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Consideration of habitat quality in a river connectivity index for anadromous fishes

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ABSTRACT

River fragmentation is one of the main threats to diadromous fish species. We aimed to create a new and simple connectivity index to calculate habitat accessibility that considers habitat suitability for fish species, using the Bidasoa River basin in the north of Spain and Atlantic salmon (*Salmo salar*) as an example. A habitat connectivity index (HCI) was calculated for the river basin using upstream passability and segment length as variables. We then calculated a new habitat quality index for each river segment and multiplied it by river segment length to create the Breeding Habitat Connectivity Index (HCIb). These 2 indices were first calculated using only upstream barrier passability and then by adding downstream passability. In each case, the indices show different outcomes but a similar pattern: in all cases, main-stem obstacles closest to the river mouth most affected the connectivity index, even when habitat quality was considered. Although we cannot compare the indices to the real area used by salmon because spatial tracking was not performed during the study years, we consider that including habitat quality in a river connectivity index adds useful information for scientists and managers.

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Atlantic salmon; dam removal; ecological restoration; fish migration; habitat quality; river connectivity

Introduction

Longitudinal fragmentation is one of the main threats to river integrity (Olden 2016). Obstacles such as dams and weirs obstruct the movement of water, sediments, nutrients, and organisms, significantly altering river ecosystems (Nilsson et al. 2005, Vörösmarty et al. 2010, Crook et al. 2015). Diadromous fish species such as salmonids, eels, and sturgeons are the most affected aquatic organisms because obstacles hinder their migration from the ocean to the river, preventing the completion of their life cycle (Fullerton et al. 2010). Lack of longitudinal connectivity has caused population declines and local extinctions of many diadromous fish species around the world (Fullerton et al. 2011, Nieland et al. 2015, Segurado et al. 2015). However, diadromous fishes are not the only species impacted. Potamodromous fishes are also affected by river fragmentation because dams isolate populations and change river morphology, thus increasing the risk of extinction (e.g., Alexandre and Almeida 2010, Bain and Wine 2010).

In recent decades, dam removal has become a priority for improving river connectivity and freshwater ecosystem health (Hart et al. 2002), although the barrier removal selection methods are usually obscure and inefficient, and removal effects on fish communities are usually not evaluated (Rodeles et al. 2017).

Different connectivity indices have been developed to analyze longitudinal river connectivity and provide managers with a useful tool to plan obstacle removal or select locations for new dams (Grill et al. 2015). These indices are models that range in complexity from those that analyze each obstacle separately (O'Hanley and Tomberlin 2005, Solà et al. 2011) to others that use graph theory to integrate the complexity of the river network (Schick and Lindley 2007, Cote et al. 2009, Zheng et al. 2009, Erös et al. 2011, McKay et al. 2013). Indices developed following the graph theory consider the location of each dam in the river network and consider river segments as habitat patches separated by obstacles. These patches are more or less connected, depending on the location and characteristics of the obstacle (Cote et al. 2009, Branco et al. 2014, Segurado et al. 2015), river conditions (Bourne et al. 2011, Shaw et al. 2016), and biology of each fish species (Bourne et al. 2011, Maitland et al. 2016).

To accurately describe the permeability of each obstacle (passability), multiple physical and biological variables must be assessed, such as dam height, water flow, and species swimming capacity, among others (Kemp and O'Hanley 2010). In various studies, a selection of these variables related to obstacle characteristics has been used to create a connectivity index (Ovidio and Philippart

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2002, Kemp and O'Hanley 2010, Bourne et al. 2011, Shaw et al. 2016). Technically, other variables such as species biology, ecology, behavior, or habitat quality may be used to create a connectivity model for a particular species or group of fishes, but in practice, such studies are scarce (Van Looy et al. 2013, Diebel et al. 2015, Maitland et al. 2016). Connectivity indices are, in several cases, accompanied by budget optimization methods to help managers select obstacles for removal when economic limitations exist (O'Hanley 2011, Maitland et al. 2016).

Gathering information on these variables is often an extremely time-consuming or even impossible task. Inaccessibility of river stretches or the absence of appropriate tools may prevent the incorporation of these elements into the indices, especially when analyzing connectivity at larger scales (basin level and above (Ovidio and Philippart 2002, Shaw et al. 2016). In these cases, researchers use expert judgement, computer approximations, or model simplifications to calculate the passability of obstacles and river connectivity (Cote et al. 2009, Bourne et al. 2011, Branco et al. 2014). Depending on the objectives and the scale of the research, more simplified indices (using only obstacle passability and river stretch length) can be used to estimate connectivity (Kemp and O'Hanley 2010). However, adding as many variables as possible to the indices is recommended to produce suitable restoration and conservation plans adapted to each particular case (Bower et al. 2015, Maitland et al. 2016).

The Bidasoa River basin in the north of Spain harbors the easternmost population of Atlantic salmon (*Salmo salar* L.) on the Iberian Peninsula. The drastic decrease this population suffered during the 20th century was probably due to the proliferation of hydroelectric weirs that obstructed the migration of salmon to the spawning grounds upstream (Campos et al. 2008). Today the Bidasoa watershed has >150 obstacles, most of which are weirs. The autonomous government of the region of Navarra has been building fish ladders and removing obsolete obstacles during the last 20 years to improve river connectivity for Atlantic salmon, providing a unique opportunity to perform long-term studies about the effects of barriers and their removal over the longitudinal connectivity of a river basin.

The aim of this study was to provide managers with a simple index to assess river connectivity that includes habitat suitability for fish species and informs future barrier removal actions. A simple Habitat Quality Index (Q_i) for Atlantic salmon reproduction was created and added to an existing Habitat Connectivity Index (HCI) to build the Breeding Habitat Connectivity Index (HCIb). The change in Bidasoa River connectivity due to weir removal and fish ladder actions was analyzed using the HCIb and the HCI to compare the results. Because indices are models, their outcomes vary depending on the variables used to build them, and common patterns and differences can be found among the results. To add more information, connectivity was analyzed first using only upstream barrier passability and then adding downstream passability to the HCI and the HCIb. Past connectivity of the Bidasoa River basin was assessed, and barriers were ranked according to their impact on habitat accessibility.

Methods

Bidasoa River and Atlantic salmon

The Bidasoa River basin has a drainage area of 710 km^2. The river starts in the Pyrenees Mountains and ends in the Bay of Biscay in the Cantabrian Sea, delimiting the border between Spain and France in its last 10 km. The river is 69 km long, has a mean annual flow of 24.7 m^3/s, and receives water from numerous small tributaries. The climate in the river basin is oceanic, with abundant precipitation and no significant dry season. The Bidasoa River basin had 158 artificial obstacles at the beginning of the 21st century. By December 2016, 15 weirs had been removed and 3 had added fish ladders, both in the mainstem and various tributaries (Fig. 1).

Atlantic salmon (*Salmo salar* L.) is a large anadromous salmonid with a strong body suited for long migrations between the ocean and the river. This species is distributed along the European and American Atlantic coasts of the Northern Hemisphere, from the north of Spain and the United States to the Arctic Polar Circle. Salmon hatch in the river during spring, grow for 1 or 2 years in the river, and then migrate to the sea where they complete body and sexual maturation. Salmon spend 1–3 (or sometimes more) years in the ocean and then return to the river where they hatched to spawn during winter (Jonsson and Jonsson 2011).

River and weir mitigation data

The Government of Navarra provided the database of obstacles and fish ladder actions for the Bidasoa River basin. We downloaded an ESRI shapefile layer of rivers from the website IDENA (IDENA 2016), and using ArcMap (ESRI 2011) we discarded the smallest Bidasoa River tributaries (described as "other grade" in the layer attributes table) and their barriers because they are too small to sustain Atlantic salmon. The obstacle database was added to ArcMap, and obstacle coordinates were adjusted to match rivers. Obstacle upstream and downstream passability were classified separately as impassable (0), difficult

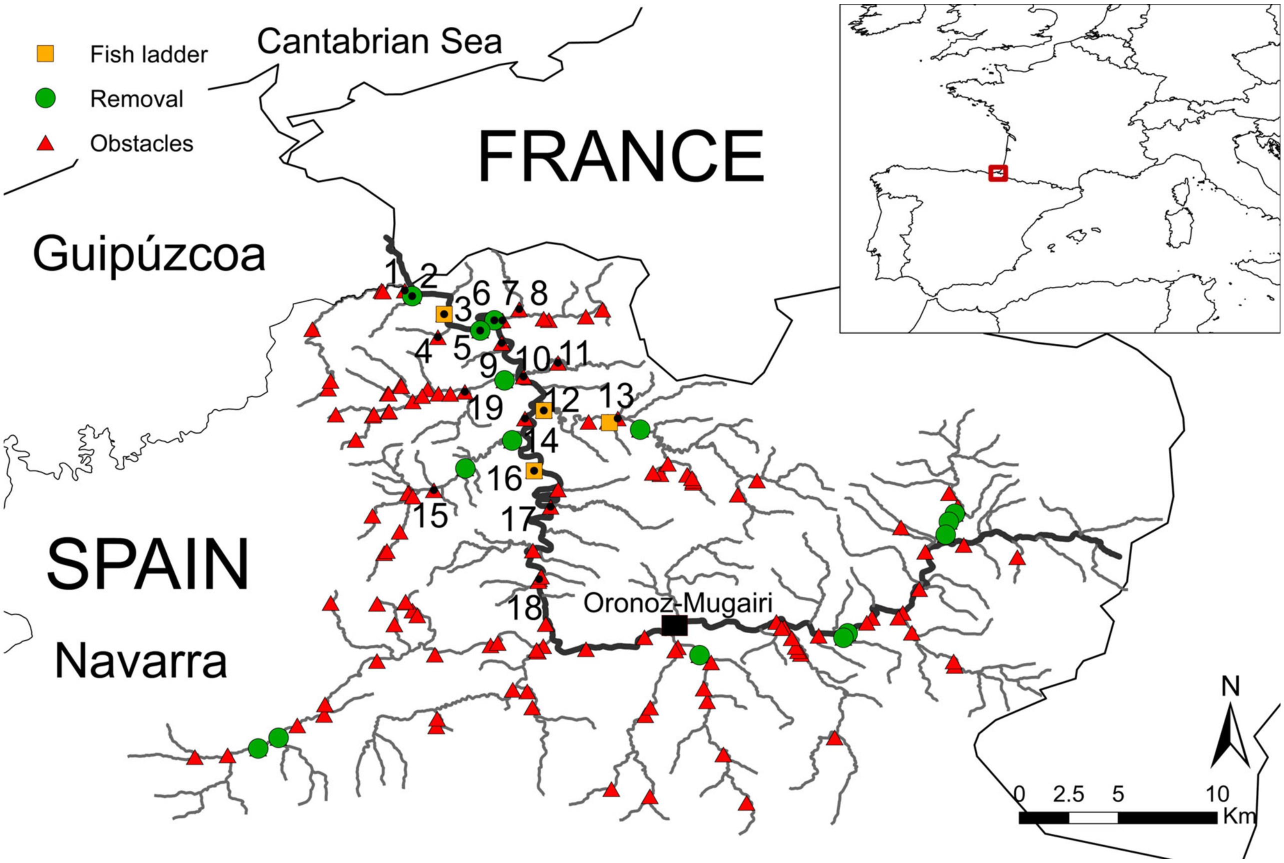

Figure 1. Bidasoa River (bold line) and its most important tributaries (gray lines), their natural and artificial obstacles (red triangles), mitigated obstacles (orange squares), and removed obstacles (green circles). Main obstacles are numbered and marked with a black dot: 1. Mill of Endaraberea; 2. Endarlatsa; 3. Nazas; 4. Mill of Zalain; 5. la Mina; 6. Central de Bera; 7. Mill Argaya-Enea; 8. Mill of Iztea; 9. Funvera; 10. Toma de la Central de Navasturen; 11. Toma de Aguas de Bera; 12. Ferrería; 13. Antsolukueta; 14. Central de Navasturen; 15. Yanci II; 16. Central de Murgues; 17. Culvert of Iruribieta; 18. Mill of Jorajuría; and 19. Mill Beheko-Errota.

passability (0.33), and passable (0.66) following expert judgement. Collectors and water flow gauging stations <0.6 m high classified as passable were eliminated from the analysis (5 total). Of the original 158 barriers, 134 remained after the others were discarded.

Rivers were then cut, creating segments separated by all their intersections and obstacles. Segments isolated entirely by natural obstacles were removed from the river network. The resulting river network had 404 segments and was used to create the HCI index described herein.

Habitat quality

To evaluate habitat quality, we assessed the suitability of the river basin for salmon reproduction and development. First, the elevation of the upstream and downstream end points of each segment was used to calculate the average percent slope, using a raster layer of elevation (30 m resolution) as a template (https://lta.cr.usgs.gov/SRTM1Arc). With these data, river stretches with slopes >7% were removed because they are unsuitable for salmon reproduction (Jonsson and Jonsson 2011). The remaining segments were characterized in situ during May and June 2017, except for the main course of the Bidasoa that reaches from the weir of Endarlatsa to Oronoz-Mugairi; that habitat information was provided by the Government of Navarra.

Each river segment was characterized by evaluating a series of regularly spaced sample points. A minimum distance of 100 m was established between points so that each segment was characterized by 1 to 13 points, depending on its length. The suitability of each point for spawning and growing was assessed using expert criteria. Several variables were collected: type of stretch (riffle, pool, glide, or swamp), type of substrate (sand, gravel, pebbles, rocks, or stone plates), width, the percentage of shade, and a visual assessment of depth and water velocity. Riffles with gravel and small pebbles and medium to high flow were considered suitable as spawning sites, and riffles with rocks and pebbles and medium to high flow were considered suitable for fry development (Moir et al. 1998, Grabowski et al. 2008). Points lacking these characteristics were classified as unsuitable. Two parameters were defined for each segment with these data: the relative abundance of suitable points for spawning (S_i), and suitable points for development (D_i):

$$0 < S_i < 1 \text{ and } 0 < D_i < 1. \quad (1)$$

We then defined the parameters p and q as constants that establish the relative importance of spawning and development points as:

$$p + q = 1. \quad (2)$$

We used a p and q of 0.5, meaning spawning and development sites have the same importance for Atlantic salmon and should be in the same proportion in a river segment. This number was chosen randomly and can be changed in future studies. Using the 4 parameters described above (S_i, D_i, p, and q), we defined the Index of Habitat Availability (A_i) as:

$$A_i = pS_i + qD_i , \quad (3)$$

and the Index of Proportionality (P_i), which explains the deviance of S_i and D_i proportions in segment i from the ideal proportions defined by p and q, as:

$$P_i = 1 - \frac{|qS_i - pD_i|}{qS_i + pD_i}. \quad (4)$$

Finally, we created the Index of Habitat Quality (Q_i), calculated for each segment i, expressed as:

$$Q_i = \frac{(A_i + P_i)}{2} , \quad (5)$$

where $i = 1, \ldots, n$, and n is the number of stream segments.

If $A_i > 0$, then equation 5 is applied; if $A_i = 0$, then equations 4 and 5 are not applied and $Q_i = 0$ because there is no suitable habitat in the segment. The result is a number between 0 and 1 that represents the proportion and importance of habitats suitable for spawning and development of salmon in each segment i of the river basin. This Q_i is multiplied by the length of its segment (l_i) to calculate the Index of Suitable Length (SL_i) for each segment.

$$SL_i = Q_i \times l_i. \quad (6)$$

The result of this multiplication is always smaller than the original segment length. The result should not be considered an estimate of the real length of suitable habitat in the evaluated segment but rather an index of suitability for that segment. Of the 202 segments (288.92 km), 76 river segments (95.04 km, 32.9% of the river basin) were not assessed because inaccessibility prevented sampling. Of the 76 river segments that were not sampled, 46 were terminal stretches and were removed from the analysis. The other 30 segments were small (<1 km) inner segments embedded between larger segments. The mean Q_i of the upstream and downstream segment was calculated for these inner segments. If the segment was the mouth of a tributary stream, the value of the upstream segment was selected because the habitat between the main river and tributaries is usually different (Jonsson and Jonsson 2011). After the removal of nonsampled segments, 2 removed weirs located on the upper Bidasoa basin were discarded from the study (Table 1).

Table 1. Summary of length, number of segments, and number of mitigations analyzed. The first column is original raw data, the second column is the network used to calculate the HCI, and the third column is the network used to calculate the HCIb.

	Original river basin	HCI river basin	HCIb river basin
Total length (km)	793.27	561.10	203.32
Number of segments	722	404	156
Number of barriers	158	134	73
Number of mitigations	19	19	17

Available habitat analysis

The HCI for diadromous species used in this study, developed by McKay et al. (2013), measures habitat availability from the river mouth upstream based on the location of each obstacle and the habitat of each river segment. This index uses adjacency matrices to assess upstream and cumulative passability from each node. Nodes without obstacles are represented by the value 1 (usually river intersections), and the nodes representing obstacles are assigned values between 0 and 1, depending on their passability. See McKay et al. (2013) for a complete description of the method. Using the river mouth as the first node, the total passability of node j is the product of the passability of node j by the cumulative passability (product of all node passabilities) of all nodes from the river mouth to node j. Accessible habitat upstream of node j is the result of the multiplication of total passability to node j and the upstream habitat from node j (in this study accessible habitat is both measured as segment length, and as SL_i). HCI is the result of dividing the sum of accessible habitat upstream of each node by the total habitat of the river basin, expressed as a percentage:

$$\text{HCI} = \frac{\sum (\text{Accessible habitat})}{\text{Total habitat}} 100. \quad (7)$$

The result of the analysis is a unique value from 0 to 100 for the entire river basin that represents the percentage of available habitat relative to total basin length. When the passability of all the obstacles of a river basin is 1, all habitat is available and HCI = 100.

The HCI was calculated after every mitigation action, first using only upstream obstacle passability and then using total barrier passability, calculated as the product of upstream and downstream passabilities (Cote et al. 2009). Segment habitat was only characterized by segment length.

We then modified the HCI to consider the breeding habitat quality value Q_i of each segment, a modification we called the Breeding Habitat Connectivity Index (HCIb). To calculate the HCIb, accessible habitat was calculated as total passability to node j multiplied by SL_i of the upstream segment i (equation 6). With this SL_i, the HCIb was calculated in the same way as the HCI. The HCIb was also calculated after every obstacle mitigation action using upstream barrier passability and total barrier passability.

In total, 4 models were created: the HCI for upstream migration (HCI_up), the HCI for the combined upstream and downstream migration (HCI_updown) and the HCIb for upstream (HCIb_up), and both upstream and downstream migration (HCIb_updown).

Finally, the improvement in accessibility was calculated when one obstacle or a pair of obstacles was removed using 2016 connectivity as a baseline. The results are reported as a percentage of the increase in connectivity.

The habitat connectivity indices were performed in R 3.4.0 (R Core Team 2015) with the addition of the R packages *igraph* (Igraph core team 2015), *abind* (Plate and Heiberger 2016), *raster*, and *rgdal* (Bivand et al. 2016). The R script is available from the authors under request.

Results

When calculating the HCI for upstream migration (HCI_up model), the available habitat for Atlantic salmon increased by 6.21 points between 1992 and 2016 (Table 2), an average of 0.33 points per mitigated dam. The dam removals of 2016 caused the highest increase in connectivity, >4.5 points (Table 2). If upstream adult migration and downstream smolt migration were both considered (HCI_updown model), the change in the HCI for Atlantic salmon was reduced considerably, with an average of 0.09 points per mitigated dam in the same period. The removals of 2016 also increased habitat accessibility the most, although the observed increase was much lower than in the former case (1.31 points; Table 2).

When calculating the HCIb for upstream migration (HCIb_up), there was an increase of 11.49 points between 1992 and 2016, which is 0.68 points per permeation (Table 2). The removals of 2016 increased habitat availability by 4.45 points (Table 2). When using both upstream and downstream migration (HCIb_updown model), the habitat accessibility increases by 2.84 points. We determined the evolution of segment accessibility at the beginning and end of the mitigation process for all models considered (Fig. 2 and 3).

When the remaining obstacles were removed one at a time, the effects described by the 4 models were similar; the removal of mainstem dams closer to the river mouth generally resulted in the highest increase of accessible habitat (see Nazas, Funvera, and Navasturen in Table 3). The removal of obstacles from tributaries closer to the river mouth had less impact on habitat accessibility, and removal of obstacles far from the river mouth had almost no effect. Nazas, Funvera, and Navasturen, representing the first, second, and third weirs salmon encounter when they enter the river, were the first, second, and third most impactful barriers in 3 of the 4 models. When modeling the removal of 2 obstacles at a time, the most important were still the Nazas, Funvera, and Navasturen weirs, the first 3 weirs encountered by salmon (Table 4). Models diverge in the intensity of the impact of the other obstacles (Table 3 and 4).

Discussion

Breeding Habitat Connectivity Index (HCIb)

Many different methods exist to measure longitudinal river connectivity and habitat accessibility to address

Table 2. The HCI and HCIb for upstream passage expressed in percentage of available habitat after each mitigation with the number of mitigations per year, the mean distance of the obstacles to the sea (mDRM), and the type of stream (mainstem or its tributaries). The total increment of connectivity in points between 1992 and 2016 is also shown (HCIb_updown). Connectivity is calculated using upstream migration only (up) and upstream and downstream combined migration (updown). The asterisk (*) indicates that 2 removed weirs were eliminated from the HCIb analyses.

Year	Mitigation	mDRM (km)	Type of stream	HCI_up	HCI_updown	HCIb_up	HCIb_updown
1992	0	—	—	1.83	1.49	4.02	3.20
1993	1	3.35	Main	2.28	1.69	4.45	3.29
2001	1	41.54	Tributary	2.28	1.69	4.45	3.29
2005	1	15.3	Tributary	2.30	1.69	4.52	3.29
2006	1	17.8	Tributary	2.32	1.69	4.57	3.29
2007	6	22.01	Tributary/main	2.89	1.76	5.69	3.47
2009	7 (5)*	48.32 (47.79)*	Tributary/main	2.96	1.76	5.79	3.47
2014	1	7.52	Main	3.40	1.81	7.05	3.74
2016	2	4.43	Main	8.04	3.12	15.51	6.05
Increment	—	—	—	6.21	1.31	11.49	2.84

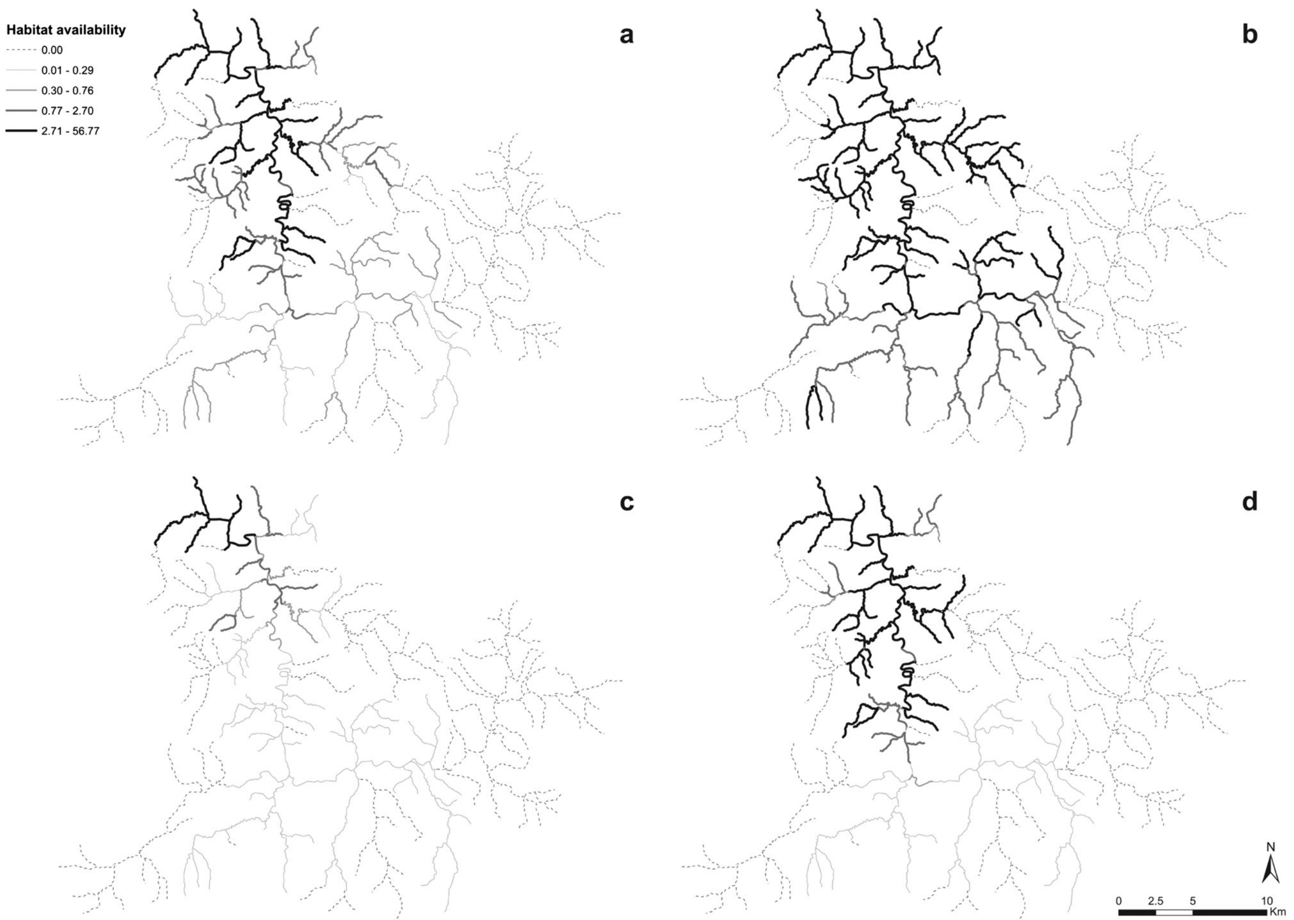

Figure 2. The HCI by segment in 1992 and 2016 using (a and b) upstream passability only, and (c and d) upstream and downstream passabilities combined. HCI is expressed as the square root of segment accessibility to help visualize the differences between the segments.

the problem of fragmentation (Kemp and O'Hanley 2010). In this study, habitat quality was included as a variable in habitat accessibility index HCIb. The suitability of a river stretch for the reproduction and development of fish species may be a deciding factor when planning connectivity restoration actions. The HCIb was compared to the HCI to understand the effect of its inclusion on an index of habitat accessibility for diadromous species. The addition of different parameters can significantly alter the outcome of an index and impact the effectiveness of restoration plans. How to choose the best index for a particular case could be a difficult task and depends on the objectives and the information available. A poor prioritization of obstacles for removal can hinder restoration plans and species management, leading to unsuccessful fish species conservation and a waste of economic resources (O'Hanley 2011).

This study showed that the available habitat for salmon reproduction increased from 1992 to 2016 in the 4 habitat accessibility models created as a result of the restoration actions conducted. However, the increase in habitat accessibility was higher in both of the HCIb models with respect to the HCI models because they describe only suitable habitat for salmon reproduction as well as the changes in river habitat caused by the disappearance of impoundments. Connecting a shorter river segment with high habitat quality may be more beneficial for Atlantic salmon reproduction than opening a larger but unsuitable river segment. The inclusion of environmental, ecological, or biological variables in connectivity indices is understood to improve the results but is not often used (Diebel et al. 2015, Maitland et al. 2016, Shaw et al. 2016) because of a lack of information and an increase in complexity. We understand that collecting breeding habitat variables such as spawning site locations might not be feasible for studies at large scales but might be worth the effort in small watershed studies like the one presented here. Other methods exist to predict local habitat variables (e.g., percent of each substrate type, width) using catchment-scale variables (e.g., length, elevation, stream order), which may be useful for analyzing habitat quality for fish species (Mugodo et al. 2006).

Habitat accessibility indices are a useful tool for habitat connectivity modeling; however, actual habitat use is sensitive to many factors, such as river flow, intraspecific

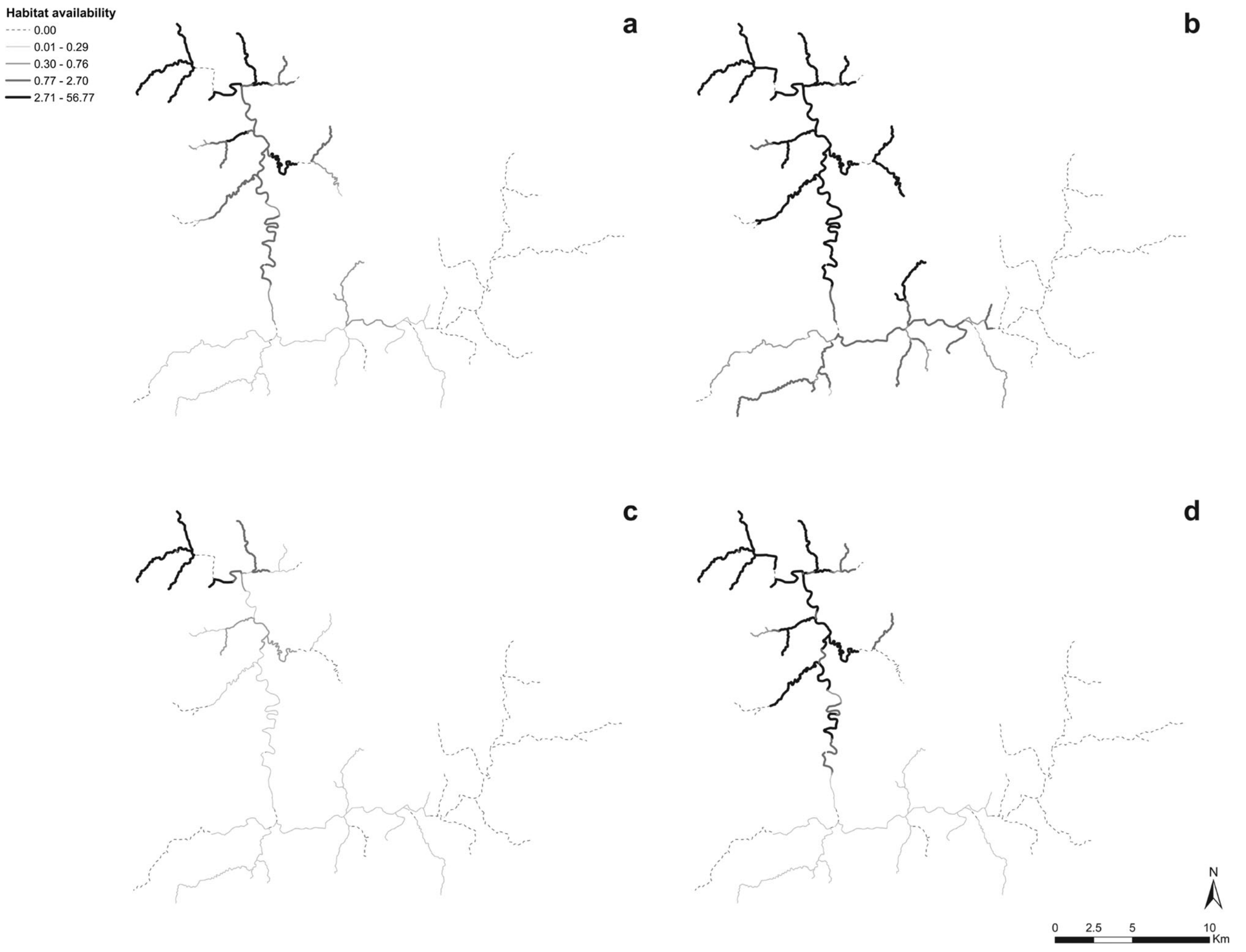

Figure 3. The HCIb by segment in 1992 and 2016, calculated using (a and b) upstream passability only, and (c and d) upstream and downstream passabilities combined. HCIb is expressed as the square root of segment accessibility.

swim capability variation, or cumulative passage (Ovidio and Philippart 2002, Thorstad et al. 2008, Bourne et al. 2011, Shaw et al. 2016). Because many of those variables are impossible to measure, certain model simplifications must be made (Cote et al. 2009, O'Hanley 2011, McKay et al. 2013), which might create bias in barrier passability and connectivity on simplified index models like the HCI and the HCIb.

The study of the individual effect of each barrier over the global connectivity of the river shows that the most

Table 3. Increment in connectivity (in points) of the 10 dam removals that further increase habitat availability for each model. The obstacles with an asterisk (*) are located in the mainstem. DRM: distance to river mouth (in km).

Name	DRM	HCI_up	HCI_updown	HCIb_up	HCIb_updown
1. Mill of Endaraberea	3.22	—	0.13	0.62	0.96
3. Nazas*	5.50	3.03	1.36	6.11	3.72
4. Mill of Zalain	6.87	0.22	0.15	—	—
7. Mill Argaya-Enea	9.49	—	0.24	1.27	1.56
8. Mill of Itzea	10.56	—	—	0.59	0.21
9. Funvera*	6.67	2.46	1.92	3.56	2.84
10. Toma de la Central de Navasturen	9.33	—	—	—	—
11. Toma de Aguas de Bera	11.97	0.25	0.04	—	—
12. Ferrería	11.62	0.37	0.08	1.01	0.32
13. Antsolokueta	17.77	0.38	—	0.27	0.03
14. Central de Navasturen*	12.29	1.13	0.29	1.58	0.52
15. Central Yanci II	10.44	—	0.04	—	—
16. Central de Murgues*	16.19	0.49	0.07	0.66	0.10
17. Culvert of Iruribieta	20.15	0.23	—	—	—
18. Mill Jorajuría	27.20	0.22	—	—	—
19. Mill Beheko-Errota	15.16	—	—	0.33	0.07

Table 4. Increment in connectivity (in points) of the top 10 removal combinations of 2 dams for the 4 models. The obstacles with an asterisk (*) are located in the mainstem.

Names	HCI_up	HCI_updown	HCIb_up	HCIb_updown
Nazas* + Funvera*	6.76	5.77	11.51	10.22
Nazas* + Central de Navasturen*	4.74	—	8.51	4.91
Funvera* + Central de Navasturen*	4.17	3.25	—	5.23
Nazas* + Central de Murgues*	3.77	—	7.11	3.94
Nazas* + Antsolokueta	3.61	—	6.53	—
Nazas* + Ferrería	3.58	—	7.64	4.46
Nazas* + Toma de Aguas de Bera	3.40	—	—	—
Nazas* + Culvert of Iruribieta	3.38	—	—	—
Nazas* + Mill of Zalain	3.36	—	—	—
Nazas* + Mill of Jorajuría	3.36	—	—	—
Funvera* + Ferrería	—	2.30	—	4.32
Funvera* + Central de Murgues*	—	2.22	—	—
Funvera* + Mill Argaya-Enea	—	2.16	—	4.39
Funvera* + Central Yanci II	—	2.10	—	—
Funvera* + Toma de Aguas de Bera	—	2.08	—	—
Funvera* + Antsolokueta	—	2.08	—	—
Fundición de * + Mill of Zalain	—	2.06	—	—
Funvera* + Mill of Endaraberea	—	2.04	—	—
Nazas* + Mill Argaya-Enea	—	—	8.04	7.30
Nazas* + Mill of Itzea	—	—	7.01	4.20
Nazas + Mill of Endaraberea	—	—	6.73	4.67
Nazas + Mill Beheko-Errota	—	—	6.62	—
Nazas + Landaburua	—	—	6.34	—

important obstacles for salmon (and probably other diadromous fishes) upstream migration are those closest to the river mouth, even when the habitat quality of river segments is considered. In all 4 models, the first 3 obstacles that salmon encounter in their migration (from river mouth and moving upstream: Nazas, Funvera, and Navasturen dams) are the most impactful (Table 3). When adding a second removed dam, the mainstem dams are still the most impactful (Table 4). This result is consistent with previous studies that denote mainstem barriers as the most impactful (Cote et al. 2009, Nieland et al. 2015). The effect of habitat quality addition to the indices is shown in the selection of tributary obstacles for removal (Table 3 and 4), in which a higher habitat quality for reproduction is usually found (Jonsson and Jonsson 2011).

Downstream obstacle passability was also added to the indices because upstream obstacle passability may not accurately predict population dynamics; adult salmon migration and reproduction is just one step in the life cycle of this species. Downstream smolt migration is also affected by obstacles but is not usually considered in diadromous fish connectivity and dam passability studies (Calles and Greenberg 2009, Roscoe and Hinch 2010, Marschall et al. 2011). Smolt injury or death upon encountering dams is due to turbines, high falls, predation, or infections (Calles and Greenberg 2009, Keefer et al. 2012, Gauld et al. 2013). Apart from direct harm, delays in downstream migration may alter smolt adaptation, growth, and survival rates (Garcia De Leaniz 2008, Marschall et al. 2011).

When downstream obstacle passability is added to the indices, the improvement in habitat availability is significantly reduced compared to the upstream-only models. This connectivity illustrates the impact of obstacles on salmon during the river stage of its life cycle (adult migration upstream as well as smolt migration downstream to the sea) and may better reflect population dynamics (Castro-Santos and Haro 2003).

Our habitat accessibility models have 2 main weaknesses. First, numerous small river streams were not accessible and were therefore removed or calculated as the mean of the quality in adjacent segments, possibly biasing the HCIb index models. Second, barrier passability was established in 3 categories (impassable, hardly passable, and passable) by expert judgement, making it less accurate than a quantitative passability (Kemp and O'Hanley 2010).

Moreover, although other studies (Diebel et al. 2015) and logic indicate that the index that includes habitat quality more accurately reflects the habitats used by Atlantic salmon, we could not assess that hypothesis because spatial tracking of salmon during the years each obstacle permeation was not conducted. Even with these shortcomings, we consider connectivity indices useful tools to analyze connectivity improvements and select obstacles for future actions, especially if habitat variables such as habitat quality and water flow are added to improve the precision of the models when possible.

Atlantic salmon situation in the Bidasoa River basin

The Bidasoa basin is a small river network formed by numerous small streams and fragmented by >150 obstacles (dams, weirs, and culverts) of different sizes. Historical data suggest >3000 salmon entered the Bidasoa River each year at the beginning of the 20th century (Sección de Ictiología y Piscicultura 1950). By contrast, the mean number of individuals entering the river in the last 20 years was 364. The mean number of spawning sites per year in the same period was 22, which were mainly concentrated in the end segments of the Bidasoa River (Álvarez and Lamuela 2001). This reduction in spawning area has been observed in other places and species (Hall et al. 2011). The likely explanation for the decrease in the Bidasoa Atlantic salmon population is the presence of obstacles, mainly dams, that block upstream river passage and constrain adult salmon to the lower river basin, which has less and lower quality spawning and parr production sites (Álvarez et al. 2003, Garcia De Leaniz 2008, Humphries and Winemiller 2009, Hall et al. 2011).

Although the accessible spawning habitat for Atlantic salmon was significantly higher in 2016 than in 1992 in the 4 models, it represents only ~10% of the watershed and is restricted to the middle and lower Bidasoa River basin (Fig. 2a–b, 3a–b). The poor breeding habitat accessibility results are the consequence of dam accumulation. Salmon must overcome numerous dams to reach high-quality spawning sites, and although many dams have fish ladders, these devices are only part of the solution because they slow migration and fatigue fish (Brown et al. 2013).

The models also showed that the mitigation efficiency per removal was low except for the 2 dams removed in 2016 (Table 2). Most mitigated weirs did not increase habitat availability for salmon by more than one point because they were likely selected not because of their effect on connectivity but for social and economic reasons. One of the most critical factors is the obsolescence of a weir. A large percentage of the Bidasoa River basin weirs are still in use, so only obsolete weirs were considered for removal. If the removed obsolete obstacles were not the most impactful, the efficacy of barrier removal was significantly reduced (Table 3 and 4), a typical result in numerous Spanish river basins (Rodeles et al. 2017).

The effects of the 2016 dam removal on salmon reproduction areas will only be accurately measured after more time (4–5 yr) has passed and by tracking adult salmon. However, dam removal in 2016 had another short-term positive effect: all individual salmon migrating into the Bidasoa River were captured and measured in an installation in the Funvera dam. After the 2016 dam removals, managers observed fewer wounds and infections in salmon captured in Funvera upstream from the removed Endarlatsa and Central de Bera dams (GAN-NIK Equipo Técnico de Pesca 2017). Healthier body condition may improve reproduction efficiency (more high-quality eggs, better fertilization) and, consequently, salmon populations (Garcia De Leaniz 2008).

Despite efforts by the Government of Navarra to stabilize and recover Bidasoa salmon, the population is still vulnerable, and salmon numbers may decrease further (GAN-NIK Equipo Técnico de Pesca 2017). Iberian salmon populations live in the southern limit of the Atlantic salmon distribution and face the stress of living in extreme climatic conditions. This unfavorable situation will intensify under some climate change conditions and may result in significant reductions and the extinction of Iberian salmonid populations (Jonsson and Jonsson 2009, Elliott and Elliott 2010, Clavero et al. 2017). To improve Atlantic salmon survival in the Iberian peninsula in the coming years, improving river connectivity is a crucial action that will provide better access to salmon spawning and smolt production sites (Horreo et al. 2011, Pess et al. 2014, Nieland et al. 2015). If salmon are constrained to small and low-quality river areas, they will likely not survive near-future climate conditions. An efficient ecological connectivity index may be essential for ensuring the recovery of the species with the least economic effort.

The Government of Navarra continues its commitment to improve river connectivity and plans to remove several other dams in the coming years (LIFE Irekibai 2016). The plan is to gradually increase potential spawning habitat by opening more suitable river stretches for salmon reproduction and development.

Dam removal is a crucial constituent of strategies to facilitate diadromous species recolonization and population recovery (Pess et al. 2014), but it is often an opportunistic action, enacted without previous ecological and cost–benefit studies (Magilligan et al. 2016) or post-monitoring efforts (Bednarek 2001, Rodeles et al. 2017). However, this study shows that habitat quality and downstream obstacle passability have a significant effect on the outcome of habitat accessibility indices and should be recognized when allowed by the conditions and scale of the watershed. This consideration will improve knowledge of the fragmentation effects on fish populations and of the selection of obstacles to remove for each species. Although the selection of dams for removal based only on ecological reasons is almost impossible (Magilligan et al. 2016), it is feasible to remove the obsolete obstacles based on their potential for connectivity. These actions will enhance the ecological benefits for river watersheds and their inhabitants in the long term.

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