

RESEARCH ARTICLE

Species and river specific effects of river fragmentation on European anadromous fish species

Peter J.T.M. van Puijenbroek^{1,2}  | Anthonie D. Buijse³  | Michiel H.S. Kraak² | Piet F.M. Verdonschot²

¹PBL Netherlands Environmental Assessment Agency, The Hague, The Netherlands

²IBED, University of Amsterdam, Amsterdam, The Netherlands

³Department, Freshwater Ecology & Water Quality, Deltares, Delft, The Netherlands

Correspondence

Peter J. T. M. van Puijenbroek, PBL Netherlands Environmental Assessment Agency, Bezuidenhoutseweg 30, Den Haag, AV 2594, The Netherlands.
Email: peter.vanpujenbroek@pbl.nl

Abstract

Fragmentation is one of the major threats to riverine ecosystems and this is most explicitly expressed by the decline in numbers of migratory fish species. Yet each species has different migration requirements and their natural distribution can include several catchments with multiple dams. Hence, to prioritize candidate rivers for improving accessibility, differences between species and between catchments have to be taken into account. The aim of this study was therefore to analyse the species and river specific effects of river fragmentation on migratory fish on a European scale. The effect of river damming on migratory fish was quantified for all 16 European long- and mid-distance anadromous species and for 33 large European rivers. The historical distribution was compared with the current upstream accessibility of the main river and the current distribution and population status of each species. The observed effects of reduced connectivity were further quantified using the Dendritic Connectivity Index for species and the Fragmentation Index for rivers. Our results showed that only very few rivers are still unaffected by dams in the main stem and that the few remaining viable migratory fish populations in Europe occur in these accessible rivers. Barriers were prioritized for making passable based on the potential accessibility gain and the number of benefitting species, showing that the main stems of the rivers Shannon and Nemunas are the best candidates. It was concluded that evaluating species and river specific effects of fragmentation strongly aids in prioritizing rivers for improving upstream accessibility.

KEYWORDS

anadromous, connectivity, dams, fish migration, river fragmentation, riverine species

1 | INTRODUCTION

Fragmentation of rivers by dams and weirs is one of the major threats to aquatic ecosystems worldwide (Dudgeon et al., 2006; Nilsson, Reidy, Dynesius, & Revenga, 2005). These dams are built for shipping, hydropower generation, flood protection, and storage of drinking and

irrigation water (Lehner et al., 2011), but fragment the aquatic landscape into isolated river sections, affecting longitudinal and lateral migration of fish species (Fuller, Doyle, & Strayer, 2015; Fullerton et al., 2010). This is most explicitly expressed by the decline in numbers of anadromous fish species (Freyhof & Brooks, 2011; Geist & Hawkins, 2016), which migrate upstream from the sea into the rivers

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to spawn. These species are particularly sensitive to the presence of dams in the main river, because a single barrier can make an entire catchment inaccessible (Parrish, Behnke, Gephard, McCormick, & Reeves, 1998; Schiemer, Guti, & Staras, 2003).

Besides limiting fish migration, barriers can also affect habitat quality, even over a long distance. Downstream effects include changes in flow regime, sediment and nutrient transport, and water temperature (Fuller et al., 2015). Upstream effects increase with size of the reservoir, because a large standing water body is uninhabitable for riverine fish (Birnie-Gauvin, Aarestrup, Riis, Jepsen, & Koed, 2017; Jepsen, Aarestrup, Økland, & Rasmussen, 1998; Pelicice & Agostinho, 2008). Even if barriers are made passable through fish passages, the habitat conditions in impoundments upstream of dams and weirs remain less favourable for riverine fish. Moreover, fish passages are not a 100% effective and vary in their efficacy per species. Higher mortality is caused by enhanced predation in impoundments and by hydropower turbine passage during downstream migration (Brevé et al., 2014; Calles, Rivinoja, & Greenberg, 2013; Jepsen et al., 1998; Wilkes, Mckenzie, & Webb, 2018). In addition, it takes time to pass through a fish passage (Baisez et al., 2011; Croze, Bau, & Delmouly, 2008). As such, fish passages need to be designed in such a way that they ensure minimal passage delay and have little to no postpassage impacts (Silva et al., 2018). Obviously, dam removal would be more effective but is certainly not always feasible (Bednarek, 2001; J. E. O'Connor, Duda, & Grant, 2015).

The combination of deteriorated habitat quality and reduced accessibility makes it difficult to separate the effects of river fragmentation from other stressors in explaining species decline. Free migration is essential for anadromous species to fulfil their life cycle. Yet each species has different migration requirements and their natural distribution can include several river basins with multiple dams. Hence, to prioritize candidate rivers for improving upstream accessibility, differences between species as well as between river basins have to be taken into account, as each river hosts a specific set of species with specific migration routes and habitat demands for spawning or seasonal migration (Fuller et al., 2015; Fullerton et al., 2010).

Earlier studies on river fragmentation did not include historical and catchment information on the level of individual fish species (Lehner et al., 2011; Nilsson et al., 2005) and were restricted to local and regional cases or included only a few species or species guilds (Baisez et al., 2011; Brevé, Buijse, Kroes, Wanningen, & Vriese, 2014; Nunn & Cowx, 2012; O'Hanley, 2011; Rincón, Solana-Gutiérrez, Alonso, Saura, & García de Jalón, 2017; Winter & Fredrich, 2003). Therefore, the aim of this study was to analyse the species and river specific consequences of river fragmentation on migratory fish on a European scale. To achieve this aim, the impact of reduced connectivity by fragmentation on 16 European riverine species with long- to mid-distance anadromous migration ranges was assessed by (a) comparing the historical distribution patterns; (b) the current accessibility of the main stem of the river; and (c) current distribution and population status. The observed effects of fragmentation were further quantified per species on a multiriver level and per river on a multispecies level. Finally, our results were used to prioritize barriers for improving accessibility based on the potential positive effects on migratory fish species.

2 | METHODS

2.1 | Study area

To analyse the effects of river fragmentation on migratory fish species, 33 large European rivers were included (using ESRI's ArcGis map: "DCW_1993_Rivers_ESRI"). The selection, with a cumulative total length of 18,600 km, comprised 13 rivers from the European Environment Agency's (EEA) "large rivers list," 18 rivers from the "other large rivers list" (EEA, 2009), and 2 Finnish rivers (Iijoki and Oulujoki). The Guadiana in Spain and Portugal and the Glomma in Norway were not considered, as fish migration is blocked by natural waterfalls. The geographical position of barriers was obtained through personal communication with expert members of the World Fish Migration Platform (www.worldfishmigrationfoundation.com) and from species or river specific literature (see Data S1 for a detailed list). For each river, the two most downstream barriers without a fish passage were localized and mapped using Google Earth. For rivers with an estuary consisting of several branches, the main branch was selected, that is, for the Rhine, this was the Nieuwe Waterweg through Rotterdam and, for the Meuse, it was the Haringvliet. Stretches of all rivers were classified into four fragmentation classes: (a) free flowing to the sea; (b) accessible by fish passage; (c) not accessible due to one barrier; and (d) not accessible due to two or more barriers.

2.2 | Selected fish species

All 16 indigenous long- or mid-distance anadromous species that occurred in Europe were included. The Danube hosted five species: Russian sturgeon (*Acipenser gueldenstaedtii*), ship sturgeon (*Acipenser nudiventris*), stellate sturgeon (*Acipenser stellatus*), beluga sturgeon (*Huso huso*), and pontic shad (*Alosa immaculata*; Froese & Pauly, 2016). The remaining 11 species occurred in the other European rivers: Adriatic sturgeon (*Acipenser naccarii*), Baltic sturgeon (*Acipenser oxyrinchus*), Atlantic sturgeon (*Acipenser sturio*), allis shad (*Alosa alosa*), twaite shad (*Alosa fallax*), whitefish (*Coregonus maraena*), houting (*Coregonus oxyrinchus*), river lamprey (*Lampetra fluviatilis*), sea lamprey (*Petromyzon marinus*), Atlantic salmon (*Salmo salar*), and sea trout (*Salmo trutta*). From these 16 species, 15 are now listed on the IUCN Red List; one, the Baltic sturgeon, is listed as being extinct in Europe, but the species was recently reintroduced from North American populations; and six are listed as critically endangered (IUCN, 2015). All species, except the sea trout, are included in the EU Habitats Directive (Table 1; EEC, 1992).

2.3 | Analysis of fragmentation and connectivity

The historical distribution was compared with the current upstream accessibility of the main river and the current distribution and population status of each species. The former was based on the rivers where each species has its present native distribution and where the species was extirpated; rivers where the species was introduced or was invasive were excluded (Kottelat & Freyhof, 2007). Both the historical distribution and the current distribution were mapped using the GBIF database (GBIF, 2016) and supporting literature (Kottelat & Freyhof,

TABLE 1 Number of each catchment as depicted in Figure 1c, the number of migratory fish species: historical, currently affected by fragmentation and information on population status; current accessible river length and accessible river length after improving accessibility of the most downstream obstacle (km); and the Fragmentation Index (F) before and after improvement

River		Number of migratory fish species			Current situation		First obstacle passable	
Number	Name	Historical	Affected	Pop. status available	Length (km)	F	Length (km)	F
33	Danube	5	5	5	860	297	940	279
8	Daugava	4	4	2	50	345	120	263
25	Dordogne	6	0	6	260	0	N.A.	0
30	Douro	6	6	6	20	563	60	495
29	Ebro	3	3	3	110	203	130	190
12	Elbe	8	4	5	760	110	770	103
21	Erne	4	4	1	0	400	10	348
26	Garonne	7	7	7	310	0	N.A.	0
32	Guadalquivir	2	2	2	110	156	200	116
13	Gudenå	5	5	4	40	338	90	146
6	Ijoki	4	4	3	0	400	20	381
5	Kemijoki	4	4	3	30	374	50	346
1	Klarälven	3	3	2	0	300	30	273
24	Loire	7	5	7	680	112	790	50
3	Luleälven	4	4	3	0	400	40	361
16	Meuse	8	8	8	270	441	390	263
9	Nemunas	7	3	3	180	222	680	0
11	Odra	6	0	4	520	0	N.A.	0
7	Oulujoki	4	4	3	40	347	100	268
28	Po	2	2	2	280	109	610	0
15	Rhine	9	6	9	820	140	830	131
27	Rhone	4	2	4	200	107	250	87
17	Scheldt	8	8	8	100	505	120	448
23	Seine	7	7	7	270	373	340	283
19	Severn	6	6	1	40	493	70	433
22	Shannon	6	6	1	10	571	230	0
31	Tagus	4	4	4	100	224	190	75
20	Thames	4	4	3	60	311	80	280
4	Torneälven	4	0	2	330	0	N.A.	0
18	Trent	6	6	4	70	412	80	394
2	Vindeälven	4	0	2	480	0	N.A.	0
10	Vistula	7	5	3	880	28	890	23
14	Weser	8	8	3	110	627	120	618

2007; Tockner, Uehlinger, & Robinson, 2009). Additional information was obtained from species or river specific references (see Data S1 for a detailed list). Recently reintroduced species without observations of returning upstream migrating specimens were still considered to be extinct. The current distribution was classified as (a) viable, (b) recovered, (c) reintroduced supported by stocking, (d) small and declining, or (e) no information.

Longitudinal connectivity was quantified by using the Dendritic Connectivity Index (DCI) for diadromous species (Cote, Kehler, Bourne, & Wier, 2008). The index was slightly adapted to calculate the reduced connectivity per species and per individual river:

$$DCI_{r,s} = 100 * l_{r,s} / L_{r,s}, \quad (1)$$

where r is river, s is species, l is the current length of the river from the sea to the first barrier without fish passage, and L is the maximum

historical migration distance. Both l and L are in km. The DCI varied between 0 for fully blocked rivers and 100 for intact rivers. To compare species, the DCI per species was calculated as the average DCI of all rivers where the species originally occurred (n):

$$DCI_s = \frac{\sum_{r=1}^n DCI_{r,s}}{n}. \quad (2)$$

To compare rivers, the inverse measure of connectivity, the fragmentation (F) per river, was calculated as the sum of the impact on all species (m) for that river:

$$F_r = \sum_{s=1}^m (100 - DCI_{r,s}). \quad (3)$$

The effect of making the first barrier passable was assessed by calculating for each river two indices: the gain in kilometres and the

gain for species, respectively. Both so-called species-fragmentation indices (S_{km} , S_F) were based on the sum of the effect for each species relative to its historical distribution:

$$S_{km_r} = \sum_{i=1}^{16} (\Delta l_{r,s}) \quad (4)$$

$$S_{F_r} = 100 \cdot \sum_{s=1}^{16} (\Delta l_{r,s} / L_{r,s}), \quad (5)$$

where S_{km} (sum of species-km) is the gain in accessible kilometres and $\Delta l_{r,s}$ is the km additional accessible river section after making the first barrier passable. S_F (sum of species-fragmentation) is the sum of the gain in DCI for all affected species in a river by removing the first barrier (Data S1). Only species with a historical distribution upstream the first barrier had a $\Delta l_{r,s} > 0$. Rivers combining high values for both Equations 4 and 5 were considered to be most promising candidates for taking measures to recover migratory fish populations and should thus receive the highest priority.

3 | RESULTS

3.1 | Fragmentation and connectivity in large European rivers

High numbers of anadromous species were historically present from the Vistula to the Garonne, with the Rhine hosting the largest number (Figure 1a). Twaite shad and houting showed the shortest migration distance, migrating just upstream of the tidal limit up to several hundred kilometres inland, whereas all other species migrated from a few hundred up to a 1,000 km (Data S1).

Comparing the historical and current distribution (Figure 1a,b) of anadromous fish species shows a dramatic decline in number of species, with many rivers being devoid of any migratory fish species. The loss of anadromous fish species coincides with a strong decrease in accessibility of almost all large European rivers (Figure 1c). Currently, only two European rivers are free flowing to the sea, the Torneälven and the Odra, whereas large river sections without

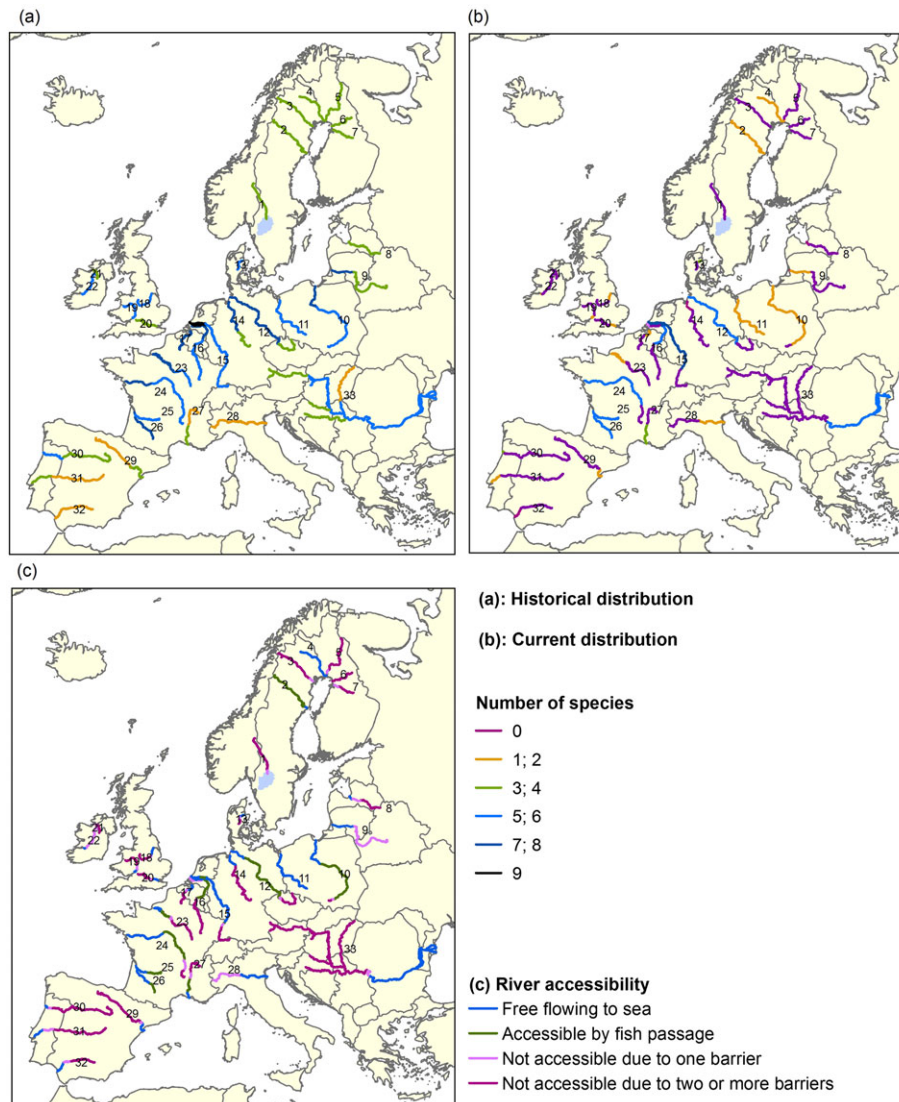


FIGURE 1 The historical (a) and current (b) distribution of the long- and mid-distance anadromous species in the main stem of large European rivers and their upstream accessibility in 2016 (c). Names of the rivers numbered 1–33 are given in Table 1. Current distribution is based on the number of species for which information on population status is available (Table 2) [Colour figure can be viewed at wileyonlinelibrary.com]

obstacles occur only in the downstream parts of the Danube and the Rhine (Figure 1c; Table 1). Major rivers with improved connectivity by means of fish passages are the Vindöälven, the Elbe, with the largest fish passage of Europe, the Loire, the Garonne, the Dordogne, and, recently, the Vistula. Of the total analysed river length, only 27% is freely accessible and 16% has improved connectivity through fish passages. Nevertheless, the restored sections have a reduced accessibility effectivity due to enhanced mortality in the reservoirs and during downstream migration. Most other rivers are not accessible for anadromous species anymore (Figure 1c). The index *F* showed that the Weser, the Shannon, the Douro, the Scheldt, and the Severn were most affected by fragmentation (Table 1).

On a scale from 0 to 100, the DCI of migratory fish species varied between 39 and 98, showing that the Danube sturgeon species and sea trout (all DCI 39) are most affected by reduced connectivity in the main stem, and twaite shad (DCI 60) and houting (DCI 67) are least affected by fragmentation (Table 2). The Baltic sturgeon (DCI 98, but, without the recently made accessible Vistula, the DCI is 77) would have been least affected by reduced connectivity, but it has become extinct nevertheless.

The current distribution of migratory species is thus strongly reduced by dams, as major parts of the rivers became inaccessible and many species went locally extinct. For six selected species for which sufficient data were available and that used to occur in many rivers, this is shown in more detail by combining the historical migration distance with the actual maximum migration distance and the current population status (Figure 2). The 1:1 lines in Figure 2 represent rivers unaffected by fragmentation or equipped with fish passages, which are obviously very few. Moreover, the most viable populations occur in these accessible rivers. The Atlantic sturgeon went extinct in five catchments that were freely accessible for more than 40% of their migratory distance, indicating that other environmental conditions

probably contributed to its current absence. The Atlantic salmon still occurs in 27 catchments and is presently reintroduced by stocking in 10 rivers, even inaccessible ones (Erkinaro et al., 2010; Östergren, Lundqvist, & Nilsson, 2011). With many reintroductions, the results for sea trout are comparable with the Atlantic salmon. In most inaccessible rivers, allis shad, river lamprey, and sea lamprey went extinct or occur presently in small, declining populations, whereas twaite shad is least affected.

Concerning the species not shown in Figure 2, extinction in Europe of Baltic sturgeon was probably caused by other factors than fragmentation, given the relative high DCI. In contrast, houting recovered in the Rhine and the Meuse after reintroduction. The Danube hosts five specific anadromous species that originally migrated over long distances. Today, migration is limited due to the Iron Gate II dam that is situated 860 km from the Black Sea and the four remaining sturgeon species are all critically endangered.

3.2 | Options for improving upstream accessibility

The gain in accessible river length by making the most downstream obstacle passable is shown by the vertical dotted line and black dot for the six species presented (Figure 2). This information is integrated in Figure 3, showing the number of species benefitting and the gain in accessible river length for all European rivers. The species and river specific gain is used to prioritize the need to improve accessibility based on the number of benefitting anadromous species, historical distribution, and the increase in accessible river length (Figure 4). Highest priority to build effective fish migration solutions is assigned to the Shannon hydropower station and the hydropower dam in the Nemunas near Kaunas (W. O'Connor, 2015; Polutskaya, 2005). These solutions would provide a gain of 220 and 500 km of free accessible

TABLE 2 Dendritic Connectivity Index (DCI); the number of rivers classified by the population status; the total number of catchments; and the status of the species in the Habitats Directive (EEC, 1992) and international IUCN Red List (IUCN, 2015) for the 16 selected species

	DCI	Population status						Total	Habitat Directive	IUCN
		Viable	Recovered	Declining	Stocked	Extinct	No information			
Russian sturgeon	39			1				1	V	CR
Adriatic sturgeon	46			1				1	II IV	CR
Ship sturgeon	39			1				1	V	CR
Baltic sturgeon	98					4		4	V	
Stellate sturgeon	39			1				1	V	CR
Atlantic sturgeon	54			1		15		16	II IV	CR
Allis shad	44	3		3	1	7	4	18	II V	LC
Twaite shad	60	3	3	3	1	3	5	18	II V	LC
Pontic shad	47	1						1	II V	VU
Whitefish	57	1	1				12	14	V	VU
Houting	67				2	1		3	II IV	EX
Beluga sturgeon	39			1				1	V	CR
River lamprey	45	7	2	1	0	7	11	28	II V	LC
Sea lamprey	55	7	2	1	0	3	6	19	II	LC
Atlantic salmon	41	6		1	11	9	0	27	II V	LC
Sea trout	41	6		1	8	6	6	27		LC

Note. The Red List status of these species includes the following: CR: critically endangered; EX: extinct; LC: least concern; LR: lower risk; VU: vulnerable.

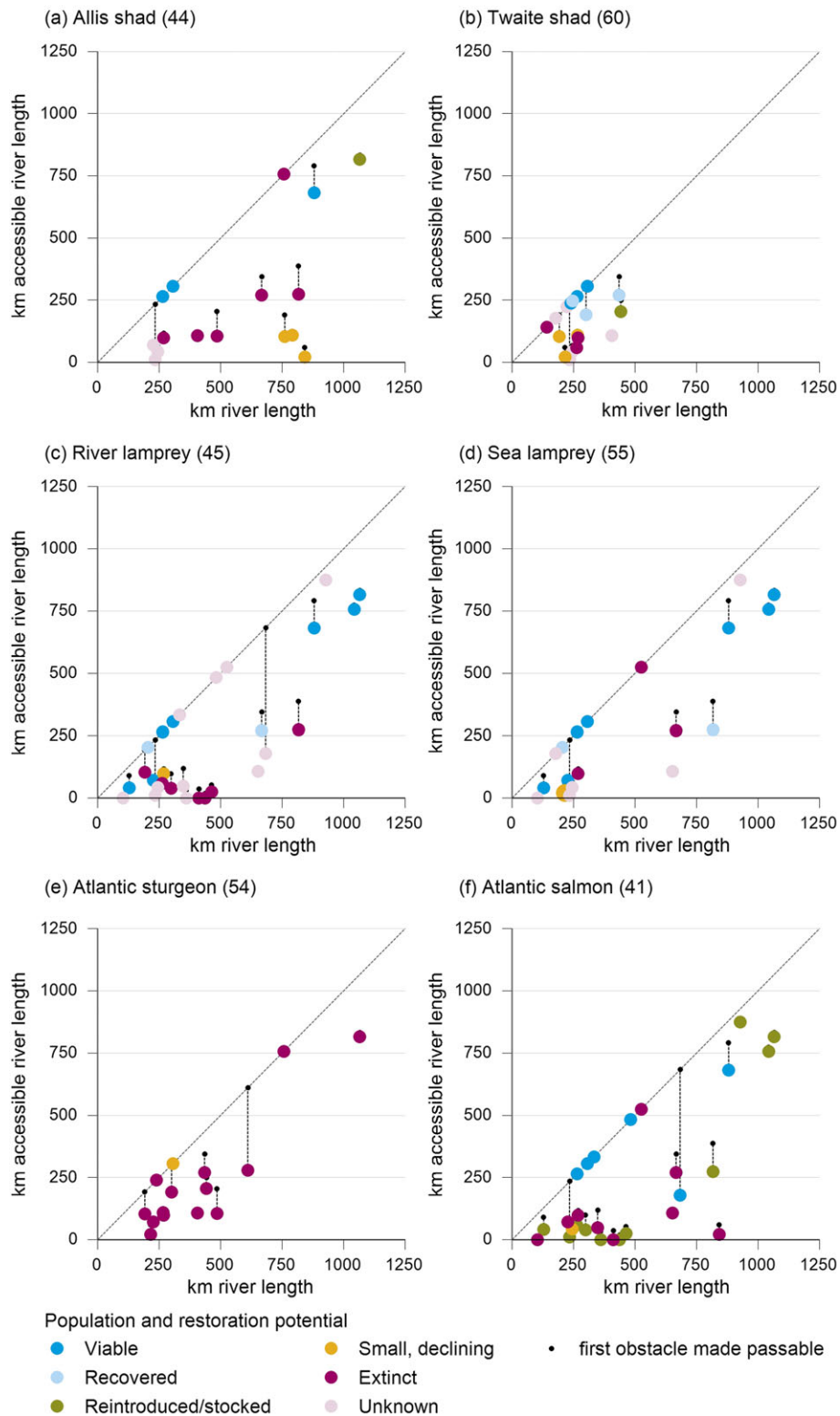


FIGURE 2 The current accessible river length (km) plotted against the accessible river length (km) for each catchment where the species historically occurred, categorized by the current population status expressed by the colour of the dots. For fully accessible rivers, the accessible river length equals the total river length. The gain by making the first obstacle passable is shown by the vertical dotted line and the black dot. For each species, the DCI is given between brackets [Colour figure can be viewed at wileyonlinelibrary.com]

river stretches for six and three species, respectively (Figure 4; Table 1). For the Danube species, building one fish passage would have no effect; on the other hand, constructing two fish passages at both the Iron Gate I and II dams would increase the accessible

river length by 1,810 km, including the large tributaries Sava and Drava and the first downstream 250 km of the Tisza tributary. A third fish passage at Gabčíkovo would return accessibility almost to the historical situation.

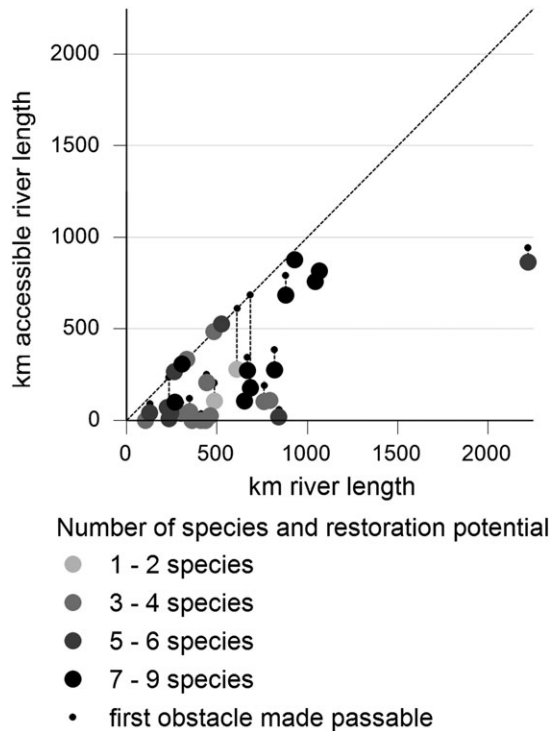


FIGURE 3 The current accessible river length (km) plotted against the historical accessible river length (km) for all species in all catchments. Catchments are grouped by the number of anadromous species. The gain by making the first obstacle passable is shown by the vertical dotted line and the black dot

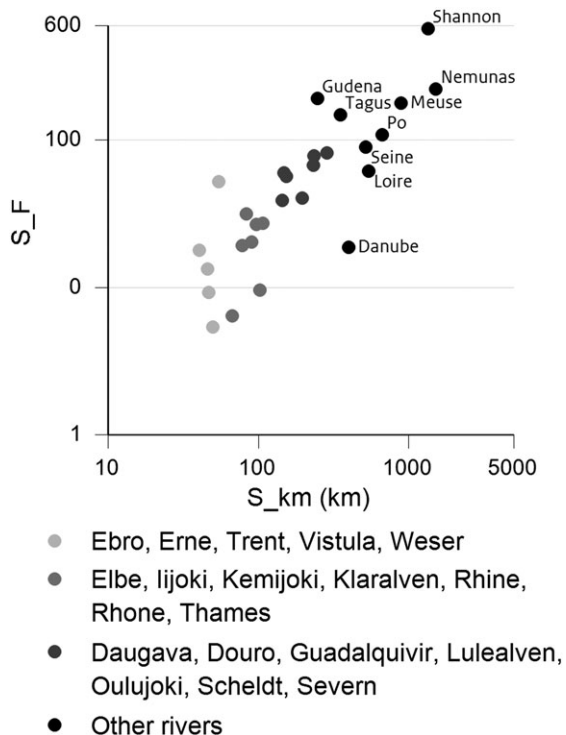


FIGURE 4 The effect of making the first obstacle accessible is expressed as the sum of the gain in DCI for all affected species (S_F , see Equation 5) plotted against the cumulative gain in km additional accessible river length for all species originally present (S_{km} ; see Equation 4)

4 | DISCUSSION

4.1 | Species and river specific effects of river fragmentation

Species specific historical and current migration distances were analysed for 16 fish species. The effect of dams was quantified by the DCI (Cote et al., 2008), an index developed to quantify the fragmentation of river basins applied in several studies (Bourne, Kehler, Wiersma, & Cote, 2011; Samia, Lutscher, & Hastings, 2015). The effect of fragmentation on anadromous species was quantified per river, taking the historical distribution into account. The use of historical distributions proved to be a crucial reference to calculate a much more accurate effect of fragmentation.

In the DCI, the fraction of the accessible river length, based on the sum of free flowing rivers and those improved by fish passages, is used as the effect indicator. Yet this effect indicator does not necessarily equal the actual impact on a species, as spawning areas generally are not evenly distributed. However, the exact location of the spawning areas is known for only two rivers. The river Rhine is accessible for 76%, covering the main river migration route to 71% of the spawning areas (ICPR, 2009). In the river Nemunas, 26% of the main river is accessible, which makes 55% of the spawning areas accessible due to the presence of one large accessible tributary (Polutskaya, 2005). These examples show that the DCI method is useful in estimating the impact of fragmentation but can be even more precisely calculated by incorporating accessible spawning areas.

Atlantic sturgeon showed the highest extinction rate. The most important causes considered are overfishing, water quality degradation, and loss of habitat (de Groot, 2002; Williot et al., 1997), which agrees with our study, showing that this sturgeon also became extinct in accessible rivers unaffected by fragmentation where barriers could not have been the primary reason for the species' absence. Atlantic salmon, the second most affected species, disappeared due to a combination of causes, including water quality degradation, fishery, extraction of sand and gravel, and building dams and weirs (de Groot, 2002; Parrish et al., 1998; Wolter, 2015). Viable populations occurred in rivers that were accessible for at least 85%, whereas, in rivers where the population became extinct or the species had been reintroduced, the accessibility was, on average, only 25%.

Reintroduction or stocking of young salmon occurred in many rivers and for many years in high numbers (Erkinaro et al., 2010; HELCOM, 2011; ICPR, 2015; Wolter, 2015). This also took, and sometimes still takes, place in inaccessible rivers where populations did not recover and stocking appeared to be inadequate without other restoration measures. Therefore, loss of connectivity is, most probably, one of the important reasons for the decline of salmon in Europe. Twait shad, river lamprey, and sea lamprey were less affected by barriers, as 50–70% of the populations were viable and have shown to recover in two to three rivers (Belliard et al., 2009; ICPR, 2015). The poor water quality in the Seine, the Rhine, and the Meuse was a main reason for local extinction and the recent water quality improvement supported a natural recovery of these species (Belliard et al., 2009; de Groot, 2002; EEA, 2010).

Lifespan is another important parameter in evaluating effects of dams or improved connectivity, especially for sturgeons. Most selected

fish species live up to 20 years, whereas sturgeons live much longer, with the beluga sturgeon having the longest lifespan: 118 years. Hence, full extinction or signs of population recovery following changes in accessibility will likely be delayed and can take up to many decades for these long-living species (Lenhardt, Jaric, Kalauzi, & Cvijanovic, 2006).

We observed a species gradient amongst the anadromous species from (a) mildly affected long- and mid-distance migrating anadromous species, such as Baltic sturgeon, houting, and twaite shad; (b) white-fish, Atlantic sturgeon, and sea lamprey; (c) seriously affected species such as pontic shad, Adriatic sturgeon, allis shad, and river lamprey; and (d) finally heavily affected species, such as the long-distance migrating anadromous species sea trout and Atlantic salmon and the four endemic, Danube sturgeon species. Our results thus clearly show that river fragmentation has species specific consequences and that fragmentation needs to be evaluated on the level of individual species and rivers.

4.2 | Options for improved accessibility

Our approach assumed that making barriers passable would be effective to improve fish migration but that may not always be the case. If the two most downstream barriers are close to each other, removing the most downstream one will hardly bring any improvement. For example, making the first barrier in the Danube, Iron Gate II, passable will have no effect when the next barrier, Iron Gate I, is not taken into consideration as well. Including the effect of removing barriers to potamodromous species could show a different priority, such as with the Gabčíkovo dam for the Danube salmon (*Hucho hucho*; Schiemer et al., 2003). Moreover, fish passages that allow migration to an upstream large reservoir could serve as an ecological trap (Pelicice & Agostinho, 2008), and small reservoirs are unfavourable habitats for migratory fish, causing high mortality (Birnie-Gauvin et al., 2017; Jepsen et al., 1998), whereas the mortality risk by turbine passage during downstream migration should also be considered (Calles et al., 2013; Wilkes et al., 2018). Therefore, dam removal is preferred above fish passages as a measure to improve connectivity (Bednarek, 2001; J. E. O'Connor et al., 2015). Other aspects that are important for prioritizing accessibility are the availability of a suitable habitat for spawning, the costs and the possibility to create fish passages.

Populations of anadromous species in European rivers have been affected by reduced accessibility, mostly due to hydropower dams and weirs. The benefit of making a barrier passable, that is, adding upstream accessible river length, depends on the number of species that occurred there in the past and on the species specific requirements. Here, we combined the number of species that would benefit from improved accessibility and the gain in accessible river length to prioritize barriers in large European rivers for being made passable. Our study indicated that making the most downstream barrier passable in the rivers Shannon and Nemunas appeared most beneficial in terms of number of species that gain accessible river length in large rivers in Europe. Other studies on prioritizing barriers for improved accessibility included habitat quality, dispersal capacity, local hydrology, and fish stocking but elaborated only on a single catchment or a

selection of species (Nunn & Cowx, 2012; O'Hanley, 2011). In this study, most obstacles in main stems are large hydropower dams. These large hydropower dams generate a major part of the hydropower electricity, much more than many small dams in tributaries, for example, 3.5% of hydropower stations in the Danube catchment generates 90% of the electricity (ICPDR, 2013). Meanwhile, these large downstream dams are also the largest obstacles hindering migration for anadromous fish. The demand for and expected increase in hydropower electricity (Bauer et al., 2017) could result in an even further increase in the number of large and small hydropower dams with subsequent deleterious effects on migratory fish (Liu, Masera, & Esser, 2013; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2014). Therefore, the potential positive effects on anadromous and potamodromous fish migration are essential steps to underpin prioritization of barriers that need to be made passable. It is concluded that evaluating the species and river specific effects of fragmentation strongly aids the prioritizing of rivers for improving accessibility and other restoration efforts.

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ORCID

Peter J.T.M. van Puijenbroek  <https://orcid.org/0000-0001-6370-2411>

Anthonie D. Buijse  <http://orcid.org/0000-0002-9759-8189>

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