote 1998), by affecting fish movements for reproduction, feeding and habitat colonization, which in turn leads to potential genetic impoverishment and loss of population portions, while probably promoting the dispersion of exotic fauna (Branco et al. 2012). In order for a body of water to achieve good ecological status, which is the main goal of the Water Framework Directive (European Commission 2000), the re-establishment of the system's longitudinal connectivity should be seen as a priority (Roni et al. 2002, Mader and Maier 2008).

Connectivity can be divided into structural and functional connectivity: structural connectivity refers to the physical relationships between structural elements (habitat patches, segments, etc.) (Keitt et al. 1997); functional connectivity, on the other hand, accounts for the response of the biological element (species, population, etc.) to the landscape structure and the landscape matrix (Tischendorf and Fahrig 2000, Taylor et al. 2006). The best method for reconnecting dam-fragmented systems is the removal of instream structures (Roni et al. 2002) – an endeavor that is usually impractical due to the high financial costs involved and to the loss of important services (flood control, irrigation and water supply) provided by these structures. A more realistic solution is connectivity enhancement via the implantation of fish transposition devices that allow fish to move both up and downstream freely, while accommodating an environmental flow. Nevertheless, both these options are increasingly being used to restore connectivity in rivers and streams (Bednarek 2001, Hart et al. 2002, Calles and Greenberg 2005), and are preferable to habitat enhancement solutions where avoiding population isolation is concerned (Auer 1996). However, when budget limitations exist there is a need to prioritize restoration actions. Numerical methods are increasingly being used to simplify data (Spellerberg 1993, Olivier and Beattie 1994, Graça and Coimbra 1998, Harris and Silveira 1999, Ladson et al. 1999). These methods aid the decision-making process while maintaining scientific accuracy (Knapp et al. 2003, Karr and Chu 1999, Paul 2003). The existing scoring-and-ranking systems only take into account the impacts of isolated barriers, neglecting the cumulative non-additive impacts of all barriers in a network (O’Hanley and Tomberlin 2005, Kemp and O’Hanley 2010). Additionally, most programs that prioritize actions for restoring connectivity do so primarily in order to increase connected river length (Mader and Maier 2008, Kocovsky et al. 2009), neglecting the habitat suitability/availability increase for each species or even for the community, and thus favoring structural connectivity over its functional counterpart.

Graph theory is based on simple concepts, and treats spatial elements as nodes and the relationship between nodes as links (Dale and Fortin 2010). Spatial graphs are a special case of graph theory in which the nodes have locations and links are defined by those locations (Fall et al. 2007). Approaches based on spatial graphs have been extensively used in landscape scale studies (Urban and Keitt 2001, Minor and Urban 2008, Dale and Fortin 2010, Galpern et al. 2011). However, recent works have extended this technique to rivers (Schick and Lindley 2007, Erös et al. 2011, 2012), and this has proved an excellent tool for assessing the connectivity of river networks. Graphs make it possible to look at a network from two perspectives: a backwards approach, understanding how the network became divided (Keitt et al. 1997, Bunn et al. 2000, Urban and Keitt 2001); and a forward approach, understanding how potential restoration actions would result in connectivity increases (Palmer et al. 2005). This technique creates the opportunity to study the non-additive cumulative effects of the barriers in a system on the reduction in connectivity by taking into account not only the isolated effect of each barrier, but also the joint effect of all barriers.

The present study aimed to provide a general spatial graph-based framework for prioritizing connectivity restoration actions. To accomplish this, a case study based on the Tagus river network was used, and the dams therein (29 built between 1928 and 2004) were evaluated considering both their chronological impact and the gains in river connectivity after their removal. This procedure made it possible to rank the dams by priority for removal, taking into account the gains in the functional connectivity of rivers for two fish species with very distinct life histories: the Iberian barbel *Luciobarbus bocagei* – representing the guild of large potamodromous fish; and the Iberian chub *Squalius pyrenaicus* – representing the guild of small water-column residents. A ranking scheme was developed for each species separately, and for the combination of the two.

4.3. Methods

4.3.1. *Study area*

The study area for the proposed case study comprised the Portuguese portion of the Tagus river basin, limited upstream by the Cedillo dam, which is located just across the border in Spain (Fig. 4.1). The Tagus river and its basin extend across 1,070 km of Portugal and Spain. They represent the largest basin on Portuguese territory and the third largest in the Iberian Peninsula, with an area of c. 80,000 km^2, of which 24,800 km^2 are in Portugal (INAG I.P. 2012). The river flows westwards towards the Atlantic coast, presenting a marked seasonal and inter-annual variability, and has been modified by dam construction since the first quarter of the 20th century. These barriers – 29 in total – have impacted fish populations by causing extirpation of or significant declines in many diadromous species, such as the shads *Alosa* spp., the sea lamprey (*Petromyzon marinus*), and the European eel (*Anguilla anguilla*). Similar decreases in native potamodromous species have been recorded following the construction of many of the barriers along the Tagus (Assis 1990, Godinho and Ferreira 2000).

4.3.2. *Species selection*

Mediterranean rivers are dominated by cyprinid fishes, ranging from large benthic potamodromous to small resident pelagic species. This diversity is accompanied by a multitude of morphologic and ecologic variations (Ferreira et al. 2007). Morpho-ecologically similar species can be grouped into guilds – assortments of organisms free of taxonomic strings that use a common array of resources (Fauth et al. 1996), where a single species can be used as representative of a given morpho-ecological guild (Chan 2001). This method is suitable for multi-specific approaches (Leonard and Orth 1988). In this study a habitat/migration functional-guild approach was adopted (Musil et al. 2012), the Iberian barbel (*Luciobarbus bocagei*, barbel hereafter) represented the guild of large potamodromous (obligatory reproduction migrations exclusively in freshwater) benthic cyprinids, and the Southern Iberian chub (*Squalius pyrenaicus*, chub hereafter) represented that of small water-column resident cyprinids.

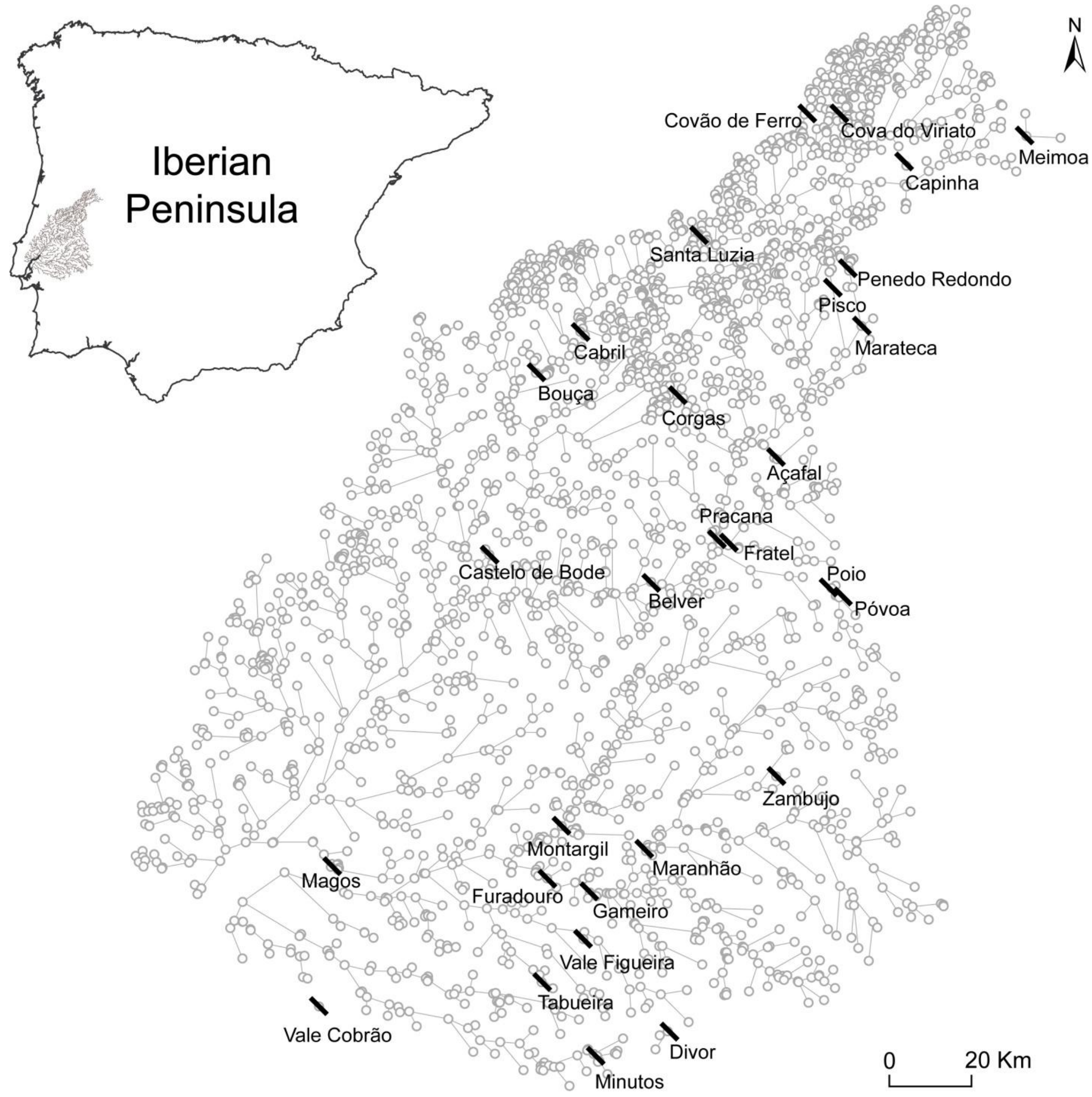

Figure 4.1 – Study area and representation of the graph model of the Tagus river network. The dams considered in this study are represented as black bold lines (****).

4.3.3. *Fish sampling*

A total of 456 sites within the species distribution range were sampled between 1996 and 2012. The sampling was performed by electrofishing – the least biased method for fish sampling (Cowx 1989) – following procedures similar to the one adopted by the European Committee for Standardization (CEN norm 14011 March 2003). Each site was sampled only once, and the fishing team progressed upstream in a zigzag pattern with single passes covering all present habitats (riffles, pools) and collecting fish with a dip net. Fish were then placed in a container filled with river water, identified to the species level and returned alive to the river.

4.3.4. *Habitat suitability modeling*

Data analysis was based on presence-absence data, which is less susceptible to inter-season and year variations, particularly for Mediterranean systems where intra and inter-annual variability is high (Magalhães et al. 2007, Hermoso et al. 2009). Additionally, this data transformation reduces the bias present in abundance data analyses when the sampling effort has disparities between sites, homogenizing data and increasing the accuracy and predictability of the analyses. The Tagus river network was divided into its constituent segments, a segment being a stretch of river between confluences. The river network segmentation followed the GIS riverscape theme CCM2 (Vogt et al. 2007) and defined 2,542 river segments.

In order to estimate the potential habitat suitability of each species in each of the river segments in the study area, fish sampling data were modeled using Boosted Regression Trees (BRT) to develop a predictive habitat model (Guisan & Zimmermann 2000). BRT is an ensemble methodology that fits statistical models in a way that differs from the traditional single parsimonious model-fitting techniques. Its strength relies on the combination of two techniques: (i) regression trees – which use recursive binary splits to adjust the response to its predictor variables; and (ii) boosting – a method that combines several models to improve predictor capability. BRT has the advantage of being able to handle several types of variables and to accommodate missing values without the need for data transformation or outlier deletion. BRT can even cope with collinearity and non-linear relationships between predictor variables (Elith et al. 2008).

To fit BRT models we followed the procedure recommended by Elith et al. (2008): in order to optimize the number of trees, we carried out a stepwise process based on 10-fold cross-validations using the area under the Receiver Operational Curve (AUC; Fielding and Bell, 1997) as the accuracy measure. The AUC assesses how far from chance the model predicts species occurrence, varying from 0.5 (random classification) to 1 (perfect classification). Two important parameters determine the number of trees required for optimal predictions: the learning rate (*lr*), which determines the contribution of each tree to the growing model; and the tree complexity (*tc*), which controls the number of interactions among variables (i.e., the number of splits of individual trees). We set *lr* and *tc* to 0.003 and 3, respectively, which are within the suggested range for the data set size and ensured that at least 1,000 trees were achieved after the stepwise process, as recommended by Elith et al. (2008). The BRT models were then used to predict (using segment and catchment scale variables – Table 4.1) the probability of occurrence (between 0 and 1) for each species in each river segment in the Tagus river network. These probability values were considered surrogates for habitat suitability. To estimate the habitat suitability of each segment for the combination of the two studied species, the respective probabilities of occurrence were multiplied. The resulting values favor segments with high probability values for both species and penalize segments with low probability values for one, and especially both, species.

Habitat suitability models were based on 29 environmental variables, including 5 variables compiled at the segment scale and 24 variables compiled at the watershed scale associated with each segment (Table 4.2). Only regionalized variables were used in habitat suitability models, in order to allow predictions for non-sampled segments. We integrated all the information using the CCM2 river network database (Vogt et al., 2007). This database includes two main GIS themes: river segments (line theme); and the respective associated watershed (polygon theme). Except for the five landcover variables, all variables were readily available in the CCM2 database, including segment hydromorphologic features, topography and climate. Landcover variables were compiled from Corine Land Cover 2006 (EEA, 2010), by computing the proportion of area occupied by each relevant landcover type (Forest, Non-irrigation crops, Irrigation crops, Agro-forestry systems and Urban) in the watershed polygons linked to each segment.

Variable extraction was performed at both the segment and catchment scales using the ArcGis 10.0 software. BRT habitat suitability modelling and prediction were performed in R 2.15.1 (R Development Core Team, 2012), using the gbm (Ridgeway 2007) and dismo (Elith et al. 2008, Hijmans et al. 2013) packages.

4.3.5. *River network topology*

In order to understand the effects of dams as river longitudinal connectivity fragmenting structures, we used an approach based on spatial graph theory (Fall et al. 2007, Erös et al. 2012), where the graph network is represented by *G = (N,L)*, where N represents a set of n nodes and L a set of l links (Erös et al. 2011). In the proposed methodology, river segments were represented as nodes and confluences as links. Dams were placed at river segments (nodes) and considered to be insurmountable barriers (impervious to fish movements in both directions) that broke up the original network into sub-networks. Each node was attributed its suitability score (derived from BRT) and the connection between nodes was considered to be binary (linked/unlinked) and undirected (connected both upstream and downstream).

In this graph-based approach the Integral Connectivity Index (IIC) was used as the overall connectivity metric. The IIC measures the degree of connectivity of a given network, increasing with augmented connectivity and ranging from 0 – no connection between landscape elements – to 1 – full connection of the landscape elements (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007). Unlike several connectivity indices, this metric has the advantage of evaluating the importance of landscape elements, individually or in combination, to the maintenance of the system’s connectivity (Pascual-Hortal and Saura 2006). It quantifies a segment’s importance using both graph structures and habitat availability/suitability.

Of the various connectivity metrics, Baranyi et al. (2011) consider that the IIC and another commonly used metric – the Betweeness Centrality (BC) (Minor and Urban 2007) – as encapsulating most of the variability in patch ranking. However, these two metrics were shown to be highly correlated in river networks (author’s unpublished data) and, in order to simplify the overall procedure, the BC was therefore not computed. The IIC was computed using Conefor v2.6 (Saura and Torné 2009, Saura and Rubio 2010).

4.3.6. *Prioritizing dam removal*

Firstly, in order to understand how dam construction incrementally impacted fish habitat availability and connectivity, we pursued a historical approach in which the impact of barriers was determined by following the temporary sequence of dam building, removing nodes (placing dams) sequentially until the current situation (29 dams) was achieved. Secondly, so as to prioritize connectivity restitution, we used the actual scenario as the starting point and added nodes (removing dams) in a backwards stepwise manner. We performed this stepwise approach by iteratively removing dams at each step, with reposition after each removal, in order to determine the isolated effect of removing a single dam. Afterwards, at each step, the dam whose removal had a higher positive impact on overall connectivity, measured as the percentage of IIC increase, was removed permanently and the process repeated until connectivity was 100% re-established.

Table 4.1 – Year of construction and principal characteristics of the dams implanted in the Tagus River network, with indication of the ranking order of removal for each species and for the combination of the two (Both). HAF – height above foundation; Area – flooded area; Service – service provided by the dam.

					Order of removal		
Name of the dam	Year	HAF (m)	Area (Km^2)	Service	Barbel	Chub	Both
Póvoa	1928	32	2.36	Energy	19	21	17
Poio	1932	18	1.1	Energy	18	20	16
Penedo Redondo	1935	21	0.0094	Water supply	28	26	26
Magos	1938	17	0.9	Irrigation	11	9	9
Santa Luzia	1942	76	2.46	Energy	14	8	8
Pracana	1950	60	5.5	Energy	4	6	6
Castelo de Bode	1951	115	32.91	Water supply/Energy/Flood control/Recreation	1	1	1
Belver	1952	30	2.86	Energy	3	5	5
Cabril	1954	132	20.23	Energy	7	2	3
Bouça	1955	63	5	Energy	6	3	2
Vale Figueira	1955	13	NA	Irrigation	27	28	27
Covão de Ferro	1956	32.5	0.065	Energy	29	23	28
Maranhão	1957	55	19.6	Irrigation/Energy	8	15	13
Montargil	1958	48	16.46	Irrigation/Energy	2	4	4
Furadouro	1959	17	0.065	Irrigation	9	13	11
Gameiro	1960	20	0.072	Irrigation/Energy	10	14	12
Divor	1965	23	2.39	Irrigation	17	24	21
Pisco	1968	24.5	0.198	Water supply/Irrigation	15	11	14
Fratel	1973	48	10	Energy	5	7	7
Tabueira	1976	23	0.46	Irrigation/Water supply/Recreation	21	25	23
Capinha	1981	18	0.097	Water supply/Irrigation	24	22	22
Cova do Viriato	1982	28	0.235	Water supply	26	17	25
Vale Cobrão	1982	20	1.1	Irrigation	23	27	24
Meimoa	1985	56	2.22	Irrigation/Water supply	22	16	19
Corgas	1991	30	0.11	Water supply	16	12	15
Marateca	1991	25	6.34	Water supply/Irrigation	12	10	10
Zambujo	1994	24	0.37	Water supply	25	29	29
Minutos	2003	36	5.3	Irrigation	13	18	20
Açafal	2004	29	0.2	Irrigation	20	19	18

Table 4.2 – Variables used to model species habitat suitability at different spatial scales.

Scale	Name	Discription
Segment	Strahler1	Order number of the river segment
	Length	Length of the river segment (m)
	Cum_len	Cumulative length of the upstream network (m)
	Drain_km2	Area drained by the river segment (km^2)
	Alt_gradie	Relief energy of the river segment (%)
Watershed	Strahler	Order of the primary catchment
	Area_km2	Area of the catchment (km^2)
	Perimeter	Perimeter of the catchment (Km)
	Elev_min	Minimum elevation in the catchment (m)
	Elev_max	Maximum elevation in the catchment (m)
	Elev_mean	Mean elevation in the catchment (m)
	Elev_Range	Elevation range in the catchment (m)
	Slope_min	Minimum slope in the catchment (%)
	Slope_max	Maximum slope in the catchment (%)
	Slope_mean	Mean slope in the catchment (%)
	Slope_Range	Slope range in the catchment (%)
	Rain_min	Minimum long-term average annual precipitation in the catchment (mm)
	Rain_max	Maximum long-term average annual precipitation in the catchment (mm)
	Rain_mean	Mean long-term average annual precipitation in the catchment (mm)
	Rain_Range	Range of long-term average annual precipitation in the catchment (mm)
	Temp_min	Minimum long-term average annual temperature in the catchment (mm)
	Temp_max	Maximum long-term average annual temperature in the catchment (mm)
	Temp_mean	Mean long-term average annual temperature in the catchment (mm)
	Temp_Range	Range of long-term average annual temperature in the catchment (mm)
	Forest	Proportion of forest area in the catchment
	Non irrigation crops	Proportion of non-irrigation crop fields in the catchment
	Irrigation crops	Proportion of irrigation crop fields in the catchment
	Agro-forestry systems	Proportion of agro-forestry systems in the catchment
	Urban	Proportion of urbanized cover in the catchment

4.4. Results

According to the graph model of the current topological connectivity of the Tagus network (Fig. 4.1), each dam – each of which represents a complete barrier to fish passage – divided the original fully connected Tagus river network into several sub-networks. The BRT modeling technique made it possible to produce habitat suitability maps (Fig 4.2) that corresponded to the probability values of the occurrence of a given species predicted for the whole set of river segments. These probabilities can be interpreted as surrogates for the ability of a river segment to sustain the species. The resultant maps are directly influenced by the physical habitat present in each of the river segments. The results of the cross-validation (AUC – 0.825 and 0.863 for the barbel and chub, respectively) indicate that the models presented a good predictive ability. The resulting habitat suitability map for barbel (Fig. 4.2a) shows that this species has a wide homogeneous distribution, occurring in large river segments, and a limited probability of occurrence at low order number streams near the extremes of the network. The chub on the other hand (Fig. 4.2b) presents a more localized potential distribution, occurring in the northern portion of the Tagus river network, especially small tributaries, and having a low affinity with high order number river segments. When the probability of occurrence of both species is combined by multiplication (Fig. 4.2c), the northern portion of the Tagus network is clearly the primary area for the sympatric appearance of both species. Here, the intermediary segments gain preponderance over high and low order number segments.

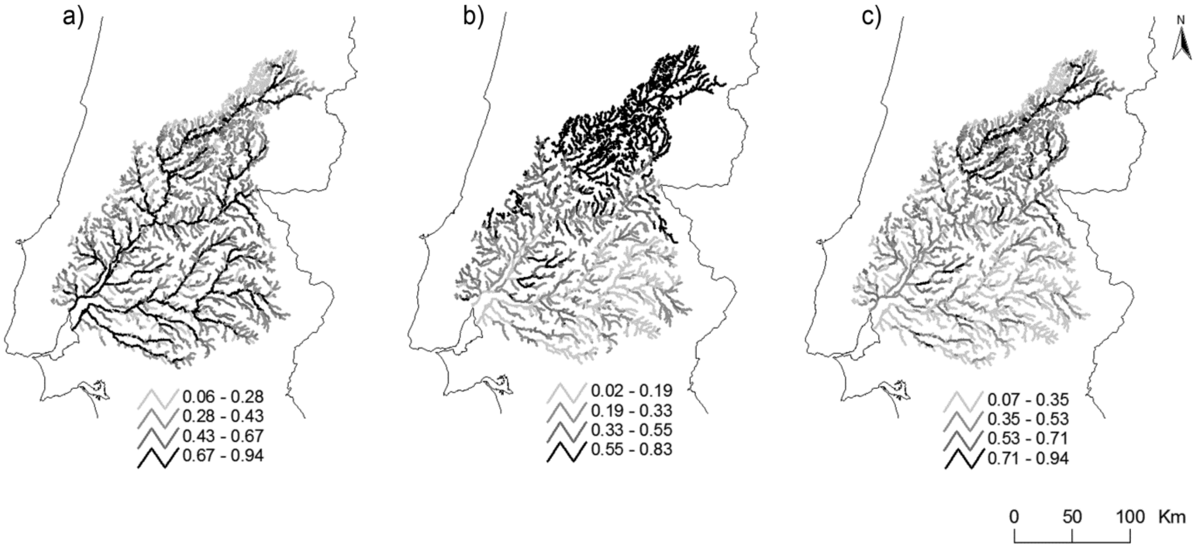

Figure 4.2 – Map representation of the habitat suitability models, expressed as modeled probability of occurrence (0 to 1), of the Tagus river network for the: a) Barbel, b) Chub, c) combination of the two species.

The construction of dams had a clear impact on the connectivity of the Tagus river network (Fig. 4.3). The current 29 dams have produced an overall connectivity reduction (measured as the variation in IIC) of 54.3% for the barbel, 49.8% for the chub, and 50.8% for both species combined. It is also shown that, besides the similarity in the overall connectivity reduction between species, the general pattern of reduction was also very similar. The first five dams to be placed had little impact (2.3 to 3.3% of overall IIC variation), while the following four had a large impact (38.4 to 41.5% of overall IIC variation). The remaining 20 dams had a comparatively low impact on connectivity, being responsible for just 6.4 to 13.6% of overall IIC variation.

The backwards-stepped process of dam removal elected dams with a different sequence for barbel, chub, and both species combined (Table 4.1). However, the order of removal was still highly correlated between species (Spearman Rank Order Correlation Rho = 0.88, $p < 0.01$) and between both species and the combination of the two (Both) (Spearman Rank Order Correlation Rho: Barbel x Both = 0.94, $p = 0.01$; Chub x Both = 0.95, $p = 0.01$). Corroborating this, the first dam to be chosen for removal was Castelo de Bode according to all three approaches. These correlations are even more evident when looking at the first 7 dams to be removed. Although not in the same order, they are the same for the three cases. Their removal constitutes a large connectivity increase (37.1 to 40.1% of overall IIC variation), while the remaining 22 dam removals only accounted for 10.7 to 17.2% of overall IIC variation. According to the stepped increase in overall IIC variation for the two species and for the combination of both (Fig. 4.4), the general pattern of overall IIC variation is similar among the three cases. There is a rapid increase in IIC until a point at which the variation flattens, at around the seventh dam removed. Nonetheless, the barbel’s pattern of variation differs slightly from the other two patterns (chub and Both), which display a closer variation, especially between the third and the ninth removals.

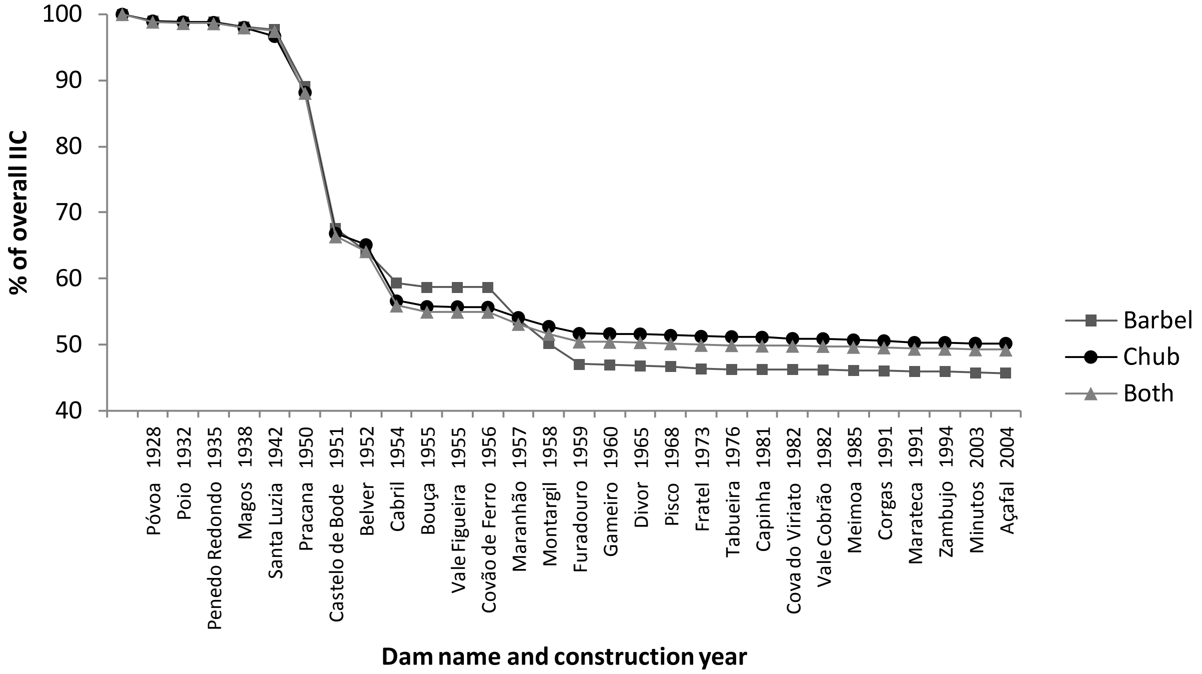

Figure 4.3 – Percentage of change in the overall connectivity (IIC) of the Tagus river network following the chronological sequence of dam construction.

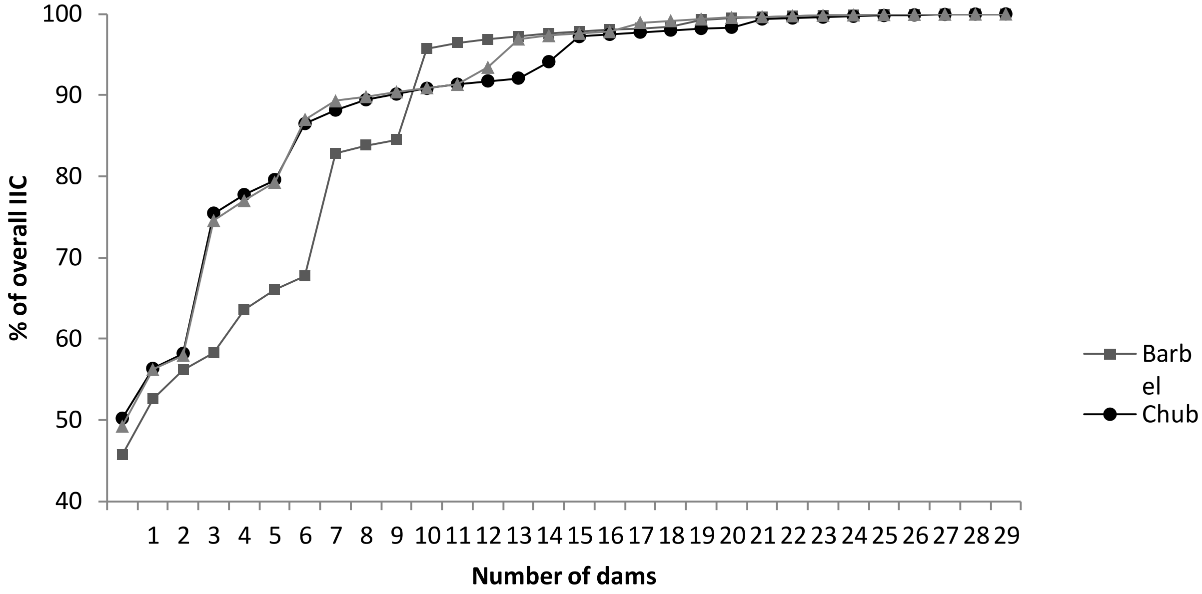

Figure 4.4 - Percentage of change in the overall connectivity (IIC) of the Tagus river network following the barrier removal sequence defined by the step-wise procedure.

4.5. Discussion

Numerous studies have documented dramatic changes in the persistence and abundance of fish populations as a result of human-induced disturbances, particularly dam construction (Marmulla 2001). Dams can block or delay fish movements and are responsible for the decline or extirpation of many native species throughout Europe (Mader and Maier 2008). Rivers represent a particular case of spatial graph analysis, since the network is already defined and rivers have a high degree of directionality imposed by flow. In addition – and contrary to landscape level analysis, in which protection provided by hubs (group of highly connected nodes) means that some networks are able to maintain connectivity even with the loss of several nodes (Urban and Keitt 2001, Barabasi and Bonabeau 2003) – river network connection suffers severely from node loss, due to the lack of alternative paths. The present article provides a new spatial graph-based approach that will help decision-makers to prioritize connectivity restoration actions in such a way as to help systems recover from past human-induced impacts. This method offers major advantages: it is a direct approach using spatial graphs that have proven to apply well to aquatic environments (Schick and Lindley 2007, Erös et al. 2011, 2012, Pereira et al. 2011); it is able to incorporate habitat suitability of a single species or a group of species into overall connectivity availability; and finally, it uses simple free software (Ridgeway 2007, Saura and Torné 2009, Saura and Rubio 2010, R Development Core Team 2012, Hijmans et al. 2013).

The results from the Tagus river network case study show that the barriers' impact on overall connectivity was higher (albeit only slightly) for the barbel. This was due to the more restricted (localized) distribution of the chub. Its wider distribution and a strong link to larger segments mean the barbel suffered a more pronounced overall impact, as dams tend to be built in larger river segments. Contrary to expectations, we verified that the first five barriers to be constructed had a small impact on overall connectivity. This differs directly from the results described by Cote et al. (2009), in which the largest losses of connectivity occurred on the implantation of the first barriers. However, the results of Cote et al. (2009) were established on the basis of a theoretical simulated network that lacked habitat analysis. The contradictory results support the need to include habitat analysis when developing conservation plans with a view to improving river connectivity. Although structural connectivity is an important overall river attribute, functional connectivity needs to be evaluated when connectivity restoration actions are focused on specific targets. The fact that the first barriers to be constructed had little impact on the overall connectivity of the Tagus river network proves that the correct placement of barriers will drastically reduce the impact of these structures on overall connectivity for freshwater fish species. Our work shows that dams produce a real decrease in the longitudinal connectivity of a river network, and that although the extent of this decrease varies among target species, in overall terms it is generally the same. The ability of potamodromous migrants to use the available habitat between barriers explains why these species were not substantially more affected than the resident species (Branco et al. 2012). BRT proved to be quite a robust technique, producing predictive models with substantial accuracy. This methodology's plasticity and robustness made it possible to predict the suitability of each segment of the network for each of the studied species. This technique has applications that can be extended to management problems, identifying areas of conservation priority and facilitating the definition of fishery areas.

When defining the ranking order of dams for removal, there was a variation among species. Even though we found the same general pattern of variation in connectivity metrics following removals, dams had different degrees of impact on the different target species. When applying this methodology in order to prioritize dam removal, attention must be paid to the purpose of the restoration. The latter has to be targeted at a species or group of species, always bearing in mind that this approach is case-specific, and that although the results may be similar, they are specific to the habitat suitability model that represents the ecology of the conservation target. One way to circumvent this specificity is to model all species present in the network, or at least a representative of each morpho-ecological guild (Leonard and Orth 1988, Fauth et al. 1996, Chan 2001), and to multiply the suitability scores in such a way to permit a holistic definition of restoration priorities.

In this study we decided to use only insurmountable barriers that limited fish movements completely in both directions. This is, however, a limitation, as even small obstacles can have a significant effect on flow, temperature regime, movement of animals and habitat quality (Larinier 2001), thereby potentially causing change in the composition, structure and distribution of fish assemblages (Alexandre and Almeida 2010). These small barriers have different impacts on fish species with different swimming abilities and can be a permanent blockage for some but not all. Some are only barriers in one direction, being pervious to downstream movements, at least for part of the year (Branco et al. 2012). Consequently, in order to increase prioritization accuracy we need to incorporate barrier permeability.

Metrics along the lines of Probability of Connectivity (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007), or the attribution of different values to the links between pairs of nodes according to their permeability (Urban et al. 2009, Schick and Lindley 2007), can facilitate the incorporation of these concerns into this spatial graph methodology. Dispersal probabilities should also be included, as different species have different life cycles and different movement abilities. A method for simplifying decision-making would also benefit from the inclusion of a cost-benefit analysis, given that economic aspects are of increasing concern.

This article proposes a connectivity rehabilitation prioritization methodology which, for the first time, uses spatial graphs and habitat suitability to model the impact of the removal or placement of an insurmountable barrier in a river network. This methodology will aid decision-making processes by prioritizing actions in relation to the actual overall connectivity increase, and can also be a useful tool for determining how to place new instream developments with less impacts. Future studies should focus on improving the method's ability to identify the real habitat increment provided by the reestablishment of the connectivity that was previously limited by a barrier. To accomplish this goal, special attention should be paid to the links between contiguous elements of the river network and to asymmetries in barrier permeability both up and downstream.

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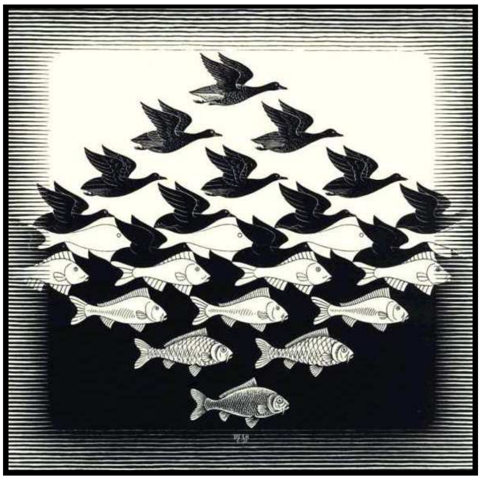
Section III

Connectivity enhancement



M. C. Escher "Sky and Water I" (1938)

Chapter 5

Boulders as building blocks: Improving habitat and river connectivity for stream fish

> "I don't want to achieve immortality through my work.
> I want to achieve it through not dying."
>
> Woody Allen

5.1. Abstract

Fragmentation of freshwater systems is one of the more common human-induced impacts on the environment, and one of the most dramatic because it leads to disconnections among riverine habitats, severely affecting fish populations. To counter this form of ecological abuse, there has been a significant increase of the number of restoration actions. This work approached stream restoration from a holistic point of view, combining habitat modeling with laboratory experimental research. A 2D hydrodynamic model was used to test the increase in Weighted Usable Area (WUA) created by different boulder placement scenarios in a disturbed site, with a widespread potamodromous cyprinid fish – the Iberian barbel (*Luciobarbus bocagei*) – as the target species. This was complemented by experimental trials in a full-scale experimental fishway with different bottom substrata arrangements in order to assess the effects of boulders on barbel movements. Results show that instream boulder placement increases WUA for barbel and facilitates fishway negotiation. The findings reflect the importance of placing instream boulders in fragmented systems in order to enhance suitable habitat area and river connectivity. However, boulder placement must be specifically designed for each case and should always be preceded by a comprehensive study for each site and target fish species.

Keywords: Boulder placement, fish habitat, 2D hydrodynamic model, pool-type fishway, 3D ADV vectrino, connectivity, potamodromous fish

5.2. Introduction

Riverine environments are among the most anthropogenically degraded systems in the world (Naiman and Turner 2000, Sala et al. 2000, Gleick 2003). Numerous studies have documented dramatic changes in the persistence and abundance of fish populations as a result of human-induced disturbances (Marmulla 2001). The fragmentation of the river continuum by obstacles, habitat alteration and habitat degradation negatively affects fish populations by increasing loss of genetic variability and risk of extinction through demographic, environmental and genetic stochasticity (Nicola et al. 1996, Peňáz et al. 1999). Migratory fish are particularly sensitive to connectivity loss caused by habitat fragmentation, because it seriously affects their ability to reach spawning grounds. Although diadromous fish are among the fish species that have been most widely studied in terms of the impacts of human pressure on the persistence and abundance of their populations, much less is known about the ecology (Lucas and Batley 1997), movements and behavior of potamodromous cyprinids. To counter this form of ecological abuse, in the last three decades there has been a significant increase of the number of (Kondolf and Micheli 1995, Bash and Ryan 2002), and money spent on (Bernhardt et al. 2005), restoration actions such as habitat improvement. However, the re-establishment of a system's longitudinal connectivity may be required for a river restoration scheme to be successful (Jansson et al. 2007, Stromberg et al. 2007), and is essential if the ecosystem is to achieve good ecological status, which is the main goal of the European Water Framework Directive (EWFD) (European Commission 2000).

Undisturbed streams harbor fish populations that are naturally well adapted to the local environment, functioning as benchmarks for rehabilitation projects (Boavida et al. 2011b). However, in disturbed sites we must address specific problems, such as the factors that limit the fish populations (Rosenfeld and Hatfield 2006). Fish habitat fragmentation and loss are often compensated for by mimicking the physical structure of the natural river environment (Shamloo et al. 2001, Katopodis 2002). This engineering design method is called physiomimesis and is appropriate to ecological solutions for habitat improvement and restoration, including fish passage design (Newbury and Gaboury 1993, Shrubsole 1994, Marsden 1995, Katopodis 1995, 1996, Katopodis et al. 2001). The placement of instream structures (IS) is a widespread rehabilitation measure for improving habitat and increasing biodiversity in response to degradation (Cowx and Welcomme 1998, Roni et al. 2006). Boulder placement (BP) is a common method for improving fish habitat. Although the effectiveness of BP as a measure for enhancing habitat for salmonid fishes has been examined in several studies (O'Grady 1995, Vehanen et al. 2003, Roni et al. 2006), few have thus far analyzed the performance of these instream structures for non-salmonids (Roni et al. 2006). BP typically helps to change the physical stream conditions, increasing pool habitats and water depth (O'Grady 1995, Vehanen et al. 2003, Roni et al. 2006), and is more effective when carried out in smaller streams (Stewart et al. 2009). These structures can also create turbulence and scour, providing fish with cover from visual predators. Additionally, BP is also known to enhance gravel retention and to provide spawning habitat for litophilic fish (Roni et al. 2006).

Fragmentation of natural river network connectivity is presumed to be one of the most generalized and important human-induced alterations forced on natural environments (Branco et al. 2012). Dams and weirs promote a breach of the systems' longitudinal connectivity, leading to significant habitat modification and alteration of the flow regime, with consequences for the existing biotic communities (Larinier 2001). The construction of fishways emerged as a powerful river restoration measure that helps fish move past the barriers (FAO/DVWK 2002). The importance of such devices was recently reinforced with the launch of water policy tools, such as the EWFD, which requires effective passage and undisturbed migration of fish as a key component for restoring the ecological quality of rivers and their drainage network (European Commission 2000). More recently, some authors (e.g. Hinch and Rand 2000, Acharya et al. 2001, FAO/DVWK 2002, Baker and Boubée 2003) have pointed out that the placement of structures like boulders (Mitchell 1995), logs or stones (Komura et al. 1996) on fishway bottoms may act as a driver for fish movements, but so far no study has addressed their real effects in terms of improving fish movements and connectivity.

The purpose of the present study was to evaluate how habitat for the potamodromous Iberian barbel – *Luciobarbus bocagei* (hereafter barbel) – is improved by boulder placement, using a 2D hydrodynamic model. 2D hydrodynamic models are increasingly employed in aquatic ecology studies, especially in river rehabilitation projects (Vehanen et al. 2003, Lacey and Millar 2004, Pasternack et al. 2004, Boavida et al. 2011a). These models quantify depth and velocity on scales of ecological relevance, such as meso and microhabitat scales (Crowder and Diplas 2000), making it possible to judge whether there is a sound modification of depth and velocity patterns following BP and to predict habitat gains and losses. When coupled with quantitative estimates of preferred physical habitat conditions, these models are a powerful tool for predicting fish habitat. In addition, given that potamodromous fish also need to move upstream, we evaluated how boulder structures may act as facilitators of fish movements and river connectivity. Fish movement was studied in an experimental full-scale fishway employing two boulder arrangements. In the present study we thus address river rehabilitation in a holistic way – from restoring and improving fish habitats to aiding fish movements and obstacle negotiation.

5.3. Methods

5.3.1. *Study area*

The study was conducted in the Ocreza River, one of the largest tributaries on the right bank of the Tagus River, Mid-Eastern Portugal. It is a medium-sized (catchment area c. 1,335 km^2) low-gradient river, running through quartzite areas that are characteristic of central Portugal. The climate is Mediterranean, with more than 80% of precipitation falling between October and April, and a variable period with low or no flow between July and September, which results in a succession of pools in the riverbed. Two study sites (Table 5.1), which were morphologically close to each other and located in a segment with Strahler's order number 3, were selected in the river. The upstream site (N39º44'11.8''; W7º44'36.6''), with a length of 138 m and an average width of 14 m, presented a high degree of naturalness and was considered to represent the reference conditions for the downstream site, which was physically disturbed but did not present pollution sources. The high complexity of habitat cover features at the reference site resulted from submerged boulders, which represented between 40 to 60% of the sheltered areas where fish could rest and hide. Main geomorphologic units included a clear pool-riffle-run sequence. The disturbed site (N39º33'50.9''; W7º48'54.7''), which was 107 m long and 20 m wide, is located 20 km downstream from the reference site. It presented unstable linear banks with occasional vegetation or woody debris providing sheltering areas, resulting from the scouring action of a small hydropower plant located 5 km upstream.

5.3.2. *Fieldwork*

The riverbed topography at the disturbed site was surveyed using a combination of a Nikon DTM310 total station (Mohave Instrument Co., Signal Hill, CA, USA) and a Global Positioning System (GPS) (Ashtech, model Pro Mark2, CRS Survey Equipment & Supplies Ltd., Concord, ON, Canada). Here, 2,188 spots were sampled. Flow velocity and depth were measured at a series of points along cross-sections where significant alterations in depth, flow velocity, substrate composition and slope were noted. Depths were measured with a ruler, and flow velocities were measured with a flow probe (model FP101, Global Water Instrumentation, Inc., Gold River, CA, USA) positioned at 60% of the local flow depth (Bovee and Milhous 1978). These data were used to calibrate the model bed roughness and to establish the boundary conditions, specifically the water surface elevation at the downstream and upstream cross-sections. Fish populations were sampled in both sites and the Shannon-Wiener diversity (H' – base *e* considering only native species) index was computed for each site.

Table 5.1 – Physical characteristics of the reference and disturbed sites (Q = 1 $m^3.s^{-1}$) in the Ocreza River. Species names are followed by the number of individuals captured. Iberian barbel – *Luciobarbus bocagei*; Iberian straight-mouth nase – *Pseudochondrostoma polylepis*; Southern Iberian spined-loach – *Cobitis paludica*; Southern Iberian chub – *Squalius pyrenaicus*; Calandino – *Squalius alburnoides*; Gudgeon – *Gobio lozanoi*; Pumpkin-seed sunfish – *Lepomis gibbosus*.

Study site	Reference	Disturbed
Total length (m)	138	107
Average width (m)	14	20
Depth (m)	0.27 ± 0.17	0.41 ± 0.22
Maximum depth (m)	0.85	1.07
Velocity ($m.s^{-1}$)	0.47 ± 0.34	0.24 ± 0.18
Species (*n*)	Barbel (297) Nase (239) Loach (6) Chub (32) Calandino (61)	Barbel (3) Loach (12) Gudgeon (39) Pumpkin-seed (7)
Shannon index*	1.14	0.50

Mean values are given for depth and velocity followed by standard error
* Base *e* considering only native species

Habitat Suitability Curves (HSC) for depth, velocity and substrate were developed for barbel, considering specific size-classes according to differences in length and age structure: < 11 and > 11 cm corresponding to the fish life-history stages of juveniles (1+) and adults (>1+) respectively (Santos et al. 2011). Fish sampling was performed during the flowing season – late May to early June – with pulsed DC electrofishing. To avoid delocation of individuals from their original optimal positions (Gorman and Karr 1978), a modified point electrofishing procedure was employed (Copp 1989). Sampling points were approached discreetly, and the activated anode was immersed in the water for 5 s at equidistant locations (every 0.5 m). Upon sighting a fish or shoal of fishes, a numbered location marker was anchored to the streambed for subsequent microhabitat use measurements. Fish were measured for total length (TL), and placed in buckets with portable ELITE aerators to avoid repeated counting. Water depth (m), mean flow velocity ($m.s^{-1}$) and dominant substrate composition (Modified Wentworth scale – Bovee 1986) were measured in 0.8 x 0.8 m quadrats below each fish location. HSC were developed by dividing microhabitat variables (depth, flow velocity and substrate composition) into classes and building frequency histograms of use and availability (Vismara et al. 2001). Suitability indexes are the normalized ratios between proportional use and availability (Boavida et al. 2011a).

5.3.3. *Boulder placement scenarios*

Different boulder placement scenarios (BP_i) were designed by increasing boulder density in the degraded site from 3 (BP_3) to more than 21 boulders ($BP_{>21}$) in ranges of 3 boulders (Table 5.2 and Fig. 5.1). The tested scenarios recreate an increasing number and density of boulders in the riverbed (Fig. 5.1), and are expected to have different influences on habitat colonization and fish movement. A two-dimensional approach using the River2D model (University of Alberta, Edmonton, AB, Canada) (Steffler 2000) was chosen, as these models have been shown to accurately represent complex mosaics of depth and velocity distributions (Ghanem et al. 1996, Crowder and Diplas 2000). The WUA (weighted usable area) – i.e. the surface (m^2) that can be used by a given fish – was computed as the product of depth, velocity and substrate suitability indexes, to evaluate the performance of BP at the disturbed site. The substrate suitability index was defined as 1 for the entire riverbed in order to account solely for the boulders' effect on suitability in terms of depth and velocity for the potential river habitat improvement. The discharge set for habitat evaluation was 1 m^3/s, which corresponds to the monthly average flow discharge in the spawning period (from March to June). Combined WUA was computed considering (for the spawning period) a predominance of juveniles – the combined value was obtained by adding 60% of the WUA for juveniles to 40% of the value for adults. The different scenarios (BP_i) were then evaluated by means of WUA values, where WUA was expressed as a percentage of the corresponding total wet area, measured in plan *X Y* using ArcGIS (ESRI, Redlands, CA, USA).

5.3.4. *Fishway experiments*

The laboratory experiments were conducted in a full-scale experimental model of a pool-type fishway (Fig. 5.2). The model structure was composed of a steel frame with lateral acrylic glass panels, allowing a simple visualization of the fish movements occurring within the fishway. The flume was composed of six pools (1.9 m long x 1.0 m wide x 1.2 m high) divided by compact polypropylene crosswalls with bottom orifices (area = 0.04 m^2) placed in an offset arrangement. The channel was set with an 8.5% slope, which is within the range of those commonly used for this type of fishway (Larinier 2008), creating a constant head drop between pools of 16.2 cm.

Two different configurations (Table 5.3) were tested by changing the density (high and low) of boulders placed at the bottom of the fishway (boulders – 15 cm x 15 cm x 10 cm high). The boulders were placed in the second downstream pool and they were positioned in five evenly spaced lines in symmetrical arrangements (Figure 5.3), and oriented according to the prevailing flow pattern to reduce recirculation behind the boulders. Low-density configurations were obtained by removing one third of the boulders, and by turning high boulder-density lines into low-density lines.

For each configuration, 20 barbels were individually monitored. The fish were captured in the River Sorraia, the largest tributary of the Tagus River in Central Portugal (Collares-Pereira et al. 1995), during the migration season, using an electrofishing methodology similar to the ones defined in the protocol adopted by the European Committee for Standardization (CEN norm 14011 March 2003). Fish were collected using a dip net and promptly placed in a container filled with river water. At the laboratory, fish were stabilized in acclimation tanks (700 L) for at least 48h before they were tested. Feeding stopped 24h prior to the experiment. Fish were placed in the tailpool, where the slope was zero, at the beginning of the experiment and allowed to enter the fishway and ascend it on their own volition. Each experiment had a maximum duration of 90 min, ending as soon as the fish successfully negotiated the boulder pool. Two independent observers and two video cameras (Sony DCR-HC23E; top and side view) monitored the fish movements within the fishway. Recorded parameters included the success (or failure) in negotiating the fishway, and fish transit times – namely the *Entrance time* (i.e. the timespan from the beginning of the experiment to the fish's successful entrance into the fishway) and the *Negotiation time* (the timespan between the beginning of the experiment and the successful negotiation of the boulder pool).

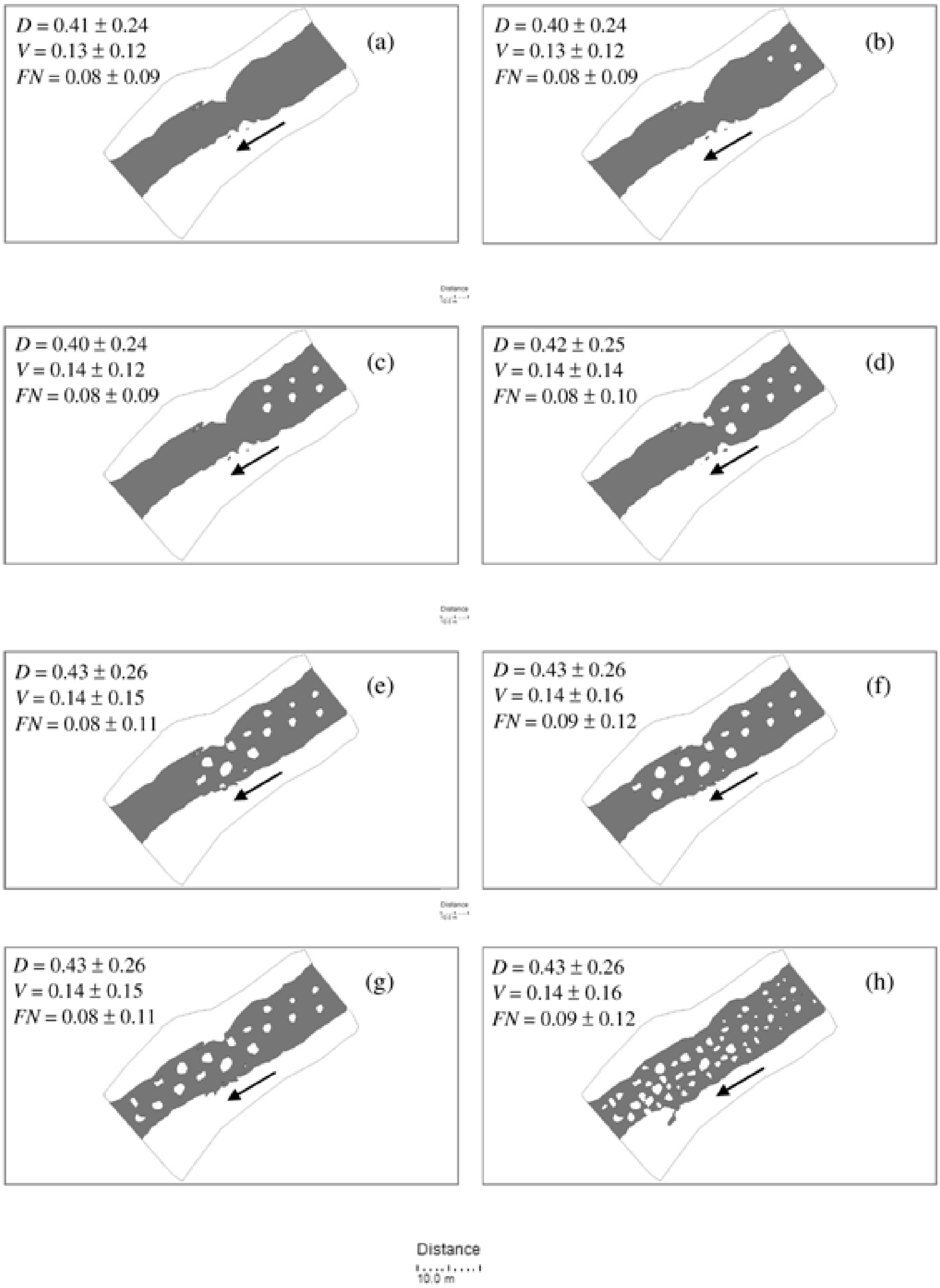


Figure 5.1 – Sketch of the disturbed site and the different boulder placement (BP_i) scenarios (horizontal plan) showing the wetted area at 1 $m^3.s^{-1}$ (a) disturbed site; (b) disturbed site with 3 boulders (BP_3); (c) disturbed site with 6 boulders (BP_6); (d) disturbed site with 9 boulders (BP_9); (e) disturbed site with 12 boulders (BP_{12}); (f) disturbed site with 15 boulders (BP_{15}); (g) disturbed site with 18 boulders (BP_{18}); and (h) disturbed site with more than 21 boulders ($BP_{>21}$). D – depth (m); V – water velocity ($m.s^{-1}$); FN – Froude number.

In order to adequately characterize existing hydraulic conditions as a consequence of BP, the three components (x, y and z) of flow velocity were measured with a Vectrino 3D ADV (Nortek AS) oriented downwards. A mesh of sampling points was created to cover the entire pool area and velocity measurements were performed at two horizontal planes parallel to the flume bed: boulders mid-height (5 cm), and 25% of pool mean depth (*h*m). Measurements were taken at a rate of 25 Hz for a period of 90s. Instantaneous measures of velocity were filtered using the Goring and Nikora (2002) phase-space threshold despiking, modified by Wahl (2003).

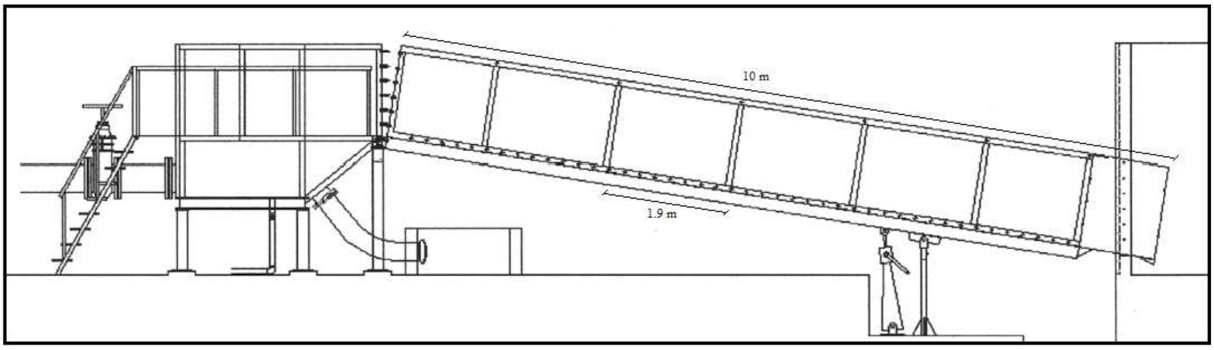


Figure 5.2 – Side view diagram of the pool-type fishway experimental model. Slope of 8.5%.

5.4. Results

5.4.1. *Boulder placement scenarios*

Fish sampling revealed a mixed array of pools, runs and riffles at the reference site. This site has a higher habitat heterogeneity and a higher diversity of native fish species evidenced by a Shannon-Wiener Index of 1.14, as opposed to the 0.5 value from the disturbed site (Table 5.1). Species sampled at the reference site included the Iberian barbel (*Luciobarbus bocagei*), the Iberian straight-mouth nase (*Pseudochondrostoma polylepis*), the Southern Iberian spined-loach (*Cobitis paludica*), the Southern Iberian chub (*Squalius pyrenaicus*), and the Calandino (*Squalius alburnoides*), with a combined total of 485 individuals, of which the barbel was the most representative species (49.3%). In contrast, at the disturbed site only 61 individuals from four different species were collected: the Iberian barbel, the Southern Iberian spined-loach, and the exotics Pumpkin-seed sunfish (*Lepomis* *gibbosus*) and Gudgeon (*Gobio lozanoi*), the latter two being the most dominant species found (75.4%).

Table 5.2 summarizes the WUA values for the barbel and its life-stages, considering the disturbed site and the BP_i scenarios. The highest habitat availability (WUA) was registered in the BP_3 scenario (combined WUA of 29.9%), followed by the BP_6 (combined WUA of 29.1%), both of which showed an improvement over the disturbed site (combined WUA of 28.9%). For the scenarios with higher boulder density, the WUA decreased in relation to the disturbed site, indicating less available habitat for fish permanency.

Table 5.2 – WUA (weighted usable area) for the barbel (*Luciobarbus bocagei*) in the disturbed site and for the different boulder placement scenarios (BP_i). WUA values are presented for the different life-stages and for a combined population.

		WUA (%)		
BP scenario	Wet area (m^2)	Juveniles	Adults	Combined (0.4 Adults + 0.6 Juveniles)
Disturbed	2223.0	42.6	8.3	28.9
BP_3	2142.3	44.1	8.6	29.9
BP_6	2104.6	43.0	8.4	29.1
BP_9	2060.7	41.5	8.7	28.4
BP_{12}	2093.0	39.0	8.7	26.9
BP_{15}	2060.2	38.1	9.1	26.5
BP_{18}	2038.2	38.1	9.1	26.5
$BP_{>21}$	2076.3	34.9	8.7	24.4

5.4.2. *Fishway experiments*

Table 5.3 summarizes the fish transit time results and the rate of success for both configurations. The high-density configuration (configuration A) had the lowest transit times, whereas the low-density one (configuration B) revealed a higher negotiation success rate, with a 60% increase in relation to configuration A.

Difference in flow velocity patterns between both configurations was non-significant for both planes (Plane 1: Sign test $p > 0.05$; Plane2: sign test $p > 0.05$). When the velocity components were analyzed independently, differences among configurations arose in both the x and y components (Plane 1 – Sign test $p_x < 0.001$, $p_y < 0.001$; Plane 2 – Sign test $p_x <$

0.001, $p_y < 0.001$). The low-density configuration yielded higher average velocities on both planes for the y component and on the first plane for the x component.

Table 5.3 – Description of the two tested configurations and summary of the mean values of the transit times for the barbel (*Luciobarbus bocagei*). The rate of successful negotiations is also presented. Conf. – configuration; Q – flow discharge; A_o – area of the orifice; *h*m – pool mean depth; P_v – volumetric power dissipation.

Conf.	Q ($L.s^{-1}$)	A_o (m^2)	Boulder density	*h*m (m)	P_v ($W.m^{-3}$)	Entrance time (min)	Negotiation time (min)	Rate of success (%)
A	38.5	0.032	High*	0.88	36.56	45.8 ± 24.8	32.4 ± 27.8	25
B	38.5	0.032	Low**	0.88	36.56	63.5 ± 14.2	79.4 ± 8.3	40

* 12 boulders; **8 boulders

Figure 5.3 shows the velocity contours and vectors of both the tested configurations at the two horizontal planes. On the boulders mid-height plane there was a clear difference in the flow pattern between the two configurations. In the low-density configuration (B) the flow pattern was characterized by a jet stream close to the side-wall adjacent to the orifice and by the presence of a recirculation zone from the jet stream to the opposite side-wall. For the configuration with a higher density of boulders (A), flow direction was diverged by the two boulders in front of the orifice, in such a way that the jet stream was interrupted, creating small areas of higher flow velocity (0.4 – 1.0 $m.s^{-1}$) followed by areas where abrupt velocity decreases were observed. For the 25% *h*m plane and for both configurations, velocity vectors and contours showed a large low-velocity circulation region that occupied the whole pool area.

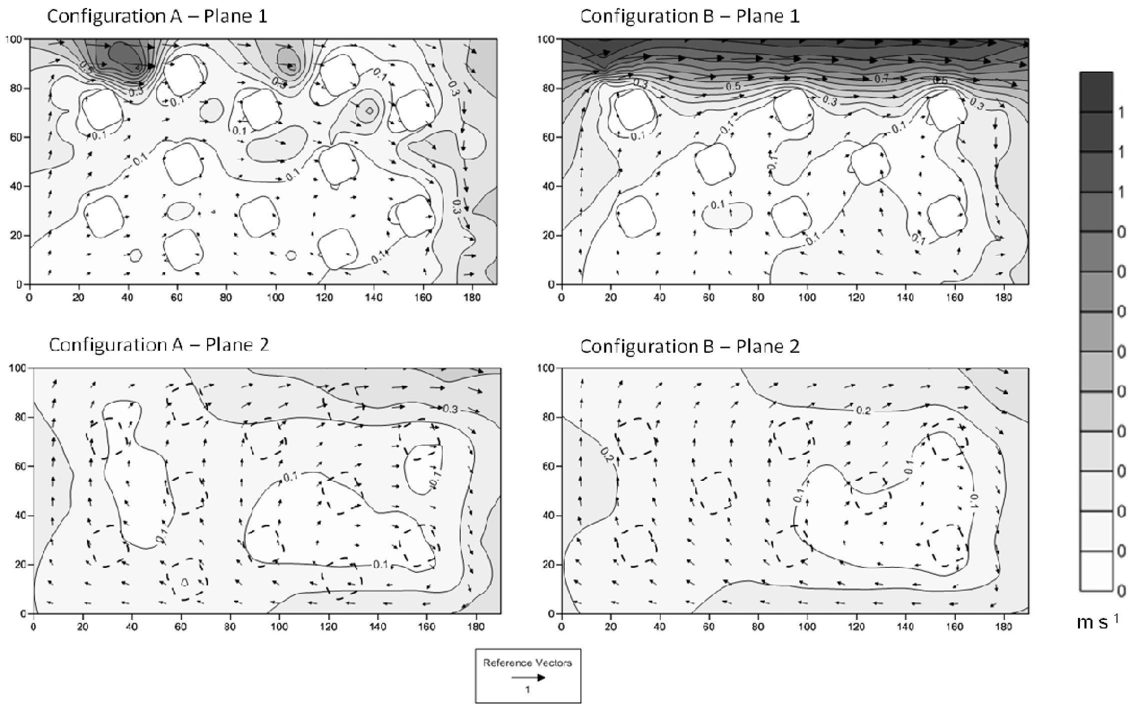


Figure 5.3 – Diagram of the velocity (m.s^{-1}) contours and direction for the two horizontal planes in the two tested configuration. Plane 1 measured at boulders mid-height (5 cm), Plane 2 measured at 25% pool mean depth (*h*m). Lined and dotted squares represent the boulders and show their position and alignment. Arrows show the direction and magnitude of flow (m.s^{-1}). Flow enters the pool at the top left corner of the diagram and exits at the bottom right corner of the diagram. Axis labels are cm.

5.5. Discussion

The present study approached stream restoration from a holistic point of view, inasmuch as it combined habitat modeling, which was used to evaluate habitat enhancement through different instream boulder placement scenarios in a disturbed river site, and laboratory experimental research, which served to assess how different boulder densities affected fish movement success and timing using an experimental fishway. The use of a full-scale experimental facility makes it possible to mimic conditions that occur in the field, and to manipulate the variables of interest while controlling for confounding variables (Kondratieff and Myrick 2005). We therefore believe that the integration of both field and laboratory research methods is a valuable system with which to plan the restoration of fragmented river systems.

Results from fish sampling showed that the higher diversity of fish species was found at the undisturbed site featuring coarser substrata, and that local fish assemblage was dominated by native species, of which barbel was the most abundant. Conversely, the disturbed site revealed a lower diversity and abundance of native species, with the exotic ones (gudgeon and pumpkin-seed sunfish) predominating. The different boulder placement scenarios attempted to approximate the substrate composition of the degraded site to that of the undisturbed site. However, the WUA tend to decrease with an increase in boulder densities. This is related to the high currents that occur in areas where the section is strangled due to the boulder placements. The shelter areas downstream the boulders were insufficient to replace the lost of habitat in other areas of the river channel. The two scenarios with the lower boulder density appeared to be the more favorable, as this increased habitat availability (i.e. WUA) for fish, and might therefore be used to restore the disturbed site. This result is in line with the results of studies with salmonids, where the placement of instream structures increased the abundance of fish (Overton et al. 1981, Ward and Slaney 1981, Moreau 1984, West 1984, House and Boehne 1985, Fuller 1990, Hvidsten and Johnsen 1992, Linlokken 1997, O'Grady et al. 2002, Dolinsek et al. 2007a, 2007b). These instream structures should preferably mimic natural features of the river channel, such as boulders and wood logs, which have displayed lower failure rates in habitat enhancement projects (Roni et al. 2006). Nonetheless, any rehabilitation measure to enhance fish habitat must start from an identification of the habitat that is limiting the population (Rosenfeld and Hatfield 2006, Vehanen et al. 2010). Bearing in mind that species' ability to respond positively to the boulder placement will also depend on whether water quality in the reach is sufficient to support them (Stewart et al. 2009). Besides this habitat improvement will also be dependent upon the source of available colonist (Pretty et al. 2003). So even if they possess an *a priori* potential for improving a species' habitat use, the boulder placement may only be effective if they are close to high-quality reaches supporting a larger number of potential colonists. Having said this, as each case is site- and species-specific, every project needs to be designed specifically for each site, target species, life stage and river type (Jungwirth et al. 2000), while considering the reference biological assemblages and ecological conditions found at undisturbed sites (Nestler et al. 2010, Boavida et al. 2011b), which should be considered benchmarks for determining the success of the restoration.

However, boulders not only affect the amount of habitat available, but also affect fish movement in the river. The present study also showed that increasing substrate heterogeneity, by placing boulders at the bottom of the experimental fishway, facilitated the upstream movements of barbel. We hypothesize that boulders altered the flow pattern and homogenized the upper portions of the pool by turning the area above the boulders into a recirculation zone without jet streams. This may have promoted a less turbulent flow, with less eddy formation, creating a large resting area with low flow velocities, which helps decrease fish disorientation phenomena (Odeh et al. 2002). Future studies should focus on assessing small-scale turbulence and eddy size in the vicinity of boulders, in an attempt to further improve our understanding of the mechanisms that aid fish passage. The low-density boulder configuration proved to be more successful at helping fish negotiate the fishway; it yielded a 60% higher success rate compared to the high-density configuration. This increased success might be due to the positioning of the boulders and to their lower density, which maintained an uninterrupted attraction flow that kept fish oriented upstream and stimulated them to negotiate the fishway, while still providing a large resting area above the boulders. Placing boulders at the bottom of pool-type fishways may therefore create a better pool environment for fish passage, while turning fishways into more nature-mimicking structures that facilitate movements of a variety of species (Katopodis 2002), providing that boulders are adequately placed (Komura et al. 1996), without interrupting attraction flows.

The results of this study highlight the usefulness of boulder placement as potential drivers for increasing fish habitat and movements. Boulders are thus a valuable tool for use in river restoration. However, boulder size, density and location in the riverbed are determinant factors in the successful improvement of river conditions for fish populations and the longitudinal connectivity between habitats. As different fish and life-stages will have different habitat needs and biomechanical characteristics, future studies should focus on the optimization of the boulder-placement structural design, in order to meet the multiple needs of fish communities.

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Chapter 6

Effect of two flow regimes on the upstream movements of the Iberian barbel (Luciobarbus bocagei) in an experimental pool-type fishway

"Rosebud"

Orson Wells, "Citizen Kane"

6.1. Abstract

Pool-type fishways related literature has seen a recent upsurge of interest in the placement of instream structures for improving fish passage. However, there is still no information on how different flow regimes created by boulder placement influence upstream fish movements. The main goal of this study is to assess the performance of two different flow regimes, characterized by the relative depth of flow (d/h), where d is the water depth and h is the height of artificial bottom substrata, in assisting fish passage in an experimental full-scale pool-type fishway. Two series of experiments consisting of 20 replicates each and representing distinct flow regimes created by boulder placement in the flume bottom – $d/h>4$ (regime 1) and $1.3<d/h<4$ (regime 2) - were carried out to analyze the proportion and timing of successful upstream movements of a potamodromous cyprinid, the Iberian barbel (*Luciobarbus bocagei*). Although no significant differences ($p> 0.05$) in passage success were observed between both regimes (55% and 60%, respectively), fish transit time was significantly lower ($p< 0.05$) in regime 2 (mean ± SD: 2.6 ± 1.6 min.) than in regime 1 (7.1 ± 5.8 min.). The results of these experiments showed that lower relative depths can be more beneficial to fish passage because they reduce the transit time for successful negotiation, thus providing a useful indication on how to improve fish passage through pool-type fishways.

Keywords: pool-type fishway, relative depth of flow, artificial boulders, Vectrino 3D ADV, Luciobarbus bocagei

6.2. Introduction

Habitat fragmentation by dams and weirs has been cited as one of the major threats to aquatic biodiversity, including freshwater fishes (e.g. Dynesius and Nilsson 1994, Aarts et al. 2003). Particularly impacted species are the ones that seasonally undergo considerable migrations within river systems (potamodromy) (Lucas and Baras 2001, Poulet 2007), since dams and weirs hinder them from reaching their spawning grounds. The restoration of the longitudinal connectivity of rivers stands therefore as a key issue for the recovery of freshwater ecosystems and the construction of fishways is a relevant *ad hoc* measure.

Pool-type fishways are one of the most common types of fishways built at small hydro-power plants (Larinier 2008). These facilities consist of a series of consecutive pools, separated by cross-walls arranged in a stepped pattern, with each pool higher than the one immediately downstream (Katopodis et al. 2001). These cross-walls are equipped with submerged orifices at the bottom and/or surface notches, which are used by the fish to move from pool to pool. However, in southern-European countries, particularly in Iberia, most of the existing pool-type fishways failed to restore connectivity for fish, because their design was biased by salmonid-based guidelines while the predominant groups of fishes needing passage are potamodromous cyprinids which exhibit different behaviour and have limited swimming ability (Pinheiro and Ferreira 2001, Santos et al. 2011). It is therefore imperative to develop adequate technical and scientific guidelines for these species to improve existing fishways or to design more suitable facilities in the future.

The placement of boulder substrata on the bottom of pool-type fishways has been advocated to improve fish passage, in particular of benthic species, such as gudgeon (*Gobio lozanoi*), loach (*Cobitis paludica*) or eel (*Anguilla Anguilla*), because it reduces flow velocities near the bottom (FAO/DVWK 2002). The increased roughness provided by embedded boulders makes it possible for species with low swimming capabilities to exploit the small velocity refuges formed by individual roughness elements to migrate upwards through the fishway. Despite the potential influence for aiding fish passage, no study has so far considered the effects on how the relative depth of flow, i.e. the ratio between the water depth of the fishway and the height of the boulders, affects upstream fish movements. Upon studying the flow around a hemispherical boulder of height h in a rectangular channel, Shamloo et al. (2001) found that the relative depth of the flow was a key parameter in determining the flow regime around an obstacle and in providing suitable hydraulic conditions for fish passage. Accordingly, they hypothesized that lower relative depths (i.e. higher boulders at lower water depths) could be more favorable for fish movements as, due to a more noticeable boulder effect, complex flow conditions that enhance fish movements, such as a greater proportion of negative horizontal velocity vectors and the presence of recirculation regions, are more likely to occur.

This study compares the effects of two different flow regimes, based on the relative depth of flow, on the upstream movements of a widespread potamodromous cyprinid species, the Iberian barbel *Luciobarbus bocagei* (hereafter barbel), migrating through an experimental pool-type fishway. Specifically, the following questions were posed: (a) are there significant differences on the horizontal and vertical velocity patterns between the two flow regimes?; (b) are there significant differences in the proportion of fish that successfully ascend the fishway between flow regimes?; and (c) do successful fish take the same amount of time (i.e. transit time) to ascend the fishway in each flow regime?

6.3. Methods

6.3.1. *Experimental facility*

The study took place in an experimental pool-type fishway installed at the Hydraulics and Environment Department of the National Laboratory for Civil Engineering (LNEC), in Lisbon. It consisted of a full-scale model (10 m long, 1 m wide and 1.2 m high), built on a steel frame and featuring acrylic glass panels on both side-walls. It was composed of 6 pools, each 1.9 m long, except the most downstream and upstream ones which were 1.8 m and 0.6 m, respectively. The pools were divided by compact polypropylene cross-walls, each one incorporating a submerged orifice and a surface notch of adjustable area. The fishway slope was set at 8.5%, which falls within the range used for these types of facilities (Larinier 2008). The fishway also encompassed an upstream and a downstream chamber. The former included a slot gate to control the discharge entering the flume, whereas the latter (4.0 m x 3.0 m x 4.0 m), separated from the flume by two mesh panels, allowed acclimation of fish prior to the start of experimentation.

6.3.2. *Hydraulics*

Two different configurations (Table 6.1) were tested by changing the relative depth of flow, i.e. the ratio between the water depth in the fishway (d) and the height of boulders (h) placed at the flume bottom, resulting in the creation of two flow regimes: regime 1 ($d/h>4$) and regime 2 ($1.3<d/h<4$). These flow regimes have been previously defined to study the flow around simple habitat structures (i.e. boulder substrata) to be used in river restoration studies (Shamloo et al. 2001). Thus, regime 1 had higher relative depth than regime 2. Discharge (Q) was kept constant (c. 62.7 L/s) among regimes. Twelve square-shaped boulders (15 cm x 15 cm) with rounded corners and presenting two heights (10 and 15 cm), were positioned along five even spaced lines in symmetrical arrangements. They were oriented with a diagonal along the flow passing through the inlet orifice, as previous studies demonstrated that it minimizes the creation of zones of strong turbulence due to vertical vortices (Heimerl et al. 2008) (Fig. 6.1).

Table 6.1 - Description of the two tested configurations based on different flow regimes. *d* – water depth; *h* – height of boulders; A_o – orifice area; h_{m1} – water depth at plane 1 (boulders mid-height) monitored by ADV; h_{m2} – water depth at plane 2 (above boulders) monitored by ADV. The number of fish (N) and mean (± SD) size of the individuals used in the experiments is also shown.

Flow regime	*d* (cm)	*h* (cm)	A_o (cm^2)	h_{m1} (cm)	h_{m2} (cm)	Fish	
						N	Size (mean ± SD (cm))
1	84	10	529	5.0	21	20	26.1 ± 6.9
2	53	15	529	7.5	21	20	25.9 ± 6.7

The efficiency of a fishway is highly dependent on how existing hydraulic conditions, in particular changes in water velocity, suit the respective target species and their behaviour (Williams et al. 2011). Consequently, to characterize the hydraulic conditions in both configurations, three-dimensional (x, y and z) instantaneous velocity measurements were conducted in two horizontal planes parallel to the flume bottom – at boulders mid-height and at 15% of the water column above the boulders (i.e., 21 cm from the flume bottom). The reason for sampling at this height is because the ADV needs a minimum depth of 5 cm from the tip of the probe to get accurate readings (Nortek AS). As the maximum high of boulders is 15 cm, measuring at 21 cm from the flume bottom guaranteed the collections of accurate velocity readings in the layer immediately contiguous to the boulders. The spacing of each measured point varied according to the measured plane. Accordingly, at the plane above the boulders, all the pool layer was available for measurement and therefore spacing was tighter (5–8 cm in x- and y-directions), than at the plane of boulders mid-height (10-13 cm in x- and y- directions), which was constrained by the physical presence of boulders. In both cases, spacing between points was narrower near the inlet and outlet orifices as these are typically areas of more pronounced velocity fluctuations (Silva et al. 2011). Altogether, a grid with 49 (plane of boulders mid-height) and 88 sampling points (plane at 21 cm above the bottom), was sampled by a Vectrino 3D ADV (Acoustic Doppler Velocimeter) (Nortek AS) oriented vertically down at a frequency of 25 Hz for a period of 90 s to characterize flow velocity. The ADV sampling period of 90 s was established from previous tests in the same fishway (for more details see Silva et al. 2011). The orifice dimensions were the same (i.e. 0.23x0.23 m) for both configurations, while the surface notches remained closed, as a previous study revealed species avoidance for these openings (Silva et al. 2009). On the whole, 2250 instantaneous measurements were recorded for each sample point. Measurements were made on the second downstream pool which was considered to be representative of hydraulic conditions within the fishway due to identical flow patterns and head drops between the pools ($\Delta h=0.162$ m).

6.3.3. *Fish*

For each configuration, twenty replicates, each one consisting in the monitoring of an upstream-migrating adult barbel individual, were performed between dusk and early night (17h-22h), to capture their nocturnal movement (Santos et al. 2002, 2005). Fish were previously captured in the Sorraia River, central Portugal, using low-voltage electrofishing during a natural reproductive migration, which generally takes place from April-June (Santos et al. 2005). Fish were all mature as shown by in situ macroscopic observations of their gonads development stage, particularly their volume, vascular irrigation and visibility of oocytes, and by the presence of nuptial tubercles. The fish were then transported to the laboratory facilities, where they were held in 800 L tanks, under a controlled environment (for further details see Santos et al. 2011) for 48h to 96h before they were tested (Romão et al. 2011). At the start of an experiment, mesh panels were removed to enable fish access to the fishway and each one was allowed to ascend on their own volition. Each replicate lasted 1.5 h (maximum) or ended when each individual fish successfully negotiated the fishway. Fish movements were continuously monitored by visual observations and video recording. For video recordings, two video cameras (Sony DCR-HC23E; top and side views) were used. Infrared lamps, scheduled to operate beginning at 20h30m, were employed whenever natural light was no longer sufficient to obtain accurate images. Recorded parameters were 1) the success (or failure) in negotiating the fishway and 2) the time fish took to successfully negotiate the fishway.

6.3.4. *Data analysis*

Instantaneous measures of velocity were first filtered using the Goring and Nikora (2002) phase-space threshold despiking method, modified by Wahl (2003). Velocity data were then analysed by quantifying at each plane, the percentage of velocity records for which the direction differed from the bulk flow (streamwise v_x), *i.e.* the proportion of negative values. This metric gives a coarse indication of the extent to which the local direction of fluid motion deviated from the prominent direction of flow, therefore describing the spatial hydraulic heterogeneity (Kemp et al. 2011). Comparisons of the proportion of streamwise negative values between the two flow regimes were then performed by χ^2 tests. Next, the v_x and v_y instantaneous measures obtained at each point on the *x* and *y* direction, respectively, were used to calculate the horizontal velocities according to the equation:

$$v_{xy} = \sqrt{{v_x}^2 + {v_y}^2}$$

Maps with the horizontal velocity contour lines were then generated for the two planes studied and their resulting patterns were then compared by Wilcoxon match-paired tests to search for differences between the two flow regimes. However, measurements and evaluation of the horizontal velocity distribution alone may not provide sufficient information about the structure of the secondary currents (Song and Chiew 2001). Deviations of the velocity vectors from the horizontal direction, i.e. the presence of the vertical component in the current velocity, are likely to perturb the fish's behaviour (Wang et al. 2010) and should be taken into account. Therefore, to adequately describe the secondary nature of flow, measurements of the vertical component, v_z, were used to generate contour maps of this variable for both flow regimes, where negative values represent descending velocities and positive values represent ascending ones. The patterns obtained at each plane for the two flow regimes were then compared by Wilcoxon match-paired tests.

A χ^2 test was performed to compare the proportion of fish that successfully ascended the fishway for each of the two flow regimes. A nonparametric Mann-Whitney U-test was also employed to test the null hypothesis that the time taken to successfully ascend the fishway was similar between the two flow regimes tested.

6.4. Results

6.4.1. *Hydraulics*

The horizontal velocity patterns are shown on Figure 6.1 for both flow regimes and for both planes: boulders mid-height and 15% of the water column above the boulders. No significant differences in velocity patterns were found between the two flow regimes (Wilcoxon match-paired test; N=49, Z=1.06; $p>0.05$) at the plane corresponding to the boulders mid-height (Fig. 6.1a and 6.1b). At this plane, two different types of regions could be distinguished for both flow regimes: i) a jet region, which emerges from the inlet orifice in a longitudinal direction with a maximum velocity of *c.* 1.60-1.70 $m.s^{-1}$, and continues until it hits the boulder immediately downstream; this caused a pronounced decay of the magnitude and direction of the primary velocity vector, as evidenced by the creation of two secondary flow paths of reduced velocity (0.20-0.25 $m.s^{-1}$) on each side of the boulder; and ii) a small recirculation region of reduced velocity (0.10-0.20 $m.s^{-1}$) which occurs below the main jet region and extends further downstream towards the opposite side-wall.

At the horizontal plane located above the boulders, significant differences on velocity patterns were found between the two flow regimes (Wilcoxon match-paired test; N=88, Z=2.37; $p<0.05$). On regime 1 (Fig. 6.1c), two regions could be easily distinguished: i) a homogenous jet region, emerging from the inlet orifice and extending along the adjacent side-wall towards the outlet and ii) a large low-velocity recirculation region (range: 0.10-0.30 $m.s^{-1}$), extending from the homogenous jet region to the opposite side-wall. Velocity patterns recorded for regime 2 (Fig. 6.1d) also revealed a jet region extending longitudinally towards the opposite cross-wall and showing a maximum velocity of c. 1.0 $m.s^{-1}$. However, in contrast to regime 1, and instead of a large recirculation region, several smaller recirculation regions were observed (velocity range: 0.1-0.3 $m.s^{-1}$) from the main jet towards the opposite side-wall, namely on the downstream 2/3 of the pool. Spatial hydraulic heterogeneity on this plane was also higher in regime 2, though marginally significant, relative to regime 1 ($\chi^2=3.89$, $p<0.10$).

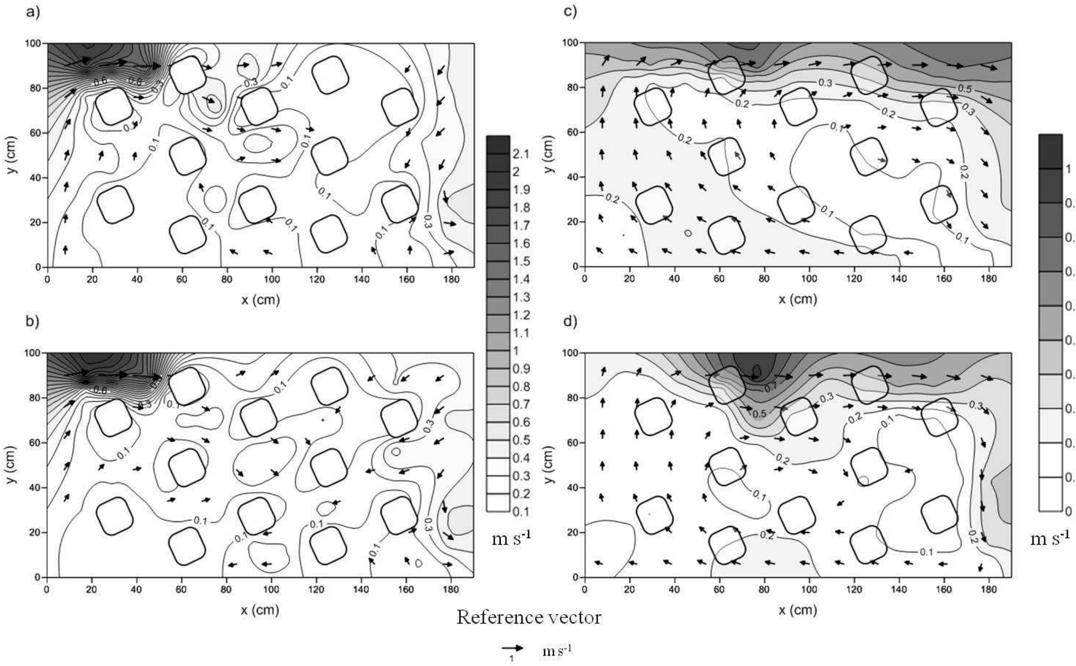

Figure 6.1 - Horizontal velocity field (magnitude and direction) in the pools according to the different flow regimes and measurement planes: (a) regime 1 at the horizontal plane corresponding to the boulders mid-height; (b) regime 2 at the horizontal plane corresponding to the boulders mid-height; (c) regime 1 at the horizontal plane corresponding to 21 cm above the flume bottom; (d) regime 2 at the horizontal plane corresponding to 21 cm above the flume bottom. Arrows show velocity direction and magnitude. Lined and dotted squares represent the boulders and show their position and alignment. Flow enters the pool at the top left corner of the diagram and exits at the bottom right corner of the diagram.

The observed vertical velocity field was significantly different between the two flow regimes (Wilcoxon match-paired test; N=49, Z=2.16; $p<0.05$). At the plane corresponding to the boulders mid-height, regime 1 (Fig. 6.2a) showed a greater predominance for positive and ascending velocities relative to regime 2 (Fig. 6.2b), particularly in the vicinity of both inlet and outlet cross-walls. At the plane located above the boulders, the pattern of vertical velocities was similar between the two flow regimes (Wilcoxon match-paired test; N=88, Z=0.87; $p>0.05$), with lower and descending values occurring near both cross-walls, while ascending velocities were noted mainly within the area between boulders (Fig. 6.2c and 6.2d).

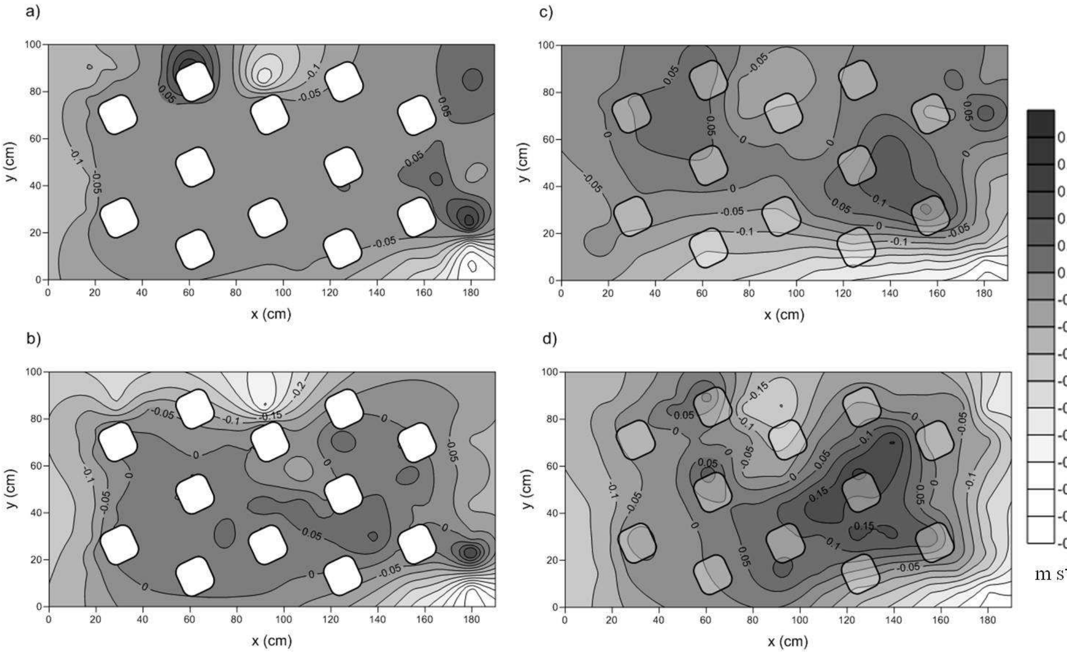

Figure 6.2 - Vertical velocity contours in the pools according to the different flow regimes and measurement planes: (a) regime 1 at the horizontal plane corresponding to the boulders mid-height; (b) regime 2 at the horizontal plane corresponding to the boulders mid-height; (c) regime 1 at the horizontal plane corresponding to 21 cm above the flume bottom; (d) regime 2 at the horizontal plane corresponding to 21 cm above the flume bottom. Lined and dotted squares represent the boulders and show their position and alignment. Flow enters the pool at the top left corner of the diagram and exits at the bottom right corner of the diagram.

6.4.2 *Fish*

The proportion of fish that successfully ascended the fishway was greater in regime 2 (60%) than in regime 1 (55%) but this was not significant ($p > 0.05$, χ^2 test) (Table 6.2). However, differences were found in the time taken to negotiate the facility. As a matter of fact, fish in regime 2 (mean ± SD: 2.6 ± 1.6 min.) took significantly less time to ascend the fishway relative to regime 1 (7.1 ± 5.8 min.) (Mann-Whitney U-test, $Z = 1.89$, $p < 0.05$).

Table 6.2 - Passage efficiency (%) and time taken by fish (mean ± SD (min.)) to successfully negotiate the experimental pool-type fishway upon the different flow regimes. χ^2 (passage efficiency) and Mann-Whitney significance levels are also shown (*ns* – non-significant).

Parameter	Flow regime		p
	1	2	
Passage efficiency (%)	55	60	ns
Time for successful negotiation (min.)	7.1 ± 5.8	2.6 ± 1.6	< 0.05

6.5. Discussion

This study analyzed the effects of two different flow regimes, based on the relative depth (*d/h*) of flow, on the passage success and timing of a widespread potamodromous cyprinid species migrating through an experimental full-scale pool-type fishway. The proportion of fish that successfully ascended the fishway was similar, 55-60%, for both flow regimes. In a recent review of 65 papers (period 1960-2011) addressing worldwide quantitative estimates of fish passage efficiency, Noonan et al. (2011) found that for conventional pool-type fishways, i.e. with no substrate embedded on the bottom, mean upstream passage efficiency for non-salmonid fishes was approximately 40%. Though the present study was not designed to compare fish passage performance between a smooth bottom (no substrate embedded) and a boulder rugosity bottom, our findings suggest that boulder placement might facilitate fish movement by increasing fish passage efficiency and point out for the usefulness of these structures as potential drivers for aiding fish passage in pool-type fishways.

Despite the similarity on the proportion of successful fish for both flow regimes, fish were able to negotiate the facility in significantly less time during regime 2. Although no differences were found between regime 1 and 2 on the horizontal velocity patterns at the plane which corresponds to the boulders mid-height, significant differences arose between the two regimes when comparing velocities at the plane above the boulders. In the latter, the use of higher boulders in association with lower water depth generated greater water velocity reductions, resulted in higher spatial hydraulic heterogeneity, and created several small recirculation regions. The presence of such small reverse-flow fields is known to aid upstream movements of many fishes in the wild. For example, Hinch and Rand (1998) found that upstream movements of sockeye salmon (*Oncorhynchus nerka*) were facilitated when fish were able to exploit these hydraulic phenomena. On the other hand, the presence of a large recirculation region occupying most of the pool area for regime 1 could have caused fish disorientation and hence a delay on fish movements. It is known that in such recirculation regions, typically much larger than the fish's body length, the hydrodynamic rotation forces introduce a torque which tends to overturn the fish and decrease stability (see Lupandin 2005 for a schematic view). Such regions may become traps for fish, thereby drastically increasing transit times in the pools (Tarrade et al. 2008). This was particularly evident in the vicinity of the orifices in regime 1, when some of these fish were seen to spread their pectoral fins in an attempt to stabilize their body position.

Vertical velocity patterns could also partially explain the shorter fish transit times observed for regime 2. The vertical velocity field was found to be significantly different between the two flow regimes, with regime 2 showing a predominance of negative (descendent) values relative to regime 1, which could have prevented fish from moving away from the preferential bottom route (Scheibe and Richmond 2002). Positive vertical velocities are known to disturb the fish's behaviour by generating a secondary flow that may force the fish to shift from one depth to another. This shift is frequently associated with a change in the hydrostatic pressure which may change fish behaviour (Pavlov et al. 2002), even in the presence of shallow water depths (< 1 m) as in the present study. These authors reported that the sensitivity threshold to the pressure change in water is within the 10 cm range of the water column. For example, minnows (*Phoxinus phoxinus*) show a hydrostatic reaction when changing the depth by 0.5 – 1 cm, ten-spined stickleback (*Pungitius pungitius*) have these reactions when changing the depth by 3 – 6 cm, and goldfish by 0.5 – 2.0 cm. This is consistent with visual and video observations from the present study, where, upon entering the pools during regime 1, fish were frequently seen to be immediately displaced to the upper portions, above the substrata, and thereafter swimming around in circles (a clear sign of the presence of a recirculation flow), before proceeding to the submerged orifice, in an attempt to proceed upstream. In contrast, during regime 2, fish tended to swim within the pathways created by the boulders. These pathways, often referred to as micro-channels, are expected to provide interconnected, preferential low stress routes along which fish may swim (Acharya et al. 2001). We therefore believe that such behaviour reflected the adoption of an energy-minimizing tactic in which fish selected the paths with higher spatial hydraulic heterogeneity, i.e. where velocity vectors were more likely to be opposite to the direction of bulk flow, thus facilitating fish movements. It is clear that future studies should focus on testing the effect of density, with different combinations of boulder spacing, and height to optimize the timing and success of fish passage and understand how the resulting micro-channels can be specifically incorporated into the design of future fishways.

The results of this study showed that, in spite of similar proportions of successful fishway negotiation, flow regimes with lower relative depth can be more beneficial to fish passage in pool-type fishways since they reduce the fish transit time. The approach used can also be a template for river restoration studies that try to quantify relations between fish passage and instream boulder placement.

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Chapter 7

Pool-type fishways: Two different morpho-ecological cyprinid species facing plunging and streaming flows

7.1. Abstract

Fish are particularly sensitive to connectivity loss as their ability to reach spawning grounds is seriously affected. The most common way to circumvent a barrier to longitudinal connectivity, and to mitigate its impacts, is to implement a fish passage device. However, these structures are often non effective for species with different morphological and ecological characteristics so there is a need to determine optimum dimensioning values and hydraulic parameters. The aim of this work is to study the behaviour and performance of two species with different ecological characteristics (Iberian barbel *Luciobarbus bocagei* – bottom oriented, and Iberian chub *Squalius pyrenaicus* – water column) in a full-scale experimental pool-type fishway which offers two different flow regimes - plunging and streaming. Results showed that both species passed through the surface notch more readily during streaming flow than during plunging flow. The surface oriented species used the surface notch more readily in streaming flow, and both species were more successful in moving upstream in streaming flow than in plunging flow. Streaming flow enhances upstream movement of both species, and seems the most suitable for fishways in river systems where a wide range of fish morpho-ecological traits are found.

7.2. Introduction

The increasing demand of water for human consumption propels the construction of dams and weirs that become insurmountable barriers to the migration of fish, thus imperiling the completion of the life cycle of several fish species. Indeed, more than half of the world's largest rivers are currently negatively impacted by dams and weirs (Nilsson et al. 2005), which have caused serious declines of both resident and migratory fish populations (Northcole 1998) by affecting upstream adult migration, reproduction, feeding and colonization movements, while promoting genetic impoverishment and dispersion of exotic species (Branco et al. 2012).

To overcome this problem, barriers must become negotiable by fish. To achieve this goal, the construction of fish transfer devices, commonly known as fishways, has been considered the most feasible measure to improve and restore connectivity. The problem with this measure is the often low efficiency of such devices for weak swimming species (Noonan et al. 2011). Fishways have traditionally been constructed based on guidelines developed and tested for salmonids, known strong swimmers with great leaping abilities, while studies of fishway performance focused on species with low economic and recreational value (e.g. cyprinids) continue to be neglected (Roscoe and Hinch 2010). This is rather unfortunate, since these species are an important biological component of fish assemblages and free instream movement is indispensable for their survival (Lucas et al. 2000). In addition, recently, several non-salmonid species have acquired greater legislative protection (e.g. under the EU Habitats Directive (Council Directive 92/43/EEC 21 May 1992)).

It is a complex problem to assure that flow and turbulence conditions within a fishway provide flow patterns suitable for an array of species. Pool-type fishways are a very common type of fish transfer device that has been built since the nineteenth century (Larinier and Marmulla 2004). They consist of a rectangular flume divided by cross-walls that create a series of consecutive pools arranged in a stepped pattern each upstream from the preceding one. The purpose of these pools is to divide the height to be negotiated by fish, while ensuring no kinetic energy of the jets coming from the bottom orifices or the notches is transmitted to the downstream basins. This creates similar flow patterns in each pool (Larinier and Marmulla 2004). Additionally, these pools offer resting areas for fish to recover after negotiating the cross-walls. The cross-walls between the pools may be equipped with different opening types - surface notches and submerged orifices at the bottom – that are used by the fish to move from pool to pool. The selection of an opening type by a fish depends on the species swimming ability and on the flow regime passing through the device (Katopodis 2005) plunging or streaming (Rajaratnam et al. 1988). In the plunging flow regime, the water level in the pool immediately below the cross-wall (producing the plunging flow) is below the crest of the notch; in the streaming flow mode, a surface stream appears to flow over the crest of the notches, skimming over the water surface of the pools in between (further details in: Clay 1995, Ead et al. 2004). Pool-type fishways, which include pool and weir and vertical slot, are the most efficient conventional or technical fishway types constructed, either for salmonids or for non-salmonids (Noonan et al. 2011). Only fishways with optimal design can be of high efficiency as their success varies according to swimming ability, size (Hinch and Bratty 2000, Castro-Santos 2005, Katopodis and Gervais 2012) and physiologic state (Pon et al. 2009, Hasler et al. 2011) of different fish species, as well as hydraulics (Katopodis and Williams 2012) and turbulence (Silva et al. 2012). The design criteria for pool-type fishways are quite well understood for diadromous species (Clay 1995, Katopodis 2005, Katopodis and Williams 2012). There is still a knowledge gap though on how to improve and make these passes more efficient and more capable to accommodate a wider range of species and size-classes. This is particularly important for potamodromous and resident cyprinid species, as international environmental legislation requirements are increasingly more stringent for species (Wang et al. 2010, Katopodis and Williams 2012).

Fish species evolved differently, to be adapted to different riverine environments. These specializations can be grouped into different morpho-ecological guilds that introduce differences in swimming abilities, behaviour and niche occupancy. The best method to understand the influence of these differences on fishway negotiation ability is to test different species, representative of different morpho-ecological guilds, on fishways with controlled conditions. Laboratory trials, where conditions found in the field are easily reproduced while manipulating variables and monitoring confounding factors are always preferable (Kondratieff and Myrick 2005), and have been proposed as the starting point of successful fishway designs (Katopodis and Williams 2012, Williams et al. 2012).

The purpose of this work is to study the behaviour and performance of cyprinid species with different ecological characteristics, in a full-scale indoor model of a pool-type fishway, fitted with bottom orifices and surface notches while subjected to one of two flow regimes - plunging and streaming. Hence, two species were used, *Luciobarbus bocagei* (Steindachner, 1864) a large-bodied potamodromous benthic fish, and *Squalius pyrenaicus* (Günther, 1868) a small-bodied water-column resident fish. It is thus hypothesized that: (1) the proportion of upstream movements through surface notches and submerged orifices will vary depending on the species and flow regime type; (2) both species will use the submerged orifices in greater proportions during the plunging flow regime, and (3) fish upstream movements and successes (when a fish reaches the top of the fishway by negotiating the fifth cross-wall) will be higher for both species during streaming flow conditions.

7.3. Methods

7.3.1. *Ethics statement*

Animal trials and sampling were conducted in agreement with national and international guidelines to maintain wellfare of the individuals (CEN 2003, INAG 2008). Fish sampling permits were obtained from the National Forest Authority. The experiments were carried out in strict accordance with the recommendations of the "protection of animal use for experimental and scientific work" of the Department for Health and Animal Protection (Direcção de Serviços de Saúde e Protecção Animal) that authorized animal experiments to be conducted in this experimental facility, and fish to be maintained in the laboratory (permit number: 16546 – 7/10/2011). All efforts were made to minimize stress and no fish were sacrificed to complete this study.

7.3.2. *Fishway facility*

The laboratory experiments were conducted in a full-scale experimental model of a pool-type fishway (Fig. 7.1). The model structure was comprised of a steel frame with side panels of acrylic glass, allowing visualization of the fish movements occurring within the fishway. The flume was composed of six pools (1.9 m long x 1.0 m wide x 1.2 m high) divided by compact polypropylene cross-walls equipped with bottom orifices and surface notches. These were placed in a double offset arrangement, i.e., each cross-wall had a bottom orifice on one side and a surface notch on the other, and this pattern alternated between pools. The flume tilted portion (10 m long) was set on an 8.5% slope, which is within the range of those commonly used for this type of fishway (Larinier 2008). The flow entering the fishway was measured and regulated by a flow meter in the supply pipe. Finer adjustments were made by a valve located at the upstream end of the fishway, where a tank (1.5 m long x 1.0 m wide x 1.2 m high), separated from the flume by a mesh screen, allowed water to flow smoothly into the flume. The water level on the other hand was regulated by a slot gate located in the downstream end of the flume at a tank (4 m long x 3 m wide x 4 m high) where the flume starts. This tank is separated from the flume by a mesh panel and mimics the hydraulic environment found downstream of the entrance to the fishway allowing for better fish acclimation. By controlling the flow discharge and the level of water in each pool, either plunging or streaming flow could be produced (Table 7.1).

Fishway hydraulic measurements

Hydraulic conditions present at each pool have direct influence on the movements of fish (Williams et al. 2012), especially flow velocity and different turbulence parameters (Bunt et al. 1999, Haro et al. 1999, Silva et al. 2012). Therefore, in order to adequately characterize the hydraulics of the fishway, the three components of flow velocity (X, Y and Z) were measured with a Vectrino 3D ADV (Nortek AS) oriented downwards following a point-wise methodology. For this, a sampling point grid was created to cover the entire pool area with tighter spacing near the openings (5 cm), as these are areas of more pronounced velocity fluctuations, and wider spacing in the middle of the grid (10-15 cm). Velocity measurements were performed at a) two horizontal planes parallel to the flume bed (plane 1 at a height of 10cm from the bottom, i.e. half the height of the bottom orifice and plane 2 at a height of *ca.* 78% of pool mean depth (*hm*), the plane directly affected by the surface notch), and b) two vertical planes, at the mid-width of each opening, parallel to the sidewalls (Fig. 7.1, Table 7.2). Measurements were performed at a 25 Hz rate for 90s as this frequency and period were previously defined to be representative (Santos et al. 2012), at the second upstream pool. The hydraulic balance attained in the fishway allowed for any pool to be representative of every pool in the fishway. Instantaneous measures of velocity were filtered afterwards using the Goring and Nikora (2002) phase-space threshold despiking method, modified by Wahl (2002), using the WINADV freeware program (Wahl 2001). Turbulence was characterized through Reynolds shear stress (RSS), which was calculated for the horizontal plane XY and for the vertical plane XZ, using the following formulas respectively:

$$-\rho\overline{\mu'v'} \quad (1) \qquad\qquad -\rho\overline{\mu'w'} \quad (2)$$

where ρ = fluid density, *μ′* = fluctuating component of the velocity in the x direction, *v′* = fluctuating component of the velocity in the y direction and *w′* = fluctuating component of the velocity in the z direction.

7.3.3. *Species selection*

The vast majority of studies on negotiating fishways use salmonids as target species. Advancing the scientific knowledge on navigating fishways requires the study of different non-salmonid species. Cyprinids are the dominant group of autochthonous freshwater fish in Mediterranean rivers ranging from large-size benthic potamodromous species to small-size pelagic ones, thus presenting different body shapes and occupying a range of ecological niches (Ferreira et al. 2007). As studying the movements of all species would be time consuming, budget prohibitive and ultimately unfeasible, two species were chosen as representative of two morpho-ecological guilds (Chan 2001): the Iberian barbel (*L. bocagei* as the representative of large-bodied potamodromous benthic cyprinids, and the Southern Iberian chub (*S. pyrenaicus*), as the representative of small-bodied water-column resident cyprinids. The use of guilds, which represent groups of organisms independent of taxonomic envelopes that use the same range of resources (Fauth et al. 1996), has been proposed as a tool for multi-specific approaches (Leonard and Orth 1988).

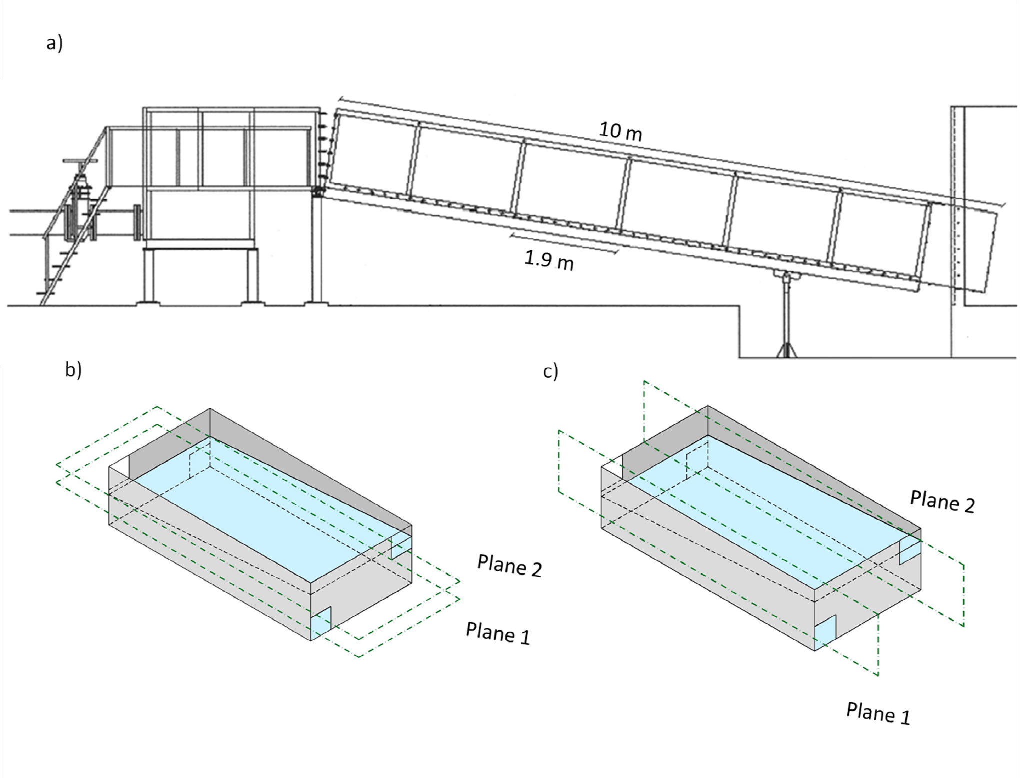

Figure 7.1 - a) Side view diagram of the pool-type fishway experimental prototype on a slope of 8.5%; b) Three dimensional representation of a pool, showing orifice arrangements and the horizontal planes (dashed green lines) where hydraulic measurements were conducted; c) Three dimensional representation of a pool, showing orifice arrangements and the vertical planes (dashed green lines) where hydraulic measurements were conducted.

Table 7.1 - Description of the two tested flow regimes. Q – fishway discharge; *h*m – pool mean depth.

Flow Regime	Q ($L.s^{-1}$)	Orifice	Notch (width)	*h*m
Plunging	59.3	0.2m x 0.2m	0.2m	0.9m
Streaming	78.5	0.2m x 0.2m	0.2m	1.0m

7.3.4. *Experiments*

Two different flow regimes - plunging and streaming - were tested (Table 7.1). Three replicates of individual schools of 5 fish for each species were studied independently for each flow regime. Barbel and chub were captured on small coastal rivers from the Tagus river basin, central Portugal, during the migration season (Spring), by means of electrofishing using the procedures adopted by the European Committee for Standardization (CEN 2003). Fish were collected using a dip net and promptly placed in a mesh container fixed to the river bed at a location away from the influence of the electric field, allowing fish to be maintained in natural temperature and oxygenation conditions for the duration of the capture period. Fish were chosen to be of comparable length, and were transported to the laboratory in aerated containers filled with river water. Care was taken to reduce stress and expedite the procedure. At the laboratory, fish were stabilized in acclimation tanks (700 L) for at least 48h before they were tested. Tests were performed in Spring during the migration season. The quality of the water was examined on a daily basis and changed at a ratio of 150 L per day. Feeding stopped 24h before each experiment. Fish were acclimatized to the fishway environment as for each experiment they were introduced in the tailwater-pool where the fishway openings were obstructed by a mesh panel that was removed after a period of 30 minutes. Each experiment lasted 90 minutes and was performed during the period of dusk and early night (17h-01h) to reflect the natural period of migration (Santos et al. 2002, 2005). Each fish was only used once and was allowed to ascend the fishway on its own volition. Two independent observers monitored the fish movements within the fishway. It was considered a “movement” whenever a fish negotiated a cross-wall in the upstream direction (a pool-to-pool displacement by one fish); it was considered a “success” when a fish reached the top of the fishway by negotiating the fifth cross-wall. All upstream pool-to-pool displacements performed by any fish in the school during the full length of the experiment (90 min.) were registered. After each experiment fish were observed carefully to see if any injury, tissue damage, bruising and direct or delayed mortality was induced by excessive turbulence (Cada 2001, Odeh et al. 2002, Neitzel et al. 2004).

7.3.5. *Data analysis*

Differences in the number of upstream movements performed by the species during each flow regime - plunging and streaming - and through both opening types - bottom orifice and surface notch - were tested using proportion tests based on Chi-square distribution. The same procedure was applied to test for differences in the number of successful fishway negotiations attained individually and by both species in each of the flow regimes. To test the influence of flow regime, opening type and their interaction (flow regime x opening type) on the upstream movements of both species, a PERMANOVA test (permutation of residuals under a reduced model (Anderson and Robinson 2001)) was applied. This statistical analysis is a powerful non-parametric approach that uses a permutational technique to enable significance tests for small sample sizes to be conducted (Walters and Coen 2006) and was used to test the null hypotheses: (1) flow regime had no effect on the upstream movements of fish; (2) opening type had no effect on the upstream movements of fish; (3) effects of flow regime and opening types did not interact. Additionally, Mann-Whitney U tests and Sign tests were applied to the hydraulic data, to test for differences in flow velocities and turbulences (i.e. the Reynolds shear stress) between the two flow regimes. Chi-square proportion tests were performed in MedCalc software (MedCalc Software bvba). Mann-Whitney U tests and Sign tests were carried out in the software STATISTICA (STATSOFT INC. 2000). PERMANOVA tests were performed with the package PERMANOVA for PRIMER+v6.0 (Clarke and Gorley 2006, Anderson et al. 2008).

Table 7.2 – Point-grid information for the measurements performed with the Acoustic Doppler Velocimeter (ADV) at the 4 planes for each flow regime

Flow Regime	Orientation	Plane	# points in the grid	Measured at
Plunging	Horizontal	1	97	10 cm from the bottom
Plunging	Horizontal	2	97	70.5 cm from the bottom
Plunging	Vertical	1	104	10 cm from the lateral wall adjacent to the notch inlet
Plunging	Vertical	2	104	10 cm from the lateral wall adjacent to the orifice inlet
Streaming	Horizontal	1	97	10 cm from the bottom
Streaming	Horizontal	2	97	78.2 cm from the bottom
Streaming	Vertical	1	105	10 cm from the lateral wall adjacent to the notch inlet
Streaming	Vertical	2	106	10 cm from the lateral wall adjacent to the orifice inlet

7.4 Results

7.4.1. *Hydraulics*

Figure 7.2 shows the flow velocity contours and vectors of both tested flow regimes at the two horizontal planes measured. On horizontal plane 1 of the plunging flow configuration, a jet-flow region could be distinguished from the water inlet to the opposite cross-wall. Horizontal plane 2 of this flow regime was characterized by a velocity peak close to the inlet of the water plunge that shaped a short downstream jet-flow region, interrupted by the main upstream flow. At horizontal plane 1 of the streaming flow regime, a large jet-flow region going from the water inlet to the opposite cross-wall could be observed. Horizontal plane 2 of this flow regime was characterized by a jet-flow from the water inlet to the opposite cross-wall. When compared, through a Sign test, the flow velocity pattern (XYZ resultant) in the two tested flow configurations differed on horizontal plane 2 (Sign test $Z = 4.67$, Non-ties = 97, $p < 0.001$), closest to the water surface. Differences between flow regimes also arose in both horizontal planes, when the patterns of the horizontal and vertical components of Reynolds shear stress, were compared through Sign tests (Plane 1: RSS_{xy} - $Z = 3.66$, Non-ties = 97, p-value < 0.001; RSS_{xz} - $Z = 3.66$, Non-ties = 97, $p < 0.001$; Plane 2: RSS_{xy} - $Z = 2.64$, Non-ties = 97, $p = 0.008$; RSS_{xz} - $Z = 3.45$, Non-ties = 97, $p < 0.001$).

Figure 7.3 shows the water velocity contours and vectors of both tested flow regimes at the two vertical planes considered. In the plunging flow, vertical plane 1, there was a noticeably high velocity plunge of water that was interrupted by an upstream flow. Vertical plane 2 of the same regime showed a strong jet stream region t from the water inlet to the opposite cross-wall. The streaming flow regime is characterized by a vertical plane 1 where the water flows, through the entire water column, from the water notch inlet towards the water outlet. Vertical plane 2 of this regime shows a strong jet stream from the water inlet up to the opposite cross-wall. When compared, through a Mann-Whitney U test, the water velocities (XYZ resultant) in the two tested flow regimes differed on vertical plane 1 ($U = 4526$, $N_1 = 104$, $N_2 = 105$, $p = 0.033$). This is the vertical plane which is under the direct influence of the surface notch inlet. In this vertical plane differences also arose when the same comparison was made for the Reynold’s Shear Stress horizontal and vertical components (RSS_{xy} - $U = 4343$, $N_1 = 104$, $N_2 = 105$, $p = 0.011$; RSS_{xz} - $U = 4139$, $N_1 = 104$, $N_2 = 105$, $p = 0.0025$).

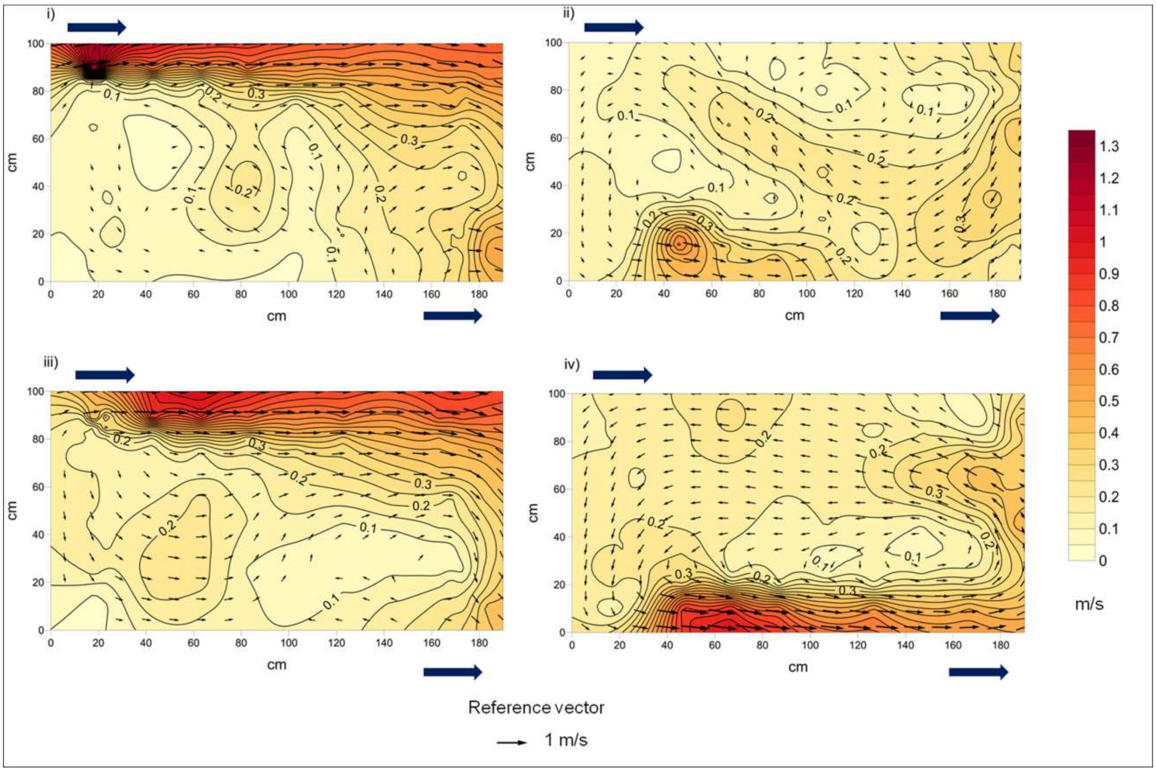

Figure 7.2 - Velocity contour lines and vectors for the two horizontal planes in the two flow regimes. Plane 1 measured at 10 cm, Plane 2 measured at 78% pool mean depth (*h*m). Arrows within the diagram show the direction and magnitude of flow. Arrows outside of the diagram show the water inlet and outlet points. i) Plunging flow regime horizontal plane 1; ii) Plunging flow regime horizontal plane 2; iii) Streaming flow regime horizontal plane 1; iv) Streaming flow regime horizontal plane 2.

7.4.1. *Fish*

The fishway experiments showed that fish used the two opening types differently depending on flow regime and were closely related to the differences found in the hydraulic characterization (Table 7.3). During the plunging flow regime, 94% of all the upstream movements were conveyed through the bottom orifice opening (χ^2= 163.189, $p < 0.0001$). A different result was observed for the streaming flow where the upstream movements were conveyed preferentially through the surface notch (57%) while 43% occurred through the bottom orifice opening (χ^2= 10.208, $p = 0.0014$). The overall number of upstream movements between flow regimes was also different, with 74% of the movements occurring during the streaming flow regime (χ^2= 180.599, $p < 0.0001$). This difference in the number of movements was also reflected in a higher number of successful fishway negotiations, with 74% (χ^2= 61.725, $p < 0.0001$) occurring in the streaming flow regime.

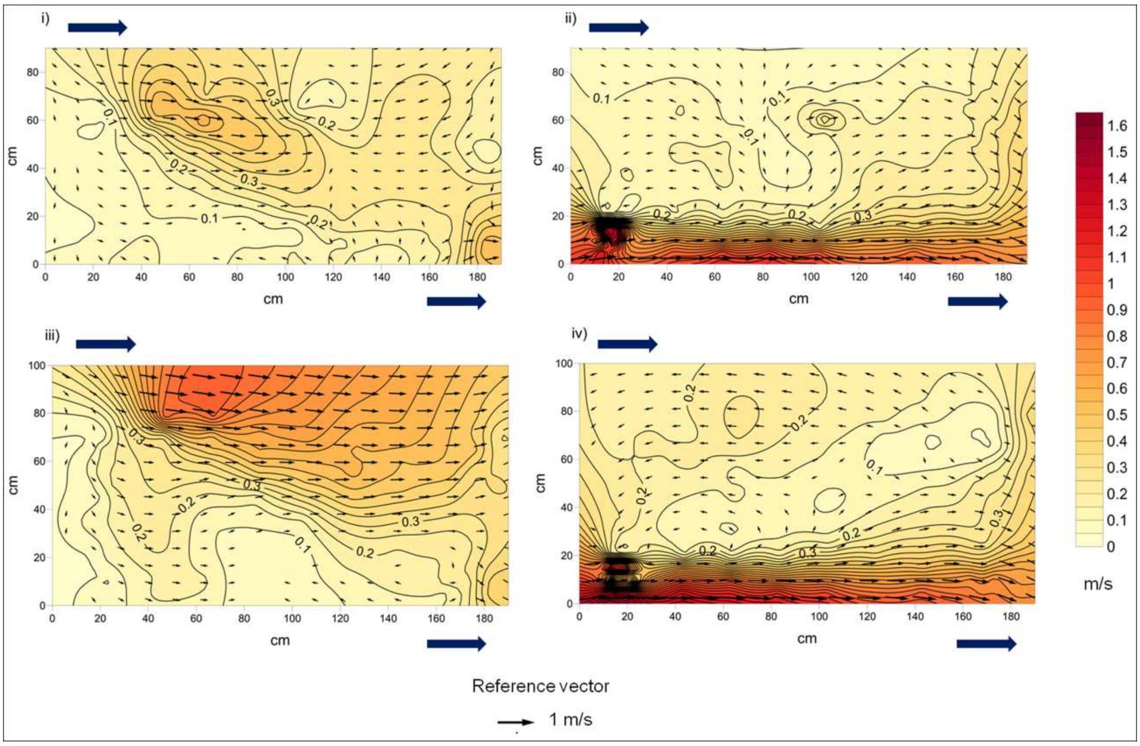

Figure 7.3 - Velocity contour lines and vectors for the two vertical planes in the two flow regimes. Planes were measured at 50% of the orifice width. Arrows within the diagram show the direction and magnitude of flow. Arrows outside of the diagram show the water inlet and outlet points. i) Plunging flow regime vertical plane 1; ii) Plunging flow regime vertical plane 2; iii) Streaming flow regime vertical plane 1; iv) Streaming flow regime vertical plane 2.

The fishway experiments showed that the barbel used the facility differently for each distinct flow regime. Results from the PERMANOVA analysis (Table 7.4) showed a significant flow regime effect on the number of upstream fish movements within the fishway: overall, experiments conducted during streaming flow conditions revealed a higher proportion of barbel movements (80%) relative to plunging flows (20%). The effect of opening type alone was not significant, as the overall proportion of fish using notches (38%) and orifices (62%) were found to be similar. This produced a non-significant regime-by-opening type interaction. Experiments conducted during plunging flow conditions revealed an unequal proportion of movements through the orifices (97%) and notches (3%) (Fig. 7.4) (χ^2 = 64.474, $p < 0.0001$). During the streaming flow conditions, barbel tended to use the two opening types an almost equal percentage of times (χ^2 = 1.571, p = 0.21), as 46% of the upstream movements were undertaken through the surface notch and 54% through the bottom orifice (Fig. 7.4). In fact, 99% of all barbel's upstream movements through the surface notch were fulfilled in the streaming flow regime (χ^2 = 132.250, $p < 0.0001$). When analyzing the number of successes registered in each of the flow regimes there was evidence of higher success in the streaming flow regime (χ^2 = 32.508, $p < 0.0001$), which had over three times more successes (76%) than the plunging flow.

Table 7.3 - Number of upstream movements (i.e. upstream pool-to-pool displacements of a single individual) performed by all the individuals of each species through the bottom orifice and surface notch in the experimental pool-type fishway in both flow regimes (Plunging and Streaming). The number of successes (i.e. the number of times a fish attained the top of the fishway by the negotiation of the fifth cross-wall) achieved by all the individuals of each species in both flow regimes is also shown. The values of Total length (cm), Standard length (cm) and Body mass (g) are also presented (average ± standard deviation).

Species	Flow regime	Bottom orifice	Surface notch	Total	# of successes	Total length	Standard length	Body mass
Barbel	Plunging	37	1	38	15	26 ± 3.9	20.6 ± 3.4	181.2 ± 88.0
	Streaming	71	83	154	48	25.5 ± 2.3	22.7 ± 2.9	239.6 ± 26.0
Chub	Plunging	63	5	68	10	12.9 ± 2.4	10.7 ± 2.0	28.6 ± 16.0
	Streaming	46	98	144	36	12.7 ± 1.5	10.6 ± 1.3	25.5 ± 8.7

The fishway experiments showed that the chub used the facility differently for each distinct flow regime. Results from the PERMANOVA analysis showed that flow regime had a significant effect on the number of fish upstream movements within the flume: in general, experiments performed in streaming flow regime revealed a higher ratio of chub movements (68%) relative to plunging flow regime conditions (32%). The isolated effect of opening type was not significant, because the overall proportions of fish using the notch opening (49%) and the bottom orifice (51%) were found to be equivalent. Nevertheless, a significant interaction between regime and opening was detected ($p < 0.01$), indicating thereby that the flow regime affected the number of upstream movements differently, depending on the type of cross-wall opening. Accordingly, tests conducted in plunging flow regime revealed an uneven proportion of movements occurring through the bottom orifice (93%) and surface notch (7%) (Fig. 7.4) (χ^2 = 95.559, $p < 0.0001$). As a result, the bulk (58%) of the upstream movements undertaken by chub through the bottom orifice were completed during the plunging flow condition (χ^2 = 4.697, p = 0.0302). In contrast, chub were more likely to use the surface notches (68%) for streaming flows to the detriment of bottom orifices (32%) (χ^2 = 36.126, P < 0.0001), and, as a result, 95% of all upstream movements through the surface notch were accomplished during streaming flow conditions (χ^2 = 164.349, P < 0.0001). When analyzing the successes registered in each of the flow regimes there was evidence of higher success achieved during streaming flow conditions (78%) relative to plunging flows (χ^2 = 27.174, P < 0.0001). After the experiments, fish did not present any signs of injury produced by turbulence.

Table 7.4 – Levels of significance of the two-factor PERMANOVA – permutation of residuals under a reduced model – testing the effects of flow regime plunging/streaming (Regime) and surface notch/bottom orifice (Opening type) on the upstream movements of barbel and chub. * - Significant with an α = 0.05.

		Sum of Squares	Degrees of freedom	Mean Squares	Pseudo-F	P (perm)	Unique permutations
Barbel	Regime	1121.3	1	1121.3	11.317	0.010*	891
	Opening type	192.0	1	192.0	1.938	0.272	917
	Regime*Opening type	48.0	1	48.0	0.484	0.536	936
	Residuals	792.7	8	99.1			
Chub	Regime	481.3	1	481.3	11.460	0.008*	910
	Opening type	3.0	1	3.0	0.007	0.792	927
	Regime*Opening type	1008.3	1	1008.3	24.008	0.006*	921
	Residuals	336.0	8	42.0			

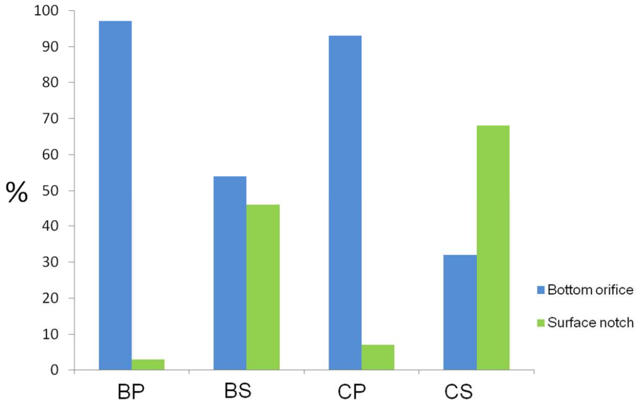

Figure 7.4 – Proportions of upstream movements through both opening types by each species for both flow regimes. BP – Barbel in plunging flow regime; BS – Barbel in streaming flow regime; CP – Chub in plunging flow regime; CS – Chub in streaming flow regime.

7.5. Discussion

The morphology of a fish species, its body size and shape (Videler and Wardle 1991, Videler 1993, Katopodis and Gervais 2012) can determine the swimming ability and hydraulic suitability of the species to a specific environment (Chan 2001). This study allowed the assessment of movements and navigation behaviour of cyprinid species representing different morpho-ecological guilds (benthic/potamodromous *vs*. water-column/resident) within a full-scale model of a pool-type fishway with different flow regimes. It contrasts with the majority of studies on fish transfer devices that often lack balanced experimental designs. It overcomes study limitation conducted in the wild by enabling the variables of interest to be manipulated while controlling for confounding effects (Kondratieff and Myrick 2005). The importance of this study is highlighted by the fact that it is the first study that examines and compares the movements and navigation behaviour of two morpho-ecologically different fish species in a pool-type fishway with streaming or plunging flow. The vast majority of studies have neglected the streaming flow regime of pool-type fishways and only studied the plunging flow regime (Katopodis and Gervais 2012). The philosophy behind fishway research, design, and construction has evolved over the years and has been moving towards more holistic fishways, i.e. fishways that can serve a wide spectrum of species with different ecological niches. By focusing on the nature of movements of different species guilds within a fishway, this work moves a step forward towards holistic multi-species fishways.

The upstream movements of any fish are, as those of other animals (Goedmakers and Pinkster 1981, Erman 1986), always non-random and are a consequence of colonization, reproductive or feeding needs. During the experiments both fish species showed to be able to negotiate the fishway in both flow regimes. After the experiments, fish did not present any signs of injury produced by turbulence, indicating that fish probably limited their exposure to high RSS and flow velocities to a minimum.

Recent studies have defined the critical swimming speed of barbel (Mateus et al. 2008) – 0.81 $m.s^{-1}$ (3.1 $BL.s^{-1}$) – and of chub's sister species the bordallo (*Squalius carolitertii* (Doadrio, 1988)) (Romão et al. 2012) - 0.54 $m.s^{-1}$(4.4 $BL.s^{-1}$). The flow velocity in the bulk of the pool area for the two flow regimes never surpassed 0.3 $m.s^{-1}$ attaining only higher velocities near the water inlets. This demonstrates that the velocity fields in both flow regimes were acceptable for these species and allowed fish to recover from negotiating the cross-wall where they had to undertake burst movements to offset the high flow velocities found at the cross-wall openings.

The findings of this study showed that during the plunging flow regime, the surface notch was seldom used by either species, which was not surprising since cyprinids are known to have a limited leaping ability (Bunt 2001). An opposite trend was found for a salmonid species, the Atlantic salmon (*Salmo salar*), that preferred to use the surface notch opening for its upstream movements in an experimental pool-type fishway during plunging flow regime (Stuart 1962). Guiny et al. (2003) studied salmonids (Atlantic salmon parr and brown trout (*Salmo trutta*)) and found that both species used almost exclusively the bottom orifice to negotiate a cross-wall. It is important to note though that in the Guiny et al. (2003) experiments the water column below the cross-wall was just 20 cm deep, and with this reduced depth the plunging water touched the flume bed and rebounded. This effect created flow vectors moving in different directions and may have reduced fish movements through the surface notch. In the present study, the vast majority of upstream movements during plunging flow by both tested species occurred through the bottom orifice. This result is in line with the findings of Silva et al. (2009), where barbel also preferred to use the bottom orifices in contrast to the surface notch opening type for their upstream movements during plunging flows. Ficke et al. (2011) also concluded that pool-type fishways that require fish to leap over the crest of the surface notch and instream structures that produce a vertical drop of more than 10 cm will not allow significant upstream passage of small-sized fish species. In the current study, only a few individuals of both species, most likely those with stronger swimming capacity, were able to negotiate the pool through the surface notch during plunging flow. These results confirm the hypothesis that species would not be able to use the surface notch during plunging flow, and will be forced to use the bottom opening. On the other hand, streaming flow facilitated access to the surface notch, allowing species to move upstream more successfully with fewer constraints and possibly with less energy expenditure, increasing the number of movements. By turning the surface notch into a more accessible opening type, the streaming flow regime increased the area available for negotiating cross-walls. However, species displayed different choices of opening types for their upstream movements. These preferences are congruent with their different morpho-ecologic guilds: the chub, a water column species, had a clear preference for the surface notch opening. In contrast, the barbel, a bottom oriented species, divided their upstream movements between opening types, demonstrating that this is a plastic species with the ability to use the entire water column.

The positive rheotactic behaviour during their upstream migrations (Bunt 2001, Williams et al. 2012) guides fish upstream by orienting them against the downstream flow. Fish may also display rheotactic responses to turbulence promoting migratory movements (Coutant 1998, Williams et al. 2012). Based on these facts, the hydraulics of the two tested flow regimes allowed a simple explanation of the experimental results. The plunging flow regime provided little or no attraction to the surface notch, since an upstream flow circulation was generated which interrupted the downstream flow possibly miss-orientating fish. The same does not happen for the streaming flow, where there was a continuity of downstream flow allowing fish to be attracted to the surface notch. Looking at vertical plane 1, this pattern becomes even more evident. In streaming flow there was continuity of flow in the entire length of the pool and throughout the pool water column. This is in contrasting with the sudden change in flow direction observed in vertical plane 1 of the plunging flow regime. The fact that the flow regimes differed in their RSS patterns also supports the difference in movements and successes attained in both flow regimes. This proves that not only velocity but also turbulence parameters can explain fish preferences when navigating through a fishway (Coutant 1998, Silva et al. 2012).

Streaming flow proved to be a more efficient flow regime by enhancing upstream movements, facilitating the movement of the surface oriented species and increasing the options of the bottom oriented species. Through a more suitable hydraulic environment, streaming flow increased the negotiation success of both species. Thus, the streaming flow configuration is the most suitable for fishways constructed in river systems in which a wide range of fish morpho-ecological traits are found. Existing fishways should be retrofitted to accommodate the behaviour and swimming capabilities of the species present at the site (Johnson et al. 2012). The present study shows that enabling streaming flows on future and on existing fishways is desirable. This must be considered during fishway design to allow this flow regime to be attained even with low flows. Future studies should concentrate on the behaviour of other non-salmonid species in pool-type fishways. Focusing on the swimming capabilities of different species, finding the best fishway configuration that maximizes attraction (Francis 1870, Green et al. 2011, Katopodis and Williams 2012), keeping velocity gradients (Williams et al. 2012) and turbulence levels acceptable (Silva et al. 2012), ensuring negotiation success of all fish species present in the target system, and minimizing fishway selection of species, size-classes and ages (Agostinho et al. 2002, 2007, Mallen-Cooper and Brand 2007, Naughton et al. 2007) is the best way to move towards the objective of an holistic fishway that accommodates the entire range of species present at a given system.

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Section IV

General discussion

> *"The great tragedy of science – the slaying of a beautiful hypothesis by an ugly fact."*
>
> Thomas Huxley

Chapter 8

Discussion

“Science never solves a problem without creating ten more.”

George Bernard Shaw

River connectivity is regarded as one of the most important variables to be considered when developing studies in freshwater systems (Cowx and Welcom 1998, Roni et al. 2002, Kondolf et al. 2006, Rahel 2007). Of the four classic dimensions of connectivity (Ward 1989), longitudinal connectivity is accepted as the most important for fish species (Fausch et al. 2002). This dimension has been seriously affected by the construction of horizontal instream obstacles that fragment the river systems into isolated reaches, frequently incapable of maintaining healthy fish communities, and hamper fish movements limiting the completion of their life-cycle. The disconnection created by obstacles leads to a loss of genetic variability and potentiates extinction risk (Nicola et al. 1996, Peňáz et al. 1999). Such alterations of structural connectivity inevitably lead to functional changes of the systems and, as such, to alterations of functional connectivity of rivers. To counteract these impacts, connectivity enhancement actions are urgent and are emerging vigorously (Amoros and Roset 2002, Bash and Ryan 2002, Ormerod 2003). But ever present budget limitations require that restoration actions be effective and provide significant reconnection effects, and so correct resource allocation must be a priority.

The purpose of the present thesis was to understand the impacts of longitudinal connectivity losses on potamodromous and resident fish species and to define ways to reduce these impacts by enhancing connectivity. The studies pursued here point towards an impact of full barriers on the structural and functional connectivity of river networks. A methodology to assist resource allocation, by prioritizing barriers to be intervened to enhance connectivity is defined; and an input on best practices and designs for fishway construction, or retrofitting actions, to improve fish movements on fragmented systems is also given. Contrarily to other studies, this thesis is anchored on quantification of longitudinal connectivity, based on analytical techniques.

In this section, the results and conclusions attained in sections II and III are summarized and an integrated overview of the works therein is given to provide a better understanding on how those studies, while providing responses to specific scientific questions, are connected to deliver a solid thesis on river longitudinal connectivity for fish species.

8.1. Is the distribution of fish species affected by longitudinal connectivity losses?

This question is answered in the first work (Chapter 2), where barriers of different sizes were pooled together to determine if the presence of instream barriers affected the distribution of several fish species grouped into three ecological guilds (potamodromous, residents and exotic species). To accomplish that, and because the use of models can be a limitation due to their simplification of ecological reality, multiple modelling techniques were used (Segurado and Araújo 2004). It was theorized that barriers would negatively impact the distribution of potamodromous and, to a lesser extent, the distribution of resident species. It was also hypothesized that due to their preference for lentic habitats, exotic species would be favoured by flow regulation. Albeit these literature supported theorizations, the results of this study pointed towards the impossibility to isolate the influence of barriers on defining the distribution of freshwater fish species of all three ecologic guilds. Results showed that the effect of environment and pressure variables exceeded the isolated effect of connectivity related variables. Most of the analysed barriers were of reduced dimensions and produced small low-depth lentic environments that do not homogenize large extensions of habitat, allowing for a certain degree of habitat heterogeneity to be maintained. The results could also have been limited by the lack of historic data about the distribution of fish species in the absence of barriers situation, which forced the adoption of a spatial treatment instead of a temporal approach. Another important fact that may have limited the discrimination of barrier impacts on fish distribution was that barriers of all sizes were pooled together. While it can be assumed without an element of risk that big barriers (dams and small hydropower plants) are completely insurmountable, the same may not be valid for small weirs (< 2m) that cease to act as full barriers with increasing water levels (Ovidio and Phillipart 2002) allowing passive and possibly active movements of the species to occur. There is the possibility, untested in this study, that suitable habitat between barriers exist, which might have also covered the impact of barriers. It is however apparent that understanding the effects of connectivity loss on freshwater fish species and communities is an aim that needs to be further pursued. This study showed that although barriers may affect community structure, recruitment and abundance, the distribution of freshwater fish species is not affected by barriers, given that, for some barriers, the blockage effect is only intermittent. This presents a change in the way large-scale approaches deal with connectivity.

8.2. Can structural and functional connectivity be determined for a river network?

This question is answered in the second and third studies presented in this thesis (Chapters 3 and 4). In these works it is defined a methodology, based on spatial graphs, that allows to quantitatively define the current connectivity of a given river network, and it is applied as an example to the Tagus River. This methodology also allows understanding the historical evolution of the connectivity of the network following the chronologic implantation of barriers starting from the situation of no barriers being present.

Rivers are a special case of spatial graph, where the network is pre-determined and has a strong directionality obliged by natural, downstream, river flow. A clear distinction between these and terrestrial landscape analysis, where even with the loss of several nodes it is possible to maintain a high degree of connectivity (Urban and Keitt 2001, Barabasi and Bonabeau 2003), is that the protection of highly connected groups of nodes (hubs) is impossible since there is only one link between elements of the network. River network connectivity is thus severely affected by the loss of even a single node, due to the lack of an alternative pathway.

Chapter 3 focuses particularly on the structural connectivity of river networks, looking at the length of segments that constitute the aforementioned network. Here the node weighting scheme is based on the principle that longer connected patches sustain bigger, more diverse, and thus healthier and more resilient fish communities (Perkin and Gido 2012). Chapter 4, on the other hand, is more focused on functional connectivity, appending to the methodology defined in the previous chapter a technique to model fish habitat suitability. This technique, based on Boosted Regression Trees (Elith et al. 2008), allows nodes to be weighted with the habitat suitability of that node for the species, group of species or guild of species targeted in each study.

The connectivity of a river network is deleteriously affected by barrier placement. The results from the applied case study (Tagus River) point towards a continuous decrease of overall river connectivity with the succession of barrier implantation. This result is concurrent for both structural and functional connectivity. In both cases, contrarily to the expected, the first few barriers had a limited effect on connectivity, due to the locationt of the first implanted dams, in lower order streams. Cote et al. (2009) found an opposite trend in relation to the impact of the first implanted barriers, but was collinear to the results of chapters 3 and 4 when stating that beyond a certain point barrier additions affect increasingly less the network connectivity. Additionally, the results of chapter 3 also point towards a non existing relationship between isolated and joint impact of barriers on overall network connectivity. The impact of each barrier is thus, dependent on the location of previously implanted barriers. Correct barrier placement can produce a limited connectivity reduction, allowing the network to maintain a high degree of connectedness.

The methodology defined here has several advantages: i) it is a direct approach, using spatial graphs that apply well to aquatic environments (Schick and Lindley 2007, Erös et al. 2011, 2012, Pereira et al. 2011); ii) it is able to incorporate different node weighting techniques (segment length, habitat suitability for a species, a group of species or ecologic guilds); iii) allows connectivity studies to be undertaken at large spatial scales; iv) it is able to determine the impact of an isolated barrier but it is also able to determine the cumulative effect of all existing barriers, which has been pointed out as the main limitation of existing methods (O'Hanley and Tomberlin 2005, Kemp and O'Hanley 2010); v) it is based on single measures quantified in relation the reference conditions of the network – free from barriers – which helps to establish a benchmark for connectivity restoration; vi) it is able to predict connectivity reductions upon the building of new barriers, helping decision-makers to select locations of least impact; and vii) it does this while recurring to freely available software (Ridgeway 2007, Saura and Torné 2009, Saura and Rubio 2010, R Core Team 2012, Hijmans et al. 2013).

8.3. Can the enhancement of structural and functional connectivity be prioritized for river networks?

This question is answered in the second and third studies presented in this thesis (Chapters 3 and 4). In these works it is defined a methodology based on spatial graphs that allow barriers to be ranked according to their structural (chapter 3) or functional (Chapter 4) connectivity enhancement priority. This is a stepped method that, iteratively at each step, defines the amount of overall connectivity gained by the removal of a single barrier. The second and following steps perform the same evaluation but accommodate the removal of the barrier elected in the preceding step. This technique allows defining connectivity restoration goals as the percentage of overall connectivity to restore. It is a very advantageous methodology because it shares most of the advantages described in the section above for the connectivity definition techniques, as these are the basis for the prioritization.

Numerical techniques that aid decision making while maintaining scientific accuracy are of the utmost importance (Karr and Chu 1999, Knapp et al. 2003, Paul 2003). Connectivity restoration prioritization schemes are increasingly needed to promote a correct allocation of finite resources. The existing ranking and ordering systems ranging from simple benefit-cost ratio to more elaborated optimization models (e.g. O'Hanley and Tomberlin 2005) are generally constituted by three measures: i) net increase in accessible habitat after barrier removal, in terms of quality-weighted area or river length, ii) degree to which a barrier limits movements, and iii) cost of connectivity restoration. These methods, contrarily to the one proposed in this thesis, do not consider the contribution of disrupted links to the overall connectivity of the river network. In the proposed technique, a barrier located at a key river segment, with high contribution to the overall integrity of the river network, is favoured in the prioritization.

The present methodology is innovative by being able to define restoration priorities in accordance to the restoration target: structural connectivity - applicable regardless of species or species group; and functional connectivity – species or guild based or for the entire fish community. As for all restoration plans, when applying this methodology to prioritize connectivity restoration actions, the purpose of restoration must be considered carefully. Restoration directed to a species or a group of species, although yielding similar results, is case-specific.

8.4. Can boulders enhance habitat availability and thus connectivity?

This question is answered in the fourth study presented in this thesis (Chapter 5). When planning connectivity restoration actions, almost as important as ensuring that fish species are able to negotiate barriers, is the insurance that fish species are able to move towards the connectivity enhanced barrier. In such cases, habitat availability has to be, in some cases, increased to allow for habitat connectivity to facilitate species' movement along the river network.

Instream structures placement should try to mimic conditions found at undisturbed nature-like segments of the same river network. Boulders and logs have proved to be the most adequate structures to accomplish this by displaying lower failure rates when applied in habitat enhancement actions (Roni et al. 2006). The placement of boulders is even known to increase salmonids abundance (Overton et al. 1981, Ward and Slaney 1981, Moreau 1984, West 1984, House and Boehne 1985, Fuller 1990, Hvidsten and Johnsen 1992, Linlokken 1997, O'Grady et al. 2002, Dolinsek et al. 2007a, 2007b). Nevertheless, species will only give a positive response to habitat enhancement actions if the water has enough quality to sustain them (Stewart et al. 2009). Another requisite for the increase of fish density is the existence of a source of colonists (Pretty et al. 2003), the intervened reach has to be near high quality reaches that support a high number of potential colonists. To accomplish the restoration goal, rehabilitation has to begin by identifying the limiting habitat (Rosenfeld and Hatfield 2006, Vehanen et al. 2010) for fish density and diversity. This reinforces the fact that restoration plans are always case-specific and that they need always to consider the reference fish assemblages as benchmarks for restoration success (Nestler et al. 2010, Boavida et al. 2011).

In this study, several boulder placement scenarios were modeled on a degraded site in an attempt to mimic the conditions found at an undisturbed site. This undisturbed site had, in relation to the disturbed one, coarser substrata, was dominated by native species and presented a higher native species diversity. The scenarios with the lower boulder density promoted a measurable increase in habitat availability (i.e. wet usable area) for fish. These structures do not affect solely habitat availability, they also affect fish movements by connecting habitats. The results of Chapter 5 emphasize the convenience of boulder placement to increment fish habitat and fish movements. Boulder substrata is a valuable instrument for river restoration, but variables such as boulder size, density and location of placement are important for the successful enhancement of river conditions and connectivity between habitats.

8.5. Can boulder placement improve fishway negotiation?

This question is answered in the fourth and fifth studies presented in this thesis (Chaper 5 and 6). The most common way to circumvent an obstacle, and to mitigate its impacts, is to implant a fish passage device. However, the majority of these structures are not suited for native cyprinids, their design is influenced by guiding principles defined for salmonid fish species (e.g. Pinheiro and Ferreira 2001), known strong swimmers. Adequate design parameters for native freshwater species with different morphological and ecological characteristics must be determined. Several authors (e.g. Hinch and Rand 2000, FAO/DVWK 2002, Baker and Boubée 2003) believe that the increase of the bottom heterogeneity of fishways, using materials like logs, boulders or stones, may facilitate fish navigation of such facilities.

The works presented herein approached boulder placement at the bottom of fishways from two ways: in Chapter 5 two boulder arrangements of different density were studied, and in Chapter 6 two relative depths of flow were studied. Noonan et al. (2012) in a review of fish passage efficiency discovered that conventional fishways, with smooth bottom, yielded a mean upstream efficiency of 40%. When comparing this result to the results of the present studies, it seems to exist a positive impact of boulder placement at fishways bottom, facilitating fish movement by increasing the ability of fish to negotiate pool-type fishways.

Lower substrata density attained a higher fish negotiation success since this configuration allows for the maintenance of an uninterrupted attraction flow that maintains fish oriented upstream and stimulates fish to negotiate the facility. Additionally, the arrangement of higher boulders with lower water depths was shown to be advantageous for fish passage of fishways. This low relative depth of flow provides for great velocity reductions, creating high spatial hydraulic heterogeneity with small recirculation regions that aid fish movements (Hinch and Rand 1998). It can be hypothesized thus, that the combination of low relative water depths with low boulder density will provide better environment inside the pool, which will potentiate fish passage movements. The use of these structures can originate the formation of low stress pathways for fish movements, often defined as micro-channels (Acharya et al. 2001). These micro-channels have high hydraulic heterogeneity with velocity vectors likely to oppose the main flow and, as such, allow fish to navigate fishways while minimizing energy expenditure.

This work demonstrates that boulder placement on the bottom of fishways creates a better pool hydraulic environment to facilitate fish movements, while turning the fishway into a nature-mimicking structure. The placement of boulders at the base of fishways should be considered when designing new fish transposition facilities and should be regarded as a useful technique to retrofit existing ill-working facilities.

The combination of the present question with the previously stated one proves that the integration of both field and controlled laboratorial methods is a valuable system to research and plan connectivity restoration of barrier impacted river networks. The combined results suggest that boulder placement may act as a whole system driver for fish movement enhancement: facilitating fish movements in the river network by the increase of river habitat availability and connection between habitats, and increasing fish negotiation ability of pool-type fishways.

8.6. Does the flow regime of fishways matter?

This question is answered in the sixth study presented in this thesis (Chapter 7). This was the first study to analyze and compare the passage behaviour of two distinct morpho-ecologic fish species in an experimental pool-type fishway upon distinct flow regimes (plunging and streaming). The vast majority of studies is focused exclusively of plunging flows, neglecting the seemingly more advantageous, for a wide range of species, streaming flow (Katopodis and Williams 2012). Fishway design has to be able to project a fishway that is holistic, that has the capacity to accommodate movements of all native species present at a given system. This work, by focusing on different morpho-ecologic guilds gives a clear contribution to achieve the goal of a more holistic technical fishway.

In this study, the streaming flow showed itself as the most favorable flow regime, it augmented volitional upstream movements and successful fishway negotiations of both fish species. Migrating fish are positively rheotactic (Bunt 2001, Williams et al. 2012), orienting themselves against the direction of the predominant flow. This rheotatic behaviour can also be observed as a response to turbulence (Coutant 1998, Williams et al. 2012). Streaming regime provided a more suitable hydraulic environment where, by a continuous downstream flow in the entire pool length and throughout the water column, fish were attracted and oriented upstream. The results presented herein reinforce the fact that fish fishway navigation preferences can be explain not only by flow velocity vectors, but also by turbulence parameters (Coutant 1998, Silva et al. 2012).

Streaming flow configuration clearly showed to be the best flow regime to be applied to new or existing fishways, placed in river systems that encompass a variety of morpho-ecologic guilds. During the dimensioning phase care must be taken to ensure that streaming flows are attained even at low flows. Existing fishways should be improved to accommodate suitable hydraulics to fit the behaviour and swimming capabilities of the species present in the network (Johnson et al. 2012).

8.7. Final considerations

This thesis contributed significantly to the assessment of the impacts of instream barrier placement on freshwater fish species. It constitutes a holistic approach to the longitudinal connectivity problematic. A clear definition of the problem was elaborated by identifying the impacts of barriers for stream fish species, and a solution was presented by developing a methodology to prioritize connectivity restoration actions, by testing instream boulder placement scenarios to increase habitat availability for fish species, and by testing different fishway configurations to facilitate fish movements.

Barriers do not affect all fish species in the same way. Intermittent barriers do not alter fish distribution as full insurmountable barriers do. These full barriers have severe implications on connectivity of river networks. This thesis allowed progressing a step forward by providing a general framework that determines quantitatively the impact of each barrier, isolated or cumulatively, to the overall structural and functional connectivity of a river network. It also allows prioritizing connectivity restoration actions by analyzing the positive impact of removing each individual barriers as well as a succession of barriers, showing that it is possible to achieve a determined connectivity restoration goal with a reduced restoration effort. This thesis also shows that boulder placement instream or within fishways increases habitat availability and potentiate fish negotiation of fishways, improving overall fish movements in the river network and augmenting thus, connectivity among habitat patches. Boulder placement can be used to retrofit ill-functioning fishways, increasing the range of species and of individuals’ size that are able to navigate through them. Flow regime is also an important variable when designing fishways, because streaming flow, although less common that plunging flow, is in fact more adequate for a variety of species. Nevertheless, each connectivity restoration project is unique and the variables (boulder density, boulder height, flow regime, etc.) must be adapted to the case at hand. This thesis proved that longitudinal connectivity infringement impact evaluation and connectivity enhancement/restoration action planning have much to gain with the inclusion of ecologically valuable insights into the analysis.

8.8. Furthering this…

The present thesis was produced with the aim of answering a series of questions. In the process of doing the work and studies that conduced to this document, several questions were answered but, as often is the case, several other were raised. This is a recurring process in science, the answer to one question generally sparkles interest in new questions. Several questions are still to be answered and must be addressed to fully understand the problems imposed by barriers to longitudinal connectivity. Additionally, these problems must be dealt with in a way to improve connectivity in connectivity hampered systems.

To quantify connectivity more thoroughly, future studies should give special consideration to the directionality of the links between contiguous spatial elements of the river network. Another important step to define the specific impact of single barrier for each species is the definition of its movement permeability asymmetry, thus providing a better understanding of barrier impacts on overall connectivity. To correctly allocate resources to river restoration actions, cost benefit analyses should be appended to connectivity enhancement priority methods. This will allow basin-wide management, integrating all impacts, even those that are cumulative and variable over different temporal and spatial scales.

Different fish species and different life-stages have different habitat and fishway negotiation needs, so fishway design must be adaptable in order to be able to accommodate the needs of the fish community. Future studies should aim at defining optimal instream structures arrangements that convene the requirements of multiple species. Small-scale turbulence as well as different spacing and height of boulders should be studied to enhance fish passage success. The biomechanics of different species should also be determined, in order to ascertain velocity gradients and turbulence levels acceptable for the different species or species guild. The attraction to the fishway is something that still needs to be further investigated to provide maximum attraction for the species present in a given system: a fish can only negotiate a fishway if it finds the entrance. By pursuing the above stated points, there is the assurance of moving towards the creation of holistic fishways that allow successful migration of all the species present in a given system, and minimize fishway selectivity.

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