**Effects of altered river network connectivity in the distribution of *Salmo trutta*:
insights from a metapopulation model**

**Alexia M. González-Ferreras¹, Enrico Bertuzzo², José Barquín¹, Luca Carraro^{3,6},
Carlos Alonso⁴ & Andrea Rinaldo^{3,5}**

*1: Environmental Hydraulics Institute, Universidad de Cantabria - Avda. Isabel Torres,
15, Parque Científico y Tecnológico de Cantabria, 39011, Santander, Spain*

*2: Dipartimento di Scienze Ambientali, Informatica e Statistica. Università Ca' Foscari
Venezia, Venice, Italy*

*3: Laboratory of Ecohydrology, École Polytechnique Fédérale Lausanne, 1015
Lausanne, Switzerland*

*4: Laboratorio de Hidrobiología, ETSI Montes, Forestal y Medio Natural, Universidad
Politécnica de Madrid, Camino de las Moreras s/n, Madrid 28040, Spain*

5: Dipartimento ICEA, Università di Padova, 35131 Padova, Italy

*6: Aquatic Ecology Group, Swiss Federal Institute of Aquatic Science and Technology
(Eawag), 8600 Dübendorf, Switzerland*

Correspondence to: Alexia M. González-Ferreras (gferrerasam@unican.es)

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Abstract

1. Network connectivity is a key feature of rivers that affects patterns and processes in lotic ecosystems. Few studies have considered how changes in river reach connectivity might affect ecosystem attributes at a whole river network scale. The use of population dynamics models of keystone species at a river network scale is crucial to explore how the effects of altered natural connectivity patterns might propagate through a river network.

2. In this study, we present a metapopulation model to estimate the spatial distribution of the population density of brown trout (*Salmo trutta*), an ecologically and socioeconomically important top-predator. The model accounts for the presence of barriers that limit longitudinal connectivity in upstream and downstream directions. The model estimates the spatial distribution of densities of three age-classes (young-of-the-year, juveniles and adults) in all river reaches that make up the network based on topology, connectivity and population dynamics (e.g. age-class specific mortality, spawning, age-class dispersal and spawning migration patterns).

3. 75% of the modelled results fell within the 95% confidence intervals of the empirical data (84.6% for young-of-the-year, 69.2% for juveniles and 69.2% for adults). The removal of all longitudinal barriers to migration in the river network (re-naturalization of the whole catchment) produced an increase in brown trout density in the most downstream reaches of the river network and lowered fish densities in the upstream portion of the network when bias in juvenile and adult movement direction was assumed. Furthermore, the removal of a single obstacle affected fish density even in distant tributaries.

4. The proposed model is an appropriate tool for the evaluation of spatial patterns of brown trout density at a river network scale and for the assessment of the impact of

1 altered connectivity. This might help simulate the results of management strategies
2 regarding river connectivity and showing where population decreases or increases could
3 be expected, although empirical knowledge of overall trout movement in the studied
4 river networks is required for drawing realistic scenarios.
5

1 **1 Introduction**

2 Connectivity is considered one of the fundamental properties of rivers (Moore, 2015),
3 and it influences different patterns and processes in lotic ecosystems (Benda *et al.*,
4 2004; Rodriguez-Iturbe *et al.*, 2009; Fagan, 2002; Carrara *et al.*, 2012; Muneeppeerakul
5 *et al.*, 2008; Muneeppeerakul *et al.*, 2007; Bertuzzo *et al.*, 2007). From a hydrological
6 perspective, connectivity is defined as “water-mediated transfer of matter, energy, or
7 organisms within or between elements of the hydrological cycle” (Pringle, 2001).
8 Although river networks are naturally fragmented (e.g. low flows or waterfalls), human
9 actions have further disconnected these habitats (Fuller, Doyle & Strayer, 2015),
10 changed connections within and between ecosystems over a wide range of habitat types
11 (Crook *et al.*, 2015) and altered the nature of hydrologic connectivity on local, regional
12 and global spatial scales (Rosenberg, McCully & Pringle, 2000; Pringle, Freeman &
13 Freeman, 2000). One of the most important human impacts in this regard is the presence
14 of longitudinal barriers, which may be physical (e.g. dams), biological (e.g. diseases) or
15 physicochemical (e.g. stream temperature or pollution plumes). For example, by the end
16 of the 20th century there existed more than 45,000 large dams in over 140 countries
17 (WCD, 2000) and the number of small dams was (and still is) considerably larger (in
18 the United States alone there are more than 2 million; Smith *et al.*, 2002).

19 Dams provide many benefits to society for drinking water, irrigation,
20 hydropower or recreation (WCD, 2000). However, dams and weirs also have adverse
21 effects on aquatic organisms by reducing upstream and downstream migration and
22 changing water quality and/or habitat conditions (Poff & Hart, 2002). One of the
23 biological groups that are most threatened by the loss of connectivity is migratory fish
24 (Sheer & Steel, 2006), especially migratory fish covering long distances (i.e. >100 km;
25 e.g. *Salmo salar*, Linnaeus 1758; Brevé *et al.*, 2014). Nonetheless, other groups have

1 also been affected by the presence of barriers such as mammals (Pavanato *et al.*, 2016),
2 macroinvertebrates (Cortes *et al.*, 1998), plants (Jansson, Nilsson & Renöfält, 2000) and
3 crustaceans (Miya & Hamano, 1988) among others. Site-specific and local impacts of
4 dams have been extensively investigated (e.g. Greathouse *et al.*, 2006; Lessard &
5 Hayes, 2003; Gardner *et al.*, 2013). However, small scale studies might prove
6 insufficient for understanding ecosystem repercussions at a catchment scale (Campbell
7 Grant, Lowe & Fagan, 2007). Up to date, few studies have addressed how changes to
8 river reach connectivity might affect ecosystem attributes at a river network scale (but
9 see Ziv *et al.*, 2012), for example, by determining the spatial extent of the effect of such
10 alteration throughout the entire river network (e. g. Yeakel *et al.*, 2014). Some studies
11 focusing on community assemblages have quantified the global longitudinal
12 connectivity loss in riverine systems as well as the relative contribution of every barrier
13 (Erős, Schmera & Schick, 2011; Rincón *et al.*, 2017; Segurado, Branco & Ferreira,
14 2013; Perkin & Gido, 2012; Cote *et al.*, 2009). These studies are often based on graph
15 theory and measures of connectivity to determine potential areas for conservation.
16 However, the biological information incorporated in these studies is rather limited (e.g.
17 mortality rates, survival rates) and, therefore, it is very difficult to understand how
18 different population traits interact with river connectivity to generate the observed
19 spatial patterns. In this regard, building population dynamics models of river species at
20 a river network scale is a promising approach to better understand how the effects of
21 altered connectivity might propagate through a river network (Charles *et al.*, 2000).

22 Fagan (2002) revealed how traditional metapopulation models do not capture the
23 hierarchical dendritic structure of the river networks and further metapopulation studies
24 (especially fish) have described the spatial effects that river network connectivity exerts
25 on demography and genetics of populations (see e.g. Labonne *et al.* (2008) and

Muneepeerakul et al. (2007) for abstract networks, Fagan (2002) and Muneepeerakul et al. (2008) for real-life settings and Fullerton et al. (2016) for applied/management purposes). A metapopulation is defined mainly by three conditions: 1) local populations inhabit discrete habitat patches, 2) the dynamics of occupied patches are not synchronous and 3) there are dispersal events between habitat patches (Rieman & Dunham, 2000; Schtickzelle & Quinn, 2007). Some salmonid populations have been considered as dendritic metapopulations in river ecosystems (Dunham & Rieman, 1999; Consuegra & García de Leániz, 2006; Cooper & Mangel, 1999; Falke & Fausch, 2010), although there is currently some debate about whether these populations conform or not to a true metapopulation structure (Rieman & Dunham, 2000; Schtickzelle & Quinn, 2007).

Brown trout (*Salmo trutta* Linnaeus, 1758) is a salmonid species that has been shown to present a metapopulation structure in previous studies (Massa-Gallucci *et al.*, 2010; Stelkens, Pompini & Wedekind, 2014). Brown trout is one of the most widespread salmonid fish species in European inland waters and its natural distribution is fundamentally restricted to this area (Elliott, 1989b), although it has been introduced to many countries worldwide (Elliott, 1989b). Moreover, brown trout is of great importance from an ecological and socio-economic point of view, as it is the top-predator fish in many river systems (Jensen *et al.*, 2008; Sánchez-Hernández, 2016) and one of the most popular and important sport-fishing species (Almodovar & Nicola, 1998). The ecology of brown trout has been studied for many years (Jonsson & Jonsson, 2011; Elliott, 1994) and several studies on population dynamics have been conducted in different regions (Mortensen, 1977; Baglinière *et al.*, 1989; Elliott, 1994; Lobón-Cerviá, 2012). However, there is still much uncertainty regarding knowledge of how different age-classes of brown trout move within and among river networks and how these

1 movements determine current spatial density patterns in river networks. Young-of-the-
2 year salmonids tend not to move much at the river reach scale (Steingrímsson & Grant,
3 2003) and a mean displacement of 200 m has been described (Vøllestad *et al.*, 2012),
4 while juvenile salmonids have been reported to move mainly upstream (Kahler, Roni &
5 Quinn, 2001; Peterson, 1982). Adults tend to move upstream for spawning (Banks,
6 1969), but they might also move downstream to look for more suitable habitats as they
7 grow and become larger (Sanz *et al.*, 2011). As a result of this complexity in movement
8 behavior among life stages, studies that model brown trout population dynamics at the
9 scale of a whole real river network considering the actual spatial structure of the
10 network, longitudinal connectivity and trout movement are scarce (but see Frank,
11 Piccolo & Baret, 2011).

12 The present study aims at modelling the average spatial patterns of density of
13 brown trout and exploring the effects of connectivity and dispersal on the average
14 spatial patterns of brown trout density in the Deva-Cares catchment in Northern Spain.
15 This catchment is affected by the presence of numerous longitudinal barriers, but hardly
16 by any other major impacts. Thus, it constitutes a very good location to develop a
17 metapopulation model for brown trout demography, which will be calibrated using field
18 data on fish population density. This model will allow exploring scenarios of river
19 connectivity, where either one or all longitudinal barriers are removed (to evaluate local
20 or global effects of connectivity). We hypothesize that changes in connectivity will
21 impact the average spatial densities of the considered age-classes differently, owing to
22 their different propensity to movement. We expect that restoring brown trout densities
23 to a natural pattern where longitudinal barriers are removed will increase densities of
24 adults in the main river course and young-of-the-year in the tributaries. Finally, we also

look at the effect of different brown trout movement biases on the average spatial densities of the different age-classes.

2 Methods

2.1 Study area

The study area was comprised of the Deva-Cares catchment (Northern Spain; 1200 km²), which drains into the Cantabric Sea (Fig. 1), under the regional administration of Government of Cantabria, Asturias and Castilla y Leon. Part of the catchment is located within the Picos de Europa National Park, which is part of the Cordillera Cantabrica mountain range. The geomorphology of the catchment is conditioned by the presence of the karst massif of Picos de Europa, which acts partly as a natural division between the Deva River (of length 64 km) and its main tributary, the Cares River (of length 54 km). The average altitude of the catchment is 1100 m, the mean slope is 50.36% and the rivers are characterized by high channel gradients and short channel lengths due to the proximity to the sea (less than 50 km to the coast in a straight line) and orographic effects (high mountains tops, rising up to 2600 m above sea level; Estevez *et al.*, 2017; González-Ferreras & Barquín, 2017).

The river network (Fig. 1) covers the perennial reaches of the Deva-Cares catchment in low-flow conditions (for more information see González-Ferreras & Barquín, 2017). Temporary reaches were assumed not to be permanently inhabited by brown trout, and were not considered in the study. The river network was divided into 623 river segments (hereafter termed nodes - mean length 1000 m) delimited by sources and confluences. The study area included 139 longitudinal barriers (see Fig. 1) of which 102 are of anthropogenic origin (e.g. dams and weirs) and 37 are natural (e.g. waterfall).

Other major significant pressures of different origin to the longitudinal barriers, such as stream habitat alteration, hydrological regime alteration or exotic species, are absent.

2.2 Fish surveys

Two datasets (FD1 and FD2) were employed in our study with different purposes. Both datasets were obtained from field surveys using electrofishing techniques. Each field survey was carried out on a minimum area that was representative of the river reach. A portable electric fishing motor (power 1.3 kW) was used, with direct current generation of 300 to 500 V, or pulsating up to 940 V with variable frequency (25 to 100 Hz). The successive catch method was performed and the Carle & Strub method (Carle & Strub, 1978) was used for abundance population estimates.

Dataset FD1 contains information on presence-absence of brown trout in 76 sites (see Fig. 1) of the Deva-Cares river network, representing the spatial variability of the species. Field surveys were carried out in August, September and October (low flow conditions) in 2014. These data were used to establish the initial brown trout presence-absence in each node of the network. Dataset FD2 gathers data from 13 sites sampled at least three times (once a year) between 2010 and 2015 (see Table 1 for details about topographic characterization). Field surveys were carried out in August, September or October over multiple years (between 2010 and 2015) to represent temporal variability in fish densities. Captured brown trout individuals were also classified into age-classes (young-of-the-year (0+), juvenile (1+) and adult (2+)) by means of a visual analysis based on the frequency distribution of the fork length (Petersen, 1986). This dataset was used to estimate fish carrying capacity and for model calibration, as further explained below.

2.3 Metapopulation model

A metapopulation is defined as a “set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible” (sensu Hanski & Simberloff, 1997). Our metapopulation model includes a freshwater brown trout population subdivided into three age-classes: young-of-the-year (0+), juveniles (1+) and adults (2+). The model is formulated under a spatially explicit, time-hybrid continuous-discrete framework (see Fig. 2a), in analogy with the epidemiological model for proliferative kidney disease in salmonids of Carraro et al. (2018; 2016). A set of ordinary differential equations expresses the time evolution of fish abundance throughout the year (from March to February), while a set of difference equations simulates the hatching process, which is assumed to occur at the beginning of March. The model takes into account changes in fish abundance due to dispersal (anadromous movements are not considered), reproduction and mortality. Individuals move from node i to node j according to their age-class and the presence of longitudinal barriers in the network. At the beginning of each year, individuals pass from one age-class to the next (except the adults) and the 0+ class is supplied by newborn individuals generated by adults. Reproduction takes place once a year (see Fig. 2).

Continuous model

The continuous model spans from time $t_{k,M}$ (year k , beginning of March M) to $t_{k,F}$ (year k , end of February F) and is constituted by the following set of differential equations:

$$\frac{dn_i^{0+}}{dt} = -\mu^{0+}n_i^{0+} - l^{0+}n_i^{0+} + \sum_{j=1}^N DP_{ji} l^{0+}n_j^{0+};$$

$$1 \quad \frac{dn_i^{1+}}{dt} = -\mu^{1+}n_i^{1+} - l^{1+}n_i^{1+} + \sum_{j=1}^N DP_{ji} l^{1+}n_j^{1+};$$

$$2 \quad \frac{dn_i^{2+}}{dt} = -\mu^{2+}n_i^{2+} - l^{2+}n_i^{2+} + \sum_{j=1}^N DP_{ji} l^{2+}n_j^{2+}.$$

3 where n_i^a is the abundance of individuals for each age-class (a : 0+, 1+ or 2+) in the i -th
 4 node of the river network; μ^a and l^a are the age-class specific mortality rates and
 5 dispersal rates, respectively; DP_{ji} is the dispersal probability, namely the probability
 6 that a fish moving out of node j chooses node i as destination. In order to specify the
 7 dispersal matrix **DP**, we first introduce the age-class specific probabilities of
 8 downstream (P_d^a) or upstream (P_u^a) movement

$$9 \quad P_d^a = \frac{1 + b^a}{2}; \quad P_u^a = 1 - P_d^a$$

10 where b^a is the bias in the direction of movement. The generic entry of the dispersal
 11 matrix reads then:

$$12 \quad DP_{ij}^a = \frac{P_{ij}^a}{\sum_{k=1}^N P_{ik}^a}$$

13 where $P_{ij}^a = P_d^a$ if node i drains into j and there is no impermeable barrier between the
 14 two nodes; $P_{ij}^a = A_j P_u^a / (\sum_{k \in U_i} A_k)$ if j drains into i and in the absence of impermeable
 15 barriers (A_j is the drainage area at node j and U_i the set of nodes that drain into i); $P_{ij}^a =$
 16 0 if there is an impermeable barrier between i and j . Note that **DP** is time dependent: in
 17 fact, two different **DP** matrices are computed, one for the low and one for the high flow
 18 condition, as defined below.

19 Much uncertainty exists in the literature regarding movement bias in salmonids.
 20 Some studies argue that the predominant movement is upstream (e. g. Kahler, Roni &
 21 Quinn, 2001; Fjellheim, Raddum & Barlaup, 1995), while others observed a tendency
 22 towards downstream movement (e. g. Mortensen, 1977) or reported no preferences (e.

g. Knouft & Spotila, 2002). Moreover, the direction of movement could be influenced by several factors as water flow or temperature (Jonsson, 1991). Based on literature, our expert knowledge and information provided by the regional fisheries officers, we decided to study two different situations in relation to movement bias for the different brown trout age-classes. The first situation (movement bias) assumed that adults present an overall tendency to move downstream to search for more suitable habitats (e. g. Sanz *et al.*, 2011) and to satisfy their metabolic requirements (Cucherousset *et al.*, 2005), while juvenile salmonids tend to move upstream (Vøllestad *et al.*, 2012; Kahler, Roni & Quinn, 2001; Gowan & Fausch, 1996) motivated by several environmental factors such as movement to feeding areas and away from high-density areas, or to avoid predation (Pearson *et al.*, 2001). The other situationType equation here. contemplates no bias on brown trout movement, i.e. same preference to move up or downstream. Thus, the movement bias situation was set with the following movement direction preferences: $b^{0+} = 0$; $b^{1+} = -0.2$; $b^{2+} = 0.2$, while in the opposite case all parameters were set to 0.

Obstacles were considered as permeable or impermeable (in both directions: upstream and downstream) longitudinal barriers depending on their physical characteristics, the fish age-class and the hydrological regime, following a national standard for the evaluation of fish pass permeability (MAGRAMA, 2015). Hydrological conditions were distinguished between low flow (LF) and high flow (HF) depending on the seasonality, with LF occurring between July and October and HF between November and June (see Fig. 2b). For age class 2+, permeable longitudinal barriers are obstacles with a maximum height of jump not greater than 1 m, minimum depth of the pool exceeding the height of jump at least by 25%, and maximum width crest not greater than 0.5 m during LF (see Supporting information S1 for a graphic

representation of the characterization of the barriers). During HF, the previous metrics are increased by 15%. Any other obstacle was considered permeable, unless it had a non-functional fish pass (i.e. presence of fish pass that is not functional due to design errors or lack of maintenance). For class 1+, all barriers are impermeable during LF and obstacles are treated as in the case of class 2+ during HF. For class 0+, all barriers are impermeable regardless of the hydrological regime. Based on these conditions, 79 out of 139 longitudinal barriers in the study area were permeable for adults and temporarily permeable for juveniles. Barrier locations are shown in Fig. 1.

Discrete model

The discrete model (from $t_{k,F}$ to $t_{k+1,M}$) is constituted by the following set of equations:

$$n_i^{0+}(t_{k+1,M}) = \sum_{j=1}^N 0.5 SM_{ji} n_j^{2+}(t_{k,D}) f \sigma \exp\left(-\frac{n_i^{total}(t_{k,F})}{C_i}\right)$$

$$n_i^{1+}(t_{k+1,M}) = n_i^{0+}(t_{k,F})$$

$$n_i^{2+}(t_{k+1,M}) = n_i^{2+}(t_{k,F}) + n_i^{1+}(t_{k,F})$$

The abundance of newborn individuals at the beginning of the year ($n_i^{0+}(t_{k+1,M})$) is the outcome of the spawning and hatching processes that take place during winter. Spawning and hatching dates depend on environmental conditions, and primarily on water temperature (Elliott & Hurley, 1998). In the Deva-Cares catchment, spawning and hatching activities reach a peak in December and March, respectively (Cantabria Regional Government pers. comm.). Similar spawning and hatching periods have also been found in nearby catchments (e. g. Lobón-Cerviá, 2005a). The total number of spawned eggs was estimated with a uniform sex ratio (1:1) as the product of adult females in December (half of the adult population $n_j^{2+}(t_{k,D})$) times the number of spawned eggs per individual (f). The number of newborn individuals is the product of the number of spawned eggs and the hatching probability (σ). Hatching success depends

on several physicochemical variables (Sternecker, Cowley & Geist, 2013) and can vary among sites and years. The value of σ was set equal to 0.1 based on local experience (Cantabria Regional Government pers. comm.). It is well known that inter-annual variation of recruitment is mainly governed by fry survival during hatching and emergence periods, which, in turn, is driven by flow and temperature conditions (Lobón-Cervía & Rincón, 2004; Bret *et al.*, 2015). However, this parameter is assumed constant in space and time because we want to simulate long-term stability conditions (average situation) of spatial density patterns at a river network level, rather than temporal dynamics of abundance. This argument is also applied for the other parameters (e.g. mortality rates) that are assumed constant in space and time.

Spawning migration patterns were defined according to a gravity model (Erlander & Stewart, 1990). The probability SM_{ij} that adult brown trout move from node i to j for spawning and then return to node i is proportional to a site-specific spawning suitability score SS_j and inversely proportional to the distance between the two nodes d_{ij} (through an exponential kernel with scale factor D which indicates a characteristic distance for migration):

$$SM_{ij} = \frac{SS_j \exp\left(-\frac{d_{ij}}{D}\right)}{\sum_{k=1}^N SS_k \exp\left(-\frac{d_{ik}}{D}\right)}$$

where d_{ij} is set to infinity when nodes i and j are not connected owing to topology or presence of an impermeable barrier. Spawning suitability scores were calculated as $SS_j = \log(A_j)^{-3}$, as tributaries and headwaters are generally more suitable for spawning (e. g. Gosset, Rives & Labonne, 2006).

Several authors have found population density in salmonids to be regulated by density-dependent mechanisms (associated with food availability, competition and spatial relationships) in the early life stages (Elliott, 1989a; Jonsson & Jonsson, 2011),

1 especially in locations with favorable habitats with high densities. In accordance to
2 Haldane's hypothesis (Haldane, 1956), such an endogenous regulation mechanism has
3 been rarely reported in peripheral populations in unfavorable habitats with low density,
4 like the Iberian peninsula. In contrast, external factors (especially extreme flow events
5 during the late embryo developmental stages and early emergence) have been found to
6 locally limit brown trout population density. This phenomenon of recruitment limitation
7 is modelled by means of a Ricker recruitment model (Ricker, 1954) with density
8 dependent factor $C_i = cH_i$, which represents a proxy of the carrying capacity of node i ,
9 where c is the fish density at carrying capacity and H_i is the habitat size, namely the
10 product of mean water width and length of the node. We assumed $c = 0.83 \text{ ind/m}^2$,
11 equal to the average maximum density obtained in a sample point in dataset FD2. In our
12 simulation, the Ricker recruitment model mimics the density-dependent effect of
13 suitable habitats potentially limiting the maximum numbers of successful nests in a
14 given stream (Einum, 2005) while accounting for a well-known environmental
15 limitation of recruitment by stream hydrology (Lobón-Cerviá & Rincón, 2004). Lengths
16 (m) were obtained from the subdivision of the river network into nodes, while mean
17 water widths (m) were obtained with Spatial Stream Network models (Ver Hoef *et al.*,
18 2014) from empirical data with information on section E of River Habitat Survey
19 (Environment Agency, 2003). Mean water width was used as the response variable,
20 while stream power (W/m) and the number of high flow events per year (exceeding a
21 threshold of seven times the median flow) were used as independent variables.

22 It should be noted that the model incorporates neither environmental or
23 demographic stochasticity nor environmental conditions (temperature or flow) due to
24 the arguments that have been previously proposed. Thus, the metapopulation model

only considers demographic and dispersal characteristics and river network connectivity to simulate long-term stability of spatial density patterns.

The metapopulation model was run for 50 years, with the aim of reaching a steady spatial distribution of fish densities unaffected by the initial conditions. We will hereafter focus on the results obtained for the 50th year of simulation. The initial presence-absence spatial pattern was derived from dataset FD1. We assumed that initial fish densities for 0+ and 2+ age-classes were null, while juveniles' initial densities were set to their value at carrying capacity in the nodes where initial presence had been predicted, and null otherwise.

2.3.1 Model calibration

Some parameters were not available for our study area due to the lack of observational data and hence they required calibration. These were mortality rates, dispersal rates, characteristic distance for spawning migration and the number of spawned eggs per individual. Feasible parameter ranges were obtained from literature.

As for the characteristic distance for spawning migration (D), we used a range between 500 and 9500 m, based on previous studies which show a mean upstream distance for reproduction within that range (e. g. Rustadbakken *et al.*, 2004; Gosset, Rives & Labonne, 2006). Regarding mortality rates ($\mu^{0+}, \mu^{1+}, \mu^{2+}$), our model assumes a single value for each of these parameters and does not differentiate between natural, fishing and temperature-dependent mortality rates. In this regard, there are studies that show very different values among brown trout cohorts and populations (Lobón-Cerviá, Budy & Mortensen, 2012). Thus, we chose a range of mortality values (0.001 to 0.005 d⁻¹) close to a population average value of 0.0025 d⁻¹ obtained from a nearby northern Spanish catchment (Esva basin; Lobón-Cerviá, Budy & Mortensen, 2012). Values of μ^{0+} were set slightly higher because early life stages suffer higher mortality rates

(Wootton, 2012). In relation to dispersal, salmonid populations are composed of both stationary and mobile individuals (e. g. Bridcut & Giller, 1993), being the former the predominant proportion (Aparicio *et al.*, 2018) and the latter less abundant (Young *et al.*, 2010), or even a very reduced proportion (i.e., less than 5%; Rocaspana *et al.*, 2013). Studies of fish movements have yielded different results based on genetic analysis (e. g. Vera *et al.*, 2010; Gowan *et al.*, 1994), dispersal distances (Young *et al.*, 2010) or dispersal rates (Crisp, 1991). Because dispersal of 0+ age-class trout is limited (Vatland & Caudron, 2015), the distances covered are small (Elliott, 1987; Vøllestad *et al.*, 2012) and the average node length is 1000 m, we set $l^{0+} = 0 \text{ d}^{-1}$. We further assumed that adults have the highest dispersal rate (Vera *et al.*, 2010; Olsson & Greenberg, 2004) with a maximum of 0.12 d^{-1} and half that value (0.6 d^{-1}) as maximum for the 1+ age-class. Fecundity highly depends on fish length (Lobon-Cervia *et al.*, 1997; Nicola & Almodóvar, 2002) or body mass (Jonsson & Jonsson, 1999), with the number of eggs ranging between 1000 and 2000 per kg (Doadrio, 2002). The average fecundity for resident trout with weights between 100 and 500 g is between 270 and 1100 eggs (Alonso, Cortázar & García de Jalón, 2012; Klemetsen *et al.*, 2003). Based on our empirical data (mean $\pm$ SD adult fork length: $194 \pm 49 \text{ mm}$; mean $\pm$ SD adult weight: $97 \pm 40 \text{ g}$), we choose values of f from 200 to 400. Parameter ranges are reported in Table 2.

The model was calibrated against mean observed fish density data from dataset FD2. We use dataset FD2 to reproduce the natural variability of brown trout density since population densities are not constant over years, but rather oscillate around an inter-annual mean carrying capacity that reflects the average environmental conditions over time (Jonsson & Jonsson, 2011). In particular, calibration was performed on a subset of 13 nodes of the fluvial network where more than one measurement was

available. Modelled fish densities (average of August, September and October) were deemed as appropriate if they were within the 95% confidence interval (CI) of a t -distribution based on the observed population density for each sample point. We assumed that fish density followed a t -distribution because of the low number of replicas per node (between 3 and 6 years). The maximum number of correct results would be 39 (13 nodes times 3 age-classes within the 95% CI). We selected the best-fit parameter set as that that achieved the greatest number of correct predictions for each node and age-class (see Supporting Information S2 for more information).

2.4 Simulations of scenarios

The metapopulation model was used to detect how modifications to river network connectivity due to removal of longitudinal barriers influenced patterns of brown trout population density. Three different scenarios generated by changes in network connectivity were explored. Scenario SQ (Status Quo) refers to the current situation of the river network, where all longitudinal barriers are present and connectivity is restricted. This scenario serves as a baseline for comparison with the other scenarios. Scenario ABR (All Barriers Removed) explores the condition of complete connectivity, where all longitudinal barriers are removed. Although Scenario ABR might seem unrealistic, its outcomes allow us to compare the two situations that constitute both extremes in a connectivity gradient. Finally, Scenario SBR (Single Barrier Removed) represents a situation with improved local connectivity, where a single impermeable barrier is removed. We selected one of the highest barrier (dam height = 15 m) located in the Picos de Europa Natural Park which is important because it limits the distribution of *Salmo salar* (Linnaeus, 1758), and therefore of brown trout population. We consider that this barrier limits both species since swimming performance curves for salmonids are given as a function of their length, not of the species (Larnier (2002) based on Beach

(1984)). This barrier isolates a catchment area of 266 km² and affects a total upstream river network length of around 100 km. Due to the lack of clear management scenarios in the Deva-Cares catchment, we consider that this selection could illustrate the effects of restoring longitudinal connectivity on a single river network section.

2.5 Sensitivity analysis

We performed a one-factor-at-a-time sensitivity analysis of the model outcomes with respect to dispersal parameters (l^{2+} , l^{1+} and D) focusing on scenario SQ and ABR and the assumption of movement/no movement bias to understand how model parameters affect density results. Although the other parameters (e.g. mortality rates) would also have a direct effect on the overall density, we only performed the sensitivity analysis on parameters related to movement due to our interest in the effects of movement bias in relation to river network connectivity. Explored values for these parameters slightly exceeded the feasible ranges proposed in Table 2; exact ranges correspond to the limits of the x axes shown in Fig. 7.

Maps showing the obtained results were developed for the different scenarios using ArcGIS 10.2 (ESRI, 2014). All models were run using MATLAB 8.5.0.197613 (R2015a) (MATLAB, 2015). Statistical analysis were performed in the R 3.1.3 software (R Core Team, 2015) and the editor RStudio (RStudio, 2015).

3 Results

3.1. Metapopulation model

The model parameters that obtained the best fit with empirical data (see Table 2) yielded 29 model results (11 for 0+, 9 for 1+ and 9 for 2+) within the 95% CI of the empirical data (see Fig. 3).

3.2 Simulation of scenarios

Within scenario SQ, density decreased with increasing age-class (Fig 4). Generally, modelled density of 0+ was higher in the headwater reaches and density of 1+ and 2+ was higher in the middle river reaches (see also Fig. 5: scenario SQ). The network-averaged fish densities (total number of fish divided by the habitat size) were 0.171 ind/m² (0+), 0.064 ind/m² (1+) and 0.041 ind/m² (2+) considering movement bias (see Table 3). Movement bias had a moderate effect on fish density for each age class, observing a decrease of less than 10% in relation to the no movement bias assumption.

For scenario ABR and no movement bias, the patterns of fish density were similar to the no movement bias case of scenario SQ (see Fig. 4 and Fig. 5; network-averaged fish densities were 0.192 ind/m² (0+), 0.072 ind/m² (1+) and 0.046 ind/m² (2+)). However, when movement bias is included, the decay in fish density is remarkable compared to the no movement bias case in scenario SQ (see Table 3). In the absence of longitudinal barriers, modelled density of 0+ class is higher in river reaches with small catchment areas, while 1+ and 2+ age-classes show higher densities in nodes with larger catchment area (Fig. 5). Although this is also the case for scenario SQ, the pattern is more pronounced in the complete connectivity scenario (Fig. 5). Overall, brown trout population density under scenario ABR tends to decrease in the smaller tributaries, while it increases in the lower part of the catchment (Fig. 5 and Fig. 6). In this scenario, the network-averaged mean densities are 0.130 ind/m² (0+), 0.042 ind/m² (1+) and 0.030 ind/m² (2+), namely 24%, 35% and 25% less compared to scenario SQ, respectively. It is remarkable that under scenario ABR and movement bias most river network nodes showed important changes (more than 50% increases or decreases) on fish population densities in comparison to scenario SQ (Fig. 6). When no movement bias is considered, most river network nodes also showed changes in comparison to the

analogous case scenario SQ, tending to increase the population density in the main channels (Fig. 6), however, the network-averaged mean densities are only 1% (1+) and 2% (0+ and 2+) lower compared to scenario SQ.

Scenario SBR with movement bias (Fig. 4 and Fig. 6) featured a decline in population density (mean densities: 0.010 ind/m² for 0+, 0.006 ind/m² for 1+ and 0.002 ind/m² for 2+ age-classes) upstream of the removed barrier, while an opposite trend was observed downstream (mean densities of 0.107 ind/m² for 0+, 0.032 ind/m² for 1+ and 0.025 ind/m² for 2+ age-classes). These changes represent an average percentage decrease of 94% upstream and of 4% increase downstream (Fig. 5). Overall, scenario SBR produced a decrease of less than 5% in the network-averaged density. However, it is remarkable that the effect of the local dam removal extends till the next longitudinal impermeable barrier in either both or downstream directions. When no movement bias is considered, mean densities follow a similar pattern in regard to scenario SQ, with densities decreasing upstream of the barrier but increasing downstream (see Table 3). In this case, upstream decrease is lower (44%) and downstream increase is greater (10%) than when assuming movement bias.

3.3 Sensitivity analysis

As l^{2+} increased (central column; Fig. 7), the differences between the overall fish densities (for all age classes) calculated with movement and no movement bias increased. When considering no movement bias, overall fish densities were not much sensitive to changes in this parameter, as high l^{2+} in this case only increased the speed at which adults move, but the spatial distribution of density was not affected. Instead, when movement bias was included, high values of l^{2+} enhanced the downstream tendency of adult fish, making them less likely to spawn in the upstream reaches (especially in scenario ABR, where there are no obstacles to downstream movement).

Increases in l^{I+} (left column; Fig. 7) caused an increase in the overall fish density (for all age classes), in particular when movement bias was included. In this case, the tendency of juvenile fish to move upstream was enhanced, and this contributed to push the adult fish towards more upstream reaches. On the other hand, the effects of high l^{I+} when no movement bias was considered were minor. The very high overall fish density for class 0+ when l^{I+} approaches 0 (top left panel; Fig. 7) is explained in the supporting information S3.

When D is set to high values (right column; Fig 7), the effect of movement bias tends to disappear. It is remarkable that, in this case, the overall fish density was a bit higher for scenario SQ than for scenario ABR, regardless of the assumption on movement bias. This implies that there is an effect of reduced connectivity in increasing the overall fish density beyond the movement/no movement bias issue.

4 Discussion

4.1 Metapopulation model

The metapopulation model proposed in this study is one of the first models that estimates the spatial patterns of density of native brown trout at a river network scale considering the real topology and using empirical data for the calibration. Our results produce an appropriate representation of the actual spatial variability of brown trout densities for the three age-classes, as reflected by the adjustment of the modelled results to the empirical data (i.e. 75% overall agreement). Moreover, when removing all longitudinal barriers, the spatial pattern of fish densities tends towards the expected spatial pattern for a natural river network, with higher densities of adult trout on the downstream portion of the network and higher densities of younger individuals upstream (Baglinière & Maisse, 1999). However, we need to acknowledge that these

1 modelled results are a direct consequence of a number of different assumptions and
2 issues.

3 First, the absence of other important environmental or anthropogenic drivers of
4 fish densities in the case study catchment besides connectivity provides a suitable
5 scenario to apply the proposed model. Indeed, our model was developed in a catchment
6 with a river network composed by perennial reaches (González-Ferreras & Barquín,
7 2017), but this situation is not characteristic of other catchments where the presence of
8 dry reaches or disconnected pools alters longitudinal connectivity (e.g. Larned *et al.*,
9 2011) and population dynamics (Perry & Bond, 2009). Moreover, we did not consider
10 anadromous movements because the size of the anadromous population in our study
11 area is small. Thus, the results might not hold in other catchments where other
12 environmental or anthropogenic drivers (e.g. exotic species, sewage discharges, etc.)
13 control the spatial patterns of brown trout densities (e.g. Leunda, 2010; Elvira &
14 Almodóvar, 2001).

15 Second, we made some assumptions related to key population characteristics of
16 the species (e.g. movement preference downstream or upstream, sex ratio, etc.) based on
17 previous knowledge and literature review. However, these characteristics were not
18 specifically assessed in the local population. Thus, the relevance of these assumptions
19 cannot be evaluated and the applicability of the current model in different catchments
20 will need an adequate calibration of the parameters. This is especially relevant in the
21 case of brown trout, as this species shows a high phenotypic plasticity (Jonsson &
22 Jonsson, 2011), with remarkable differences among different populations. In this regard,
23 we acknowledge that the chosen values of the population dynamic variables (mortality
24 rates, dispersal rates, characteristic distance for spawning migration, etc.) are constant in
25 space, although several studies showed that these variables could change within and

1 among populations. For instance, mortality rates are affected by many factors (age, size,
2 sex, environmental factors, fishing, etc.; Elliott, 1993) and they could be different
3 among river reaches of the same catchment (Lobón-Cerviá, 2012). In particular, we
4 believe that fishing might contribute to the high mortality rate of adults relative to
5 young-of-the-year individuals, although further investigation on this aspect would be
6 required.

7 Improvements to the current modelling approach should take into account the
8 spatio-temporal heterogeneity of the population dynamic variables, but this also implies
9 that more data on local populations and/or long-term data would be necessary. Our
10 study is focused on general spatial trends, but the inclusion of this information could
11 yield further insights on spatio-temporal population dynamics. For example, dispersal
12 rates can vary with water velocities (Crisp, 1991), patch quality (Bowler & Benton,
13 2005) or among seasons (Ovidio *et al.*, 2002). Dispersal rates also depend on carrying
14 capacity, although density-dependent dispersal rate was not included in the model
15 because densities are generally low and carrying capacity is seldom reached. Still, the
16 inclusion of density-dependent dispersal will be an enhancement of the model. In
17 addition, demographic stochasticity is also a key factor influencing temporal fluctuation
18 in vital rates, especially in small populations (Lande, 1993). Moreover, temporal
19 fluctuations of environmental variables are also important in determining changes in
20 fish densities. Thus, our model could be enhanced by including seasonality and,
21 possibly, environmental stochasticity (Borsuk & Lee, 2009) to assess the effects of
22 spatio-temporal heterogeneity in environmental conditions and demographic
23 stochasticity to assess the effects of spatio-temporal fluctuations on vital rates.
24 Environmental stochasticity could be incorporated by relating flow regimes to
25 mortalities through the existence or not of refuges (hydraulics and suitability changes to

1 flood or droughts) in each node and demographic stochasticity could be incorporated
2 through probability distributions (Melbourne, 2011). This approach would allow the
3 user to analyze how climate change (e. g. Almodovar *et al.*, 2012) or hydrological
4 alterations (e. g. Sabater & Tockner, 2010) might affect spatio-temporal patterns of
5 population dynamics, and it should constitute an improvement of the actual modelling
6 framework with results in the near future.

7 Regarding density-independent processes, our approach only considered density-
8 dependent mortality for young-of-the-year but accounted for the abundance of all age-
9 classes. We have not considered additional density-dependent processes because
10 Spanish Atlantic populations are mainly controlled by environmental stochasticity in
11 opposition to density-dependent processes (Alonso, Cortázar & García de Jalón, 2012).
12 Thus, the natural variability of brown trout densities around an inter-annual mean
13 carrying capacity reflecting environmental conditions is accounted in the model
14 calibration approach. However, future enhancement of the model could also account for
15 spatio-temporal heterogeneity as we have previously discussed. In this regard, the
16 model could incorporate additional density-dependent processes that can influence
17 brown trout populations such as density-dependent growth (Lobón-Cerviá, 2005b).

18 Lastly, our model could be also enhanced in relation to the assumption of
19 permeability of barriers incorporating semi-permeability (i.e. permeability in one
20 direction “upstream or downstream” for some specific situations instead of permeability
21 and impermeability in both directions; Rincón *et al.*, 2017) since it is possible that in
22 certain circumstances (e.g. high flows) and for some barriers fish may be able to move
23 downstream. This information could be incorporated through specific studies of gene
24 flow (Junge *et al.*, 2014) or movement monitoring (Gowans, Armstrong & Priede,
25 1999), which were not available for our study area.

4.2 Simulation of scenarios

River networks can be affected by local or macroscale phenomena (McCluney *et al.*, 2014). However, because of the longitudinal connectivity of river ecosystems, the propagation of changes in fish density is particularly sensitive to the location where an alteration occurs in the network (Charles *et al.*, 2000; Samia, Lutscher & Hastings, 2015; Thorp *et al.*, 2013). In the present study, the removal of all longitudinal barriers (scenario ABR) produced a decline of more than 25% in the network-average brown trout density considering the inclusion of movement bias. However, this result should be interpreted with caution; when no movement bias is considered the network-average densities are similar for both scenarios. However, sensitivity analysis on parameter D showed an effect of reduced connectivity in increasing the overall fish density beyond movement/no movement bias (i.e. increasing D values makes the movement/no movement bias situations converge, but scenarios SQ and ABR do not converge for all age-classes, showing higher values of density in the scenario SQ). This revealed the effect of connectivity on spatial patterns of density and showed that longitudinal barriers could be functioning as possible biomass “traps”, as we explain below. Moreover, scenario ABR produced a general increase in brown trout densities downstream and a decrease upstream in relation to the initial situation of the Deva-Cares catchment (scenario SQ). In addition to the effect caused by movement bias (see sensitivity analysis), it is possible to explain this pattern as larger brown trout do not found suitable habitat in smaller headwaters as they grow and become larger, which induces them to migrate downstream. Larger brown trout produce and lay larger quantities of eggs (Doadrio, 2002) and, in the absence of barriers, they will move downstream, increasing not only adult densities but also the densities of other life-cycle stages, since they spawn on many low order streams directly draining into high order

streams. On the contrary, barriers can act as “traps” not allowing the movement of larger brown trout to move to more suitable habitats downstream (e.g. deeper main river; Sanz *et al.*, 2011) increasing the densities of all life-cycle stages in headwaters or middle reaches “locked” by longitudinal barriers. Therefore, the current lack of longitudinal connectivity might not be sustaining an artificially higher density of brown trout, but rather locally altering the spatial distribution of age class densities. The removal of longitudinal barriers restored brown trout densities to the expected natural pattern, with increasing densities of adults in the main river course and higher young-of-the-year densities in the smaller tributaries. Such a trend has been shown in other studies (e.g. the Scorff basin in France; Baglinière & Maisse, 2002; Maisse & Baglinière, 1990). This natural spatial variability pattern has been traditionally attributed to changes in physical habitat characteristics, such as water depth, water velocity, substrate particle size or cover, that produce a spatial zonation of the age-classes (Heggenes, Baglinière & Cunjak, 1999). In this regard, studies on ecohydraulics have shown that larger trout select deeper stream areas while younger trout inhabit shallower areas (Ayllón *et al.*, 2009; Heggenes, Baglinière & Cunjak, 1999). Most of the relevant physical habitat attributes for the brown trout change longitudinally in a river network, usually scaled via power law relationships with discharge (or a proxy like drainage area; Leopold & Maddock Jr, 1953). Although these habitat attributes were not explicitly taken into account in the present study, they were implicitly considered when movement preferences of each age class were parameterized. Moreover, in the case of a single barrier elimination (scenario SBR), patterns obtained with or without movement bias are similar (i.e. decrease upstream and increase downstream, although with different densities). It could be necessary to deeply analyze this behavior in future studies by removing other barriers in the network in order to assess which is the effect

of the river network position. In this study, we decided to simulate the elimination of all barriers as an extreme scenario (although currently not a feasible option) and the elimination of one single barrier (see section 2.4 Simulation of scenarios for explanation) as a more feasible management option, but other barriers could potentially have a different effect.

In the three simulated scenarios (even with movement bias and no movement bias), the spatial distribution and densities of the three age-classes changed substantially in many river reaches (more than 50% increases or losses). Loss of connectivity tends to increase population density upstream, while movement bias locally affected or increased population density downstream. However, the construction of realistic scenarios requires a better knowledge on the overall movements of the different age classes through the river network (e.g. telemetry; Höjesjö et al., 2007).

4.3 Ecosystems implications

Ecosystem implications of obtained results in this study are very important in the case of a keystone species or top-predator such as the brown trout, as such changes on its densities might generate considerable top-down effects on biological communities and ecosystem processes. For example, the decline in Yellowstone cutthroat trout abundance (from 3.5 million in 1979 to 1.7 million in 1997) engendered by the introduction of lake trout altered the lower trophic levels via a trophic cascade (Koel *et al.*, 2007). Zooplankton biomass was doubled, while phytoplankton biovolume was three times lower in 2004 compared to the period before the introduction of the lake trout (Tronstad *et al.*, 2010). Moreover, field experiments performed in Japan by Nakano et al. (1999) showed that increasing the intensity of Dolly Varden trout predation on benthic aquatic invertebrates resulted on periphyton biomass increases of about one-third. Other examples of top-down effects are the introduction of certain trout

species around the world replacing native fishes as the main predators. In this regard, introduced rainbow trout in high-Andean tropical streams reduced by half the densities of certain invertebrate taxa in the benthos (*Andesiops*, Orthocladiinae and Simuliidae sp.) (Vimos *et al.*, 2015). Introduced brown trout in New Zealand streams also generated top-down cascading effects doubling benthic chlorophyll *a* (McIntosh & Townsend, 1996). Thus, the current situation of river connectivity alteration in the Deva-Cares catchment is generating important changes on the spatial patterns of a key species density that, in turn, might disrupt natural river biodiversity patterns and ecosystem functioning. We believe that this might be also the case in many other river networks all over the world in which natural longitudinal connectivity has also been altered (see Nilsson *et al.*, 2005). However, the expected effects of dams might not be the same in all systems, but depend on the local conditions and the purpose of the dams. For instance, an increase in brown trout density has been detected in the originally barbell-dominated fish community downstream Itoiz dam in Irati river (Ebro catchment, Spain) [unpublished data], where the irrigation scheme is currently preventing severe spates and droughts that characterize the natural regime of this Mediterranean river. Improving our understanding of how changes in key species densities affect river biodiversity and functioning patterns is paramount to improve river management and conservation strategies.

5 Conclusion

In conclusion, this study suggests that the proposed empirical data-driven metapopulation model is an appropriate tool to estimate the spatial patterns of age-specific brown trout density in a whole river network and to assess the effect of changes in connectivity. Spatial heterogeneity in fish density is highly dependent on connectivity and population dynamics, although future studies are needed to learn more about

parameters related to brown trout movement. Altering the natural river connectivity results in major changes in the spatial distribution of fish. Removing a single obstacle might have consequences on very distant tributaries, while removing all obstacles will restore brown trout density levels to a more natural pattern. Such results help us understand how variations in key species distribution affect biodiversity in lotic environments, in the perspective of implementing conservation strategies.

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Conflict of interest statement

The authors declare no conflict of interest.

1 **Authors' contributions**

2 All authors conceived the ideas and designed methodology. A.M.G.F. and J.B. collected
3 the data. E.B. and A.M.G.F. analyzed the data. A.M.G.F. led the writing of the
4 manuscript with input from all co-authors. All authors contributed critically to the drafts
5 and gave final approval for publication.

6 **Data accessibility**

7 Data will be available after manuscript acceptance. Data will be available are related to
8 barriers, fish datasets, river network and metapopulation model.

9

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21
22

1 TABLES

2 **Table 1.** Topographic characterization of the field sites from database FD2 (used in
3 model calibration).

Sites	Catchment area (km ²)	Elevation (m)	Gradient (%)	Width of the valley floor (m)	Distance to river mouth (m)
S9	26.2	340.000	0.043	39.600	41886.984
S12	32.826	910.000	0.048	44.000	47025.398
S11	31.943	228.000	0.090	29.100	37578.246
S8	10.067	590.000	0.063	29.400	49135.652
S10	26.268	963.000	0.049	54.300	55147.980
S13	36.556	929.000	0.026	89.900	54575.582
S7	631.997	60.000	0.004	47.800	15259.347
S3	40.176	73.000	0.030	29.700	19110.498
S6	474.314	232.000	0.006	128.000	31300.398
S5	152.386	310.000	0.017	75.800	39152.133
S1	7.635	629.000	0.070	33.800	47216.176
S4	79.036	666.000	0.017	111.200	50333.242
S2	9.785	1010.000	0.051	35.200	58643.211

4
5 **Table 2.** Parameters that require calibration and corresponding ranges. Note that the
6 dispersal rate for young-of-the-year fish l^{0+} was set to 0. (*) Explanation to the value
7 references is given in the text.

Variable	Units	Min. value	Max. value	References(*)	Calibrated values
D	m	500	9500	(Rustadbakken <i>et al.</i> , 2004; Gosset, Rives & Labonne, 2006)	2000
μ^{0+}	d ⁻¹	0.002	0.006		0.003
μ^{1+}	d ⁻¹	0.001	0.005	(Lobón-Cerviá, Budy & Mortensen, 2012)	0.002
μ^{2+}	d ⁻¹	0.001	0.005		0.003
l^{0+}	d ⁻¹	0	0		0
l^{1+}	d ⁻¹	0	0.06	(Rocaspana <i>et al.</i> , 2013)	0.015
l^{2+}	d ⁻¹	0	0.12		0.06
f	-	200	400	(Doadrio, 2002; Klemetsen <i>et al.</i> , 2003; Alonso, Cortázar & García de Jalón, 2012)	340

8
9
10 **Table 3.** Network-averaged mean densities (ind/m²) for the respective combination of
11 scenarios, age class and assumption on movement bias. Results for scenario SBR are

1 separately averaged for nodes upstream or downstream of the removed barrier. To
 2 facilitate the comparison, the same partition is also operated on scenario SQ and its
 3 results here reported.

4

Scenario	0+		1+		2+	
	Bias	No bias	Bias	No bias	Bias	No bias
SQ	0.171	0.188	0.064	0.073	0.041	0.045
ABR	0.130	0.192	0.042	0.072	0.030	0.046
SBR (upstream)	0.010	0.084	0.006	0.034	0.002	0.022
SQ (upstream)	0.180	0.153	0.075	0.063	0.044	0.037
SBR (downstream)	0.107	0.158	0.032	0.056	0.025	0.037
SQ (downstream)	0.102	0.143	0.032	0.052	0.024	0.034

5

FIGURE CAPTIONS

Figure 1. Map of the study area and representation of the Deva-Cares river network. Field sites from the two different datasets (FD1 and FD2) used in the study, longitudinal barriers (high flow-HF and low flow-LF) and permeability for the three age-classes (0+, 1+ and 2+) are also located.

Figure 2. a) Schematic representation of the metapopulation model. Natural mortality is not displayed. b) Timeline for the metapopulation model. See section 2.3 “Metapopulation model” in the main text for parameters definition and model description.

Figure 3. Modelled densities (grey circles) and average densities observed in the field across years (black circles; see section 2.2: FD2) for three different brown trout age-classes in 13 river reaches of the Deva-Cares catchment. Bars show 95% confidence intervals of observed average densities based on a *t*-distribution.

Figure 4. Modelled fish density (individuals/m²) for different age-classes, scenarios and inclusion or neglect of movement bias. In scenario SBR, the removed longitudinal impermeable barrier is shown within a black rectangle.

Figure 5. Distribution of fish density across all nodes as a function of drainage area. Rows identify scenarios, columns refer to age classes and colors represent inclusion or neglect of movement bias. Displayed values of fish density are the averages during August, September and October of the last year of simulation (steady state) obtained with the calibrated set of parameters of Table 2. The displayed percentiles are obtained

1 through a binning procedure: each data series is sorted in ascending order in terms of
2 drainage area and then divided in 20 equal parts; percentiles are then plotted at the
3 midpoint of each bin. Colored numbers within each subplot refer to the overall fish
4 density (in individuals/m²) for the respective combination of scenario, age class and
5 assumption on bias.

6
7 **Figure 6.** Percentage of change in the modelled population density for scenario ABR
8 and scenario SBR compared to scenario SQ with inclusion and neglect of movement
9 bias. In scenario SBR, the removed longitudinal impermeable barrier is shown within a
10 black rectangle.

11
12 **Figure 7.** Results from sensitivity analysis. Effect of variations of some meaningful
13 parameters (columns) on overall fish density for the three age classes (rows) for
14 different scenarios (line type) and inclusion/neglect of movement bias (line color).
15 Black solid lines identify calibrated parameter values from Table 2. Gray shaded areas
16 highlight feasible parameter ranges as identified in Table 2. Displayed values of fish
17 density are the averages during August, September and October of the last year of
18 simulation (steady state), where all parameters not tested for sensitivity were kept to
19 their calibrated value (Table 2).

Overall Fish Density [ind/m²]