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Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries

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Most lotic ecosystems have been heavily modified in recent centuries to serve human needs, for example, by building dams to form reservoirs. However, reservoirs have major impacts on freshwater ecosystem functions and severely affect rheophilic fishes. The aim of this review is to gather evidence that aside from direct habitat size reductions due to reservoir construction, competition for food and space and predation from generalist fishes affect rheophilic community compositions in tributaries (river/stream not directly affected by water retention). River fragmentation by reservoirs enables the establishment of generalist species in altered river sections. The settlement of generalist species, which proliferate in reservoirs and replace most of the native fish species formerly present in pristine river, may cause further diversity loss in tributaries. Generalist migrations in tributaries, spanning from tens of metres to kilometres, affect fish communities that have not been directly impacted by reservoir construction. This causes "edge effects" where two distinct fish communities meet. Such interactions temporarily or permanently reduce the effective sizes of available habitats for many native specialized rheophilic fish species. We identified gaps that need to be considered to understand the mechanistic functioning of distinct fauna at habitat edges. We call for detailed temporal telemetry and trophic interaction studies to clarify the mechanisms that drive community changes upstream of reservoirs. Finally, we demonstrate how such knowledge may be used in conservation to protect the remnants of rheophilic fish populations.

KEYWORDS

edge effects, habitat fragmentation, non-native species, biodiversity loss, biotic homogenization, freshwater fauna, potamodromous fish, fish migration

1 Introduction

Riverine ecosystems host much of the world's biodiversity (Dudgeon et al., 2006; Reid et al., 2019), yet they have been so significantly modified to meet human needs that few free-flowing rivers remain (Grill et al., 2019; Belletti et al., 2020). Rivers have always been considered as essential sources of human wellbeing, which provide food and water for domestic and agricultural use, colonization pathways and transportation corridors, as well as being recognized as sources of energy generation, which range from simple water wheels to sophisticated hydropower plants

(Grill et al., 2019). With the increasing demands of growing human populations, rivers are being regulated, impounded, and harnessed to meet electricity, irrigation, water supply, and flood management needs (Nilsson et al., 2005; Lehner et al., 2011; Reid et al., 2019). In addition to their primary purposes, artificial structures such as flumes, sluices, weirs and dams interfere with the natural processes of entire ecosystems. Such impoundments cause river fragmentation, flow regime modifications, sediment deposition, nutrient cycle alterations, and temperature changes, which lead to rapid declines in biodiversity (Belmar et al., 2010; Lehner et al., 2011; Feng et al., 2018; Grill et al., 2019; Jumani et al., 2019). Due to the overall complexity of the impacts of fragmentation on aquatic biodiversity that are caused by damming, the long-term scale of these impacts, and the time lags between causes and consequences, the changes in river functioning are likely underestimated (Fuller et al., 2015; Belletti et al., 2020; Arboleya et al., 2021).

Habitat fragmentation is a paramount topic in biodiversity conservation. One of the most important concepts is called “edge effects”, which in a broad context can be described as the changes in resource availability, physical and biological conditions at ecosystem boundaries or within adjacent ecosystems (Fischer and Lindenmayer, 2007). Its biotic component, on which we focus in this review, includes interactions among generalists occupying human-altered environments and specialized species present in the remaining pristine fragments (Andren and Angelstam, 1988). This primarily terrestrial concept has the potential to be more widely used in fish conservation due to similarities in the interactions among generalist and rheophilic fish fauna living side by side (Tamario et al., 2021). In particular, we review here evidence that reservoir construction may induce similar biotic edge effects between generalists and rheophilic fishes in interconnected rivers and streams (Figure 1), ranging from tens of meters to kilometers depending on the particular system and species.

Fish communities along river continua have evolved and are maintained by a series of biotic and continuous longitudinal gradients of abiotic variables through processes known as environmental filtering (Jackson et al., 2001; Kraft et al., 2015), which are reflected by the zonation patterns of fish communities (Aarts and Nienhuis, 2003; Buisson et al., 2008; Troia and Gido, 2014). Increasing riverbed steepness and water discharges and decreasing trophic status, conductivity, and temperature constitute natural barriers to dispersal for generalists and their proliferation in upstream lotic environments inhabited by potamodromous rheophilic species (Vannote et al., 1980; Johnson et al., 1995; Troia and Gido, 2014). These natural processes are seriously damaged by reservoir construction, and the impacts of reservoirs have been monitored with special attention paid to altered habitats below reservoir and newly established fish communities within reservoirs (Bain et al., 1988; Kubečka, 1993; Říha et al., 2009; Ganassin et al., 2021) and to river function alterations downstream and between reservoirs (Preece and Jones, 2002; Perkin et al., 2015; Bartoň et al., 2022). A significant scientific effort has been aimed to discover the effects of limited gene flow due to migration constraints between isolated sites and the way how construction of fish ladders could avert these effects (Roscoe and Hinch, 2010; Kemp, 2016; Tamario et al., 2019; Sun et al., 2022). However, the contact of two distinct fauna that occupy lentic reservoirs and their fluvial tributaries is to the authors’ best knowledge not well covered.

Although edge effects are a critical issue in the global declines of native rheophilic fish species populations in fragmented rivers (Limburg and Waldman, 2009; Deinet et al., 2020), the effect of

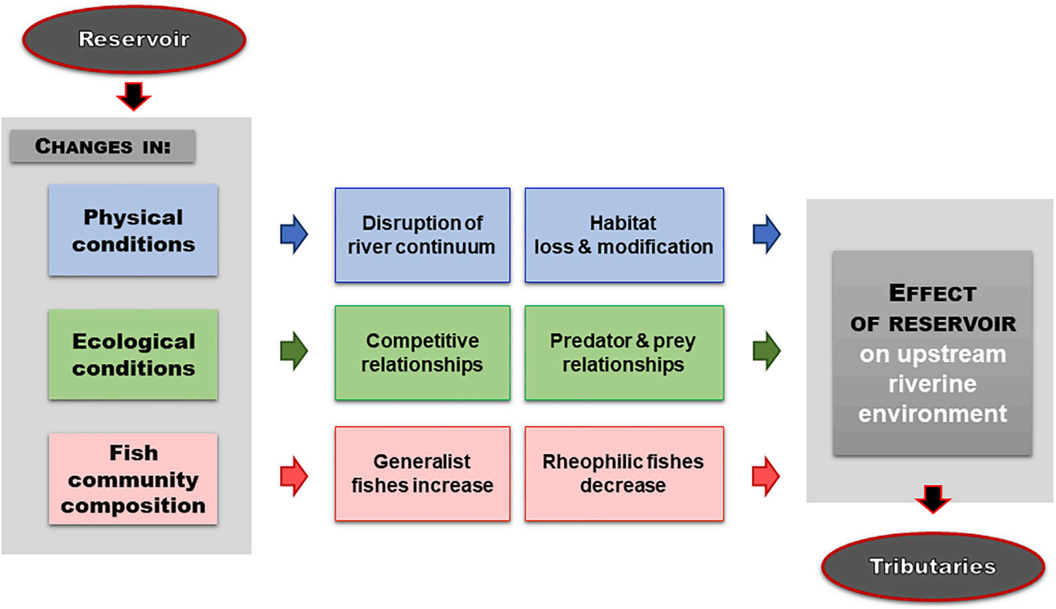

FIGURE 1
Conceptual scheme of synergistic negative effects of reservoir construction on rheophilic fishes in tributaries (river/stream not directly affected by the water retention function of a reservoir). While rheophilic fishes face a range of stressors varying from change in physical conditions to community change, this review focuses on biotic interactions that are modified by reservoir construction (green and pink color). Due to the proliferation of generalists in impounded sections of reservoirs, competitive interactions (e.g., food availability, spawning habitat, spatial niche) and predator-prey relationships (increased mortality of rheophilic fish in various life stages) are compromised, leading to community change in tributaries and negatively impacting rheophilic fishes. Please see main text for details and examples of interactions.

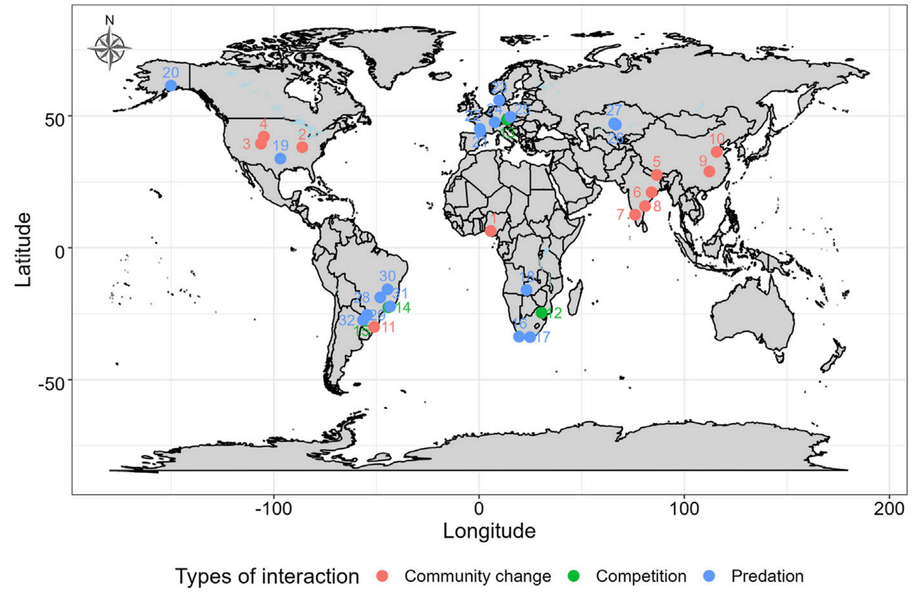

FIGURE 2
Map of evidence for interactions between rheophilic fishes and generalist fishes compiled by the study. The numbers in the map correspond to numerical order of case studies and their supporting references in Table 1.

reservoir fish fauna (which often predominantly consist of locally non-native species) on rheophilic fish has received relatively little attention. To date, most studies have evaluated biodiversity and trait-based metrics in relation to reservoir occurrences and overall river fragmentation and have provided useful insights into the biodiversity declines and functional changes in impounded rivers (Degerman et al., 2007; Wang et al., 2011; Esselman et al., 2013; Van Looy et al., 2014; Cooper et al., 2017; Turgeon et al., 2019). To much less extent were studied generalist fish migrations from reservoirs to riverine sections on habitat edges, which can further degrade river status (Andren and Angelstam, 1988; Tamario et al., 2021). While some fish community changes in rivers can be attributed to abiotic changes in ecosystems, others are likely related to biotic interactions among unnaturally close lentic and lotic fish fauna (Pringle et al., 2000; Jackson et al., 2001).

The aim of this review is to address the topic of edge effects of lentic fish fauna that are composed of generalists in reservoirs and their competitive and predation effects on rheophilic fish communities. We summarize the current state of knowledge, from reservoir settlement of generalist fish species, which is often driven by intentional or unintentional fish transport, to dynamic migrations of generalists into reservoir tributaries. Most importantly, we suggest that predation and the competitive interactions among lotic and lentic fauna are among the causes of the declining biotic integrity of reservoir tributaries. Finally, we show that it is possible to protect riverine communities by intentional fragmentation, where the conservation benefits of such measures exceed their negative impacts. We focus our attention on the impacts of generalist fishes that may come from three sources: 1) local fish species that proliferate after reservoir construction in impounded sections, 2) locally non-native species (species native in the region that were not formerly present in local communities) and 3) regionally non-native species (species not native to the focal region). We mainly focused our attention on the impacts on potamodromous rheophilic fish species, but when we did not find a good example of biotic interactions due to edge effects, we used examples of anadromous rheophilic fish species, which are better studied due to their commercial importance. We have reviewed literature and identified examples of such interactions ranging from temperate to tropical climates (Figure 2). We aim to draw attention to this topic, which is not yet explored in full, since it may help in conservation efforts aimed to preserve declining rheophilic fish species located upstream of reservoirs.

2 Proliferation of generalists in reservoirs

Dams create lentic or slow-flowing environments that are generally much deeper than the original river channels (Figure 3). Rheophilic fish are able to survive in such environments until they are occupied by other species (Irz et al., 2002; Lenhardt et al., 2009; Knott et al., 2021). However, on a longer time scale, the proportions of rheophilic fish in impounded environments generally become low, and they are replaced by quickly proliferating generalists (Figures 3, 4; Gido et al., 2009; Clavero and Hermoso 2010).

The community change has been described e.g. in mainland Europe: a typical reservoir fish community is dominated by bream (*Abramis brama*), roach (*Rutilus rutilus*), and bleak (*Alburnus alburnus*) in the final stage of community succession, although many reservoirs were constructed in rheophile-dominated community zones (Kubečka, 1993; Říha et al., 2009). Two rheophilic fish groups have been classified in Europe: More specialized rheophiles A (e.g., *Barbus barbus, Chondrostoma nasus, Leuciscus leuciscus, Squalius cephalus, Alburnoides bipunctaus, and Vimba vimba*), which require river conditions at all stages of their life histories, and less specialized rheophiles

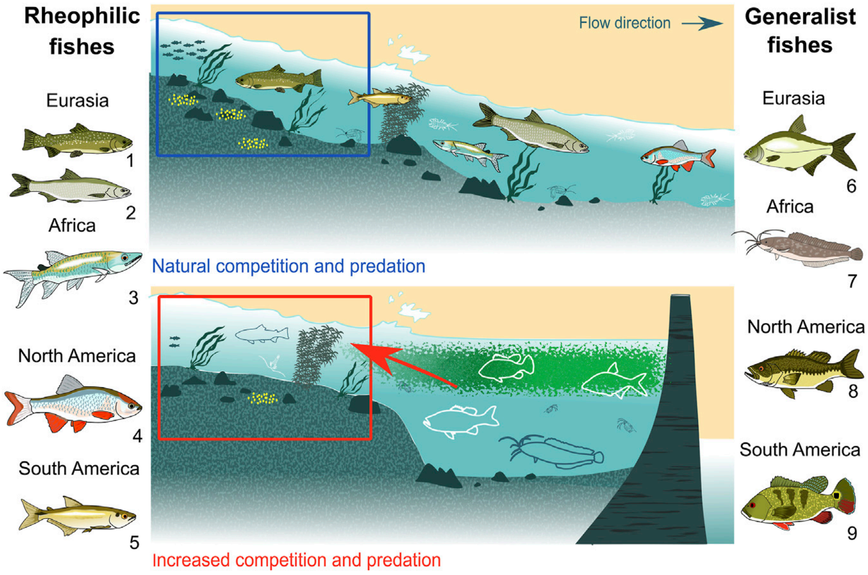

FIGURE 3
Schematic representation of the community changes before (blue rectangle) and after reservoir construction (red rectangle) and the biotic interactions among two distinct faunas of generalist fishes and rheophilic fishes in the tributary at the habitat edge. Rectangle indicates river section that is not directly influenced by increase of water level, yet the community changes due to reservoir construction. The green dots in lower panel indicate shift from littoral primary production to pelagic production and examples of invertebrates indicate the change in the major prey items for omnivorous fish within reservoir driving settlement of generalist fishes. Red arrow indicates enhanced interaction between generalist fishes in reservoir and rheophilic fishes in the tributary. Only subset of fish species reviewed is depicted to maintain clarity—rheophilic fish examples: 1—*Salmo trutta*, Salmonidae; 2—*Leuciscus aspius*, Leuciscidae; 3—*Hepsetus odoe*, Characidae; 4—*Cyprinella lutrensis*, Leuciscidae; 5—*Oligosarcus hepsetus*, Characidae; typical generalists: 6—*Abramis brama*, Cyprinidae; 7—*Clarias* sp. Clariidae; 8—*Micropterus salmoides*, Centrarchidae; 9—*Cichla ocellaris*, Cichlidae. Drawn by Zuzana Sajdlová.

B (e.g., *L. aspius, L. idus, Pelecus cultratus, Gobio gobio, Lota lota, and Cobitis taenia*), which are well adapted to lentic conditions during part of the ontogeny (Schiemer and Waidbacher, 1992). This classification appears to be valid in most systems outside Europe, and the rheophiles A formerly abundant before dam construction move upstream from lentic parts of reservoir (Agostinho et al., 1999). Adult rheophiles B can inhabit suitable reservoir habitats but usually become less abundant when reservoirs are occupied by other species. All rheophilic species require flowing water for reproduction, and their early stages have higher dissolved oxygen requirements than generalist and limnophilic species (Balon, 1975). The need for specific water flows and the risk of being displaced from suitable habitats by flow fluctuations (Bartoň et al., 2021; Bartoň et al., 2022) represent a clear disadvantage of rheophilic fishes compared to generalists, which are extremely flexible in their spawning substrate choices and do not rely on narrow ranges of optimal conditions to provide spawning sites (Hladík and Kubečka, 2004).

One of the main factors favoring the replacement of rheophilic fish by generalists in reservoirs is changes in food resources. While the main autochthonous primary production in rivers comes from benthic systems, primary production in reservoirs is mostly pelagic (Ward and Stanford, 1995). Littoral habitats with benthic food chains may be the most productive per unit area, but due to large pelagic spatial proportions of reservoirs, most production occurs in pelagic areas (Fernando, 1994; Moraes et al., 2021). The bulk of production in reservoirs goes from phytoplankton to zooplankton. For rheophilic species, benthic macroinvertebrates and algae are the main autochthonous food sources (Vannote et al., 1980; Aarts and Nienhuis, 2003; Bešta et al., 2015). These resources are generally limited in reservoirs (Agostinho et al., 1999; Moraes et al., 2021) because productive benthic habitats are limited and the benthos are also heavily used by omnivores (Agostinho et al., 1999; Schleuter and Eckmann, 2008). Another important food source for rheophilic fishes is terrestrial insects, which are generally rarely available in reservoirs and are also preyed upon by generalists (Mehner et al., 2005; Vašek et al., 2008). Although specialized, truly planktivorous fishes are often found in small numbers in reservoirs (Fernando and Holčík, 1991), while omnivorous generalists such as cyprinids, characids, percids, and centrarchids are well equipped to prey on zooplankton, which leads to zooplankton size reduction (Seďa and Kubečka, 1997; Hülsmann et al., 1999; Quintana et al., 2015). The main adaptations of omnivorous generalists for zooplankton feeding are dense branchial sieves (Van Den Berg et al., 1994) and sinusoidal swimming to detect dense aggregations of zooplankton (Jarolím et al., 2010). Rheophilic species have no such adaptations and thus cannot compete efficiently for the main food sources in reservoirs. Although rheophiles B may survive as predators or specialized benthivores, rheophiles A slowly disappear from these sites: when the barbel (*B. barbus*) was locked in the large newly filled Orava Reservoir (Slovakia), its growth rate decreased significantly despite a trophic upsurge in the newly flooded reservoir (Havlena, 1964). Additionally, study conducted in the Medjuvrsje Reservoir (Serbia) shows that the decline of rheophilic fishes gradually increases with reservoir aging (Lenhardt et al., 2009), and the increasing domination of generalists may have further negative impact on the tributaries.

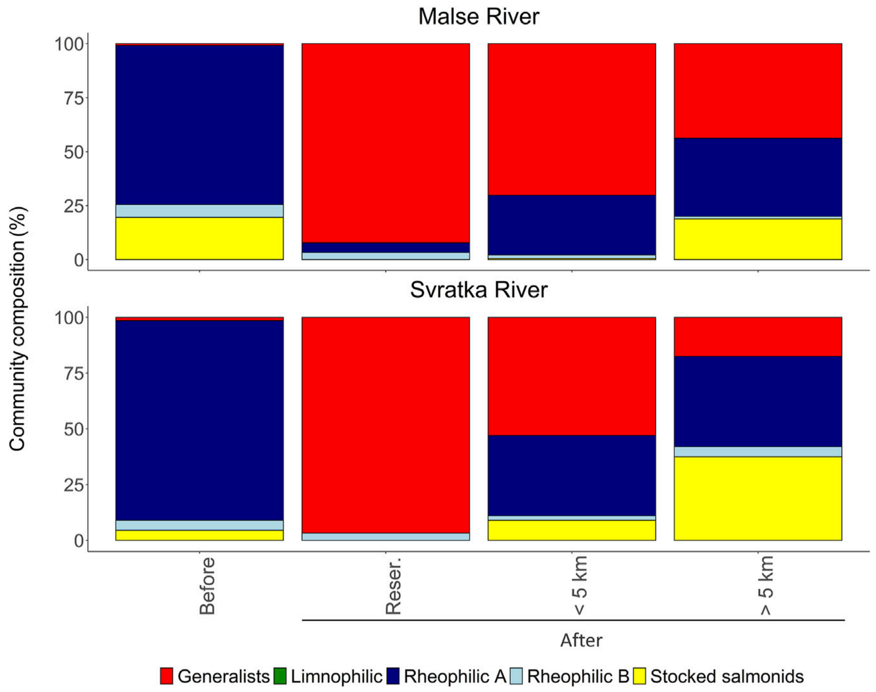

FIGURE 4
Changes in fish guild compositions after the construction of reservoirs in two rivers in the Czech Republic. Four fish faunas are considered: Former river community (Before), reservoir (Reser.), river locations less than 5 km upstream of the reservoirs (<5 km) and more than 5 km upstream of the reservoirs (>5 km). Stocked salmonids refer to brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) that are artificially supported by fisheries (according to (Peňáz et al., 1968; Hladík et al., 2008)).

3 Human-driven translocation of lowland species to upstream man-made habitats

Reservoirs often serve as stepping stones for non-native generalists, which facilitates generalists dispersal across the landscape (Havel et al., 2005; Johnson et al., 2008; Liew et al., 2016; Silva-Sene et al., 2022) and thus reservoir communities have usually high similarity with each other, despite their presence in relatively distant watersheds with distinct riverine fish communities. Therefore, reservoirs are one of the sources of biotic homogenization in river ecosystems, which is characterized by a loss of biological uniqueness (Olden and Rooney, 2006; Poff et al., 2007; Clavero and Hermoso, 2010). An example of such homogenization is introduction of *Cichla spp*. Into reservoirs of Upper Paraná river basin and other Brazilian regions resulting in the biotic homogenizations of native fish assemblages (Franco et al., 2021). This genus has been widely introduced within and outside the Neotropical region and its introduction are mostly occurring in presence of reservoirs (Franco et al., 2022a; Franco et al., 2022b).

In upper-river drainage areas, the colonization mechanisms of newly established reservoirs by non-native generalists act more slowly in the absence of fish transport (Olden et al., 2004). Considering non-human driven reservoir colonization, opportunities would often be limited to external or internal transport of fish eggs by birds, which is a process whose frequency is still unknown in the context of fish dispersal mechanisms (Hirsch et al., 2018; Silva et al., 2019; Lovas-Kiss et al., 2020) and extreme flood events (Taylor and Cooke, 2012). Therefore, the organized breeding and translocation of angler-preferred generalists into novel environments poses a serious threat to native fish communities (Copp et al., 2009; Volta et al., 2013; Early et al., 2016). In addition, many small-sized generalists are introduced accidentally with economically important stocking materials (Lusk et al., 2010) and through the release of ornamental organisms (Patoka et al., 2017) or live baitfish (Drake and Mandrak, 2014). Since these impacts are directly driven by human activities, areas with higher human population densities are more vulnerable to introductions of non-native species (Dawson et al., 2017).

4 Timing of fish migrations from reservoirs to tributaries

Animal migrations, including those of fish, are characterized as regular movements between environments (Northcote, 1984), which are influenced by individual characteristics (Chapman et al., 2011; Skov et al., 2011; Harrison et al., 2015) and can be decomposed into one-way migration events (Lucas and Baras, 2001). In general, fish migrations between lentic and lotic habitats, e.g., between lakes and their tributaries, are species-specific and depend on the food availability in lakes and their tributaries, as well as trade-offs such as predation risk or reproduction (Brönmark et al., 2008; Brodersen et al., 2014; Šmejkal et al., 2018). Some of the generalists that thrive in impounded habitats actively migrate over long distances into tributaries, such as European bream (Hladík and Kubečka, 2003; Pfauserová et al., 2021) or bleak (Šmejkal et al., 2017; Šmejkal et al., 2018) and interacting strongly with rheophilic brown trout

(*Salmo trutta*) and asp (*Leuciscus aspius*), respectively. Thus, fauna that interact at the edges of habitats can affect fish communities located hundreds of meters to more than one hundred kilometers upstream of impounded reaches (Perkin and Gido, 2011; Pfauserová et al., 2021; Tamario et al., 2021).

Reproductive migrations appear to be the main reason that cause fish to temporarily return from reservoirs to tributaries. In many species, spawning areas and spawning grounds are well defined and persist for many decades (Arnold et al., 2019), For example, lithophils that spawn on gravel and phytophils that spawn on macrophytes or flooded vegetation (Balon, 1975) migrate to tributaries when these substrates are limited in reservoirs (Hladík and Kubečka, 2003). In the case of European fish, spring migrations of rheophilic fish from reservoirs into tributaries are regularly recorded, with lithophilous asp and chub (*Squalius cephalus*) searching for gravel substrata (Benitez, et al., 2015; Pfauserová et al., 2019; Pfauserová et al., 2021; Šmejkal et al., 2021). Tributaries may also be used by reproducing generalists such as bream that are not strictly dependent on a single spawning substrate and use a wide range of available substrates (Hladík and Kubečka, 2004; Říha et al., 2013) and by phytophilous pike (*Esox lucius*) searching for submerged vegetation (Sandlund et al., 2016).

Reservoirs contain relatively high abundances of fish, with many generalist species, such as bream and roach, which are food-limited and fail to reach their maximum size due to intra- and interspecific competition and a lack of optimal food sources (benthos) (Šmejkal et al., 2015; Žák et al., 2020). As tributary temperatures drop, food resources become scarcer in the tributary, while predation risks increase (Harvey and Nakamoto, 2013). For this reason, most generalist species occupy tributaries in productive period of the year and return to reservoirs for overwintering (Pfauserová et al., 2021; Pfauserová et al., 2022). Although the mechanisms driving fish migrations from reservoirs to tributaries are not completely understood, it appears that the motivations may be similar to fish migrations from lakes to tributaries, where reproduction plays an important role (Kristiansen and Dølving, 1996; Baril and Magnan, 2002), as well as the predator-prey relationships (Skov et al., 2011).

The migratory activities between shallow lakes and their tributaries and the high species abundances in shallow lake tributaries in winter differ significantly from the dynamics of cyprinid migration between deeper canyon-shaped reservoirs and tributaries, where generalist fishes in tributaries peak in spring and summer and return to reservoirs in winter (Hladík et al., 2008; Pfauserová et al., 2021). For example, common bream, silver bream (*Blicca bjoerkna*) and roach migrate to small tributaries for overwintering to evade predation when the food availability in lakes is low and predation risks in lakes are relatively higher compared to tributaries (Skov et al., 2008; Skov et al., 2011). Whether the available depths in reservoirs are essential for fish decisions regarding where to overwinter (and thus affecting interactions with rheophilic fish) remains to be investigated.

5 Predation of rheophilic species by generalists in tributaries

One of the key factors that affects fish community structures in freshwater ecosystems is predation (Persson, 1997; Jackson et al., 2001; Temming et al., 2007). Generalist predators that thrive in the human-made lentic parts of river systems interfere with lotic waters, although the magnitude of the edge effects is unknown. In altered ecosystems, adjacent lotic river fauna may be heavily preyed upon (Table 1; Jepsen et al., 2000; Tamario et al., 2021). Introduction of predatory fish can lead to extinction of local species, destruction of unique communities, and severe loss of diversity (Chapleau et al., 1997; Hermoso et al., 2011; Pelicice et al., 2015). For example, the preys for introduced pike consist of native juvenile salmonids or other native rheophilic species where salmonids are less abundant (Sepulveda et al., 2013). Another effect observed in North America is the difference between unfragmented and fragmented streams, where in unfragmented streams more rheophilic specialists persist, and fragmented streams are significantly more dominated by generalist predatory species (Guenther and Spacie, 2006). Reservoir construction on the Laramie River, Wyoming, also caused higher abundances of non-native generalist predatory fish and led to extirpation and population reductions of selected rheophilic fishes (Quist et al., 2005). The authors of this study did not determine the specific mechanisms for the changes in the fish communities upstream of the reservoir, but they expected that non-native predators were the principal cause of community change (Quist et al., 2005). The introduction of peacock bass (*Cichla ocellaris*) in South America caused considerable negative impacts on fish assemblage composition of upper stream riverine native small-sized fish through predation (Franco et al., 2021). Another example of the influence of generalists on fish species occupying reservoir tributaries is the disappearance of red shiner (*Cyprinella lutrensis*) from streams directly connected to Lake Texoma, United States, with predation by centrarchids as a likely contributing mechanism (Matthews and Marsh-Matthews, 2011). Similarly, generalist predators threatened native rheophilic fish fauna after the construction of the Kenney Reservoir, USA (Martinez et al., 1994), although a detailed investigation of the modified interactions between species is missing in this study.

A notable example in this regard is the largest European freshwater fish, the European catfish (*Silurus glanis*), which is now regionally non-native in portions of European freshwaters (Copp et al., 2009). Catfish are typically introduced to reservoirs and spread into higher-order rivers (Gago et al., 2016); in some instances, they change fish communities during invasion (Guillerault et al., 2015). Catfish cause high mortality in the critically endangered allis shad (*Alosa alosa*) during spawning in one of Europe's most important spawning areas (e.g., Garonne River, Southwest France) (Boulêtreau et al., 2021) but also in the endangered sea lamprey (*Petromyzon marinus*) (Boulêtreau et al., 2020), Atlantic salmon (*Salmo salar*) (Boulêtreau et al., 2018) or vimba bream (*Vimba vimba*), European nase (*Chondrostoma nasus*) and barbel (*Barbus barbus*) (Lyach, 2021). Predation on native fishes by African catfish (*Clarias gariepinus*) caused a drastic reduction in the abundance of endemic and endangered *Pseudobarbus asper* and *Sandelia bainsii in* South Africa impoundments (Weyl et al., 2016).

Migratory success or mortality at early life stages can strongly influence population sizes (Larsson, 1985). Most rheophilic fish species must migrate downstream or upstream once or regularly during their lives (Lucas and Baras, 2001). As a result, they inevitably pass through altered sections of rivers with lentic waters where the risk of predation is high (Jepsen et al., 1998; Olsson et al., 2001). An example of how environmental alterations can increase mortality is the massive predation of Atlantic salmon smolts by striped bass (*Morone saxatilis*) as they pass through reservoirs (Table 1;

TABLE 1 Examples of field-based evidence of the biotic interactions among generalist fish fauna of reservoir species and rheophilic fish with negative impacts on the remaining rheophilic fish populations based in reservoir tributaries. Number (No) indicates the geographical position of the study in the map (Figure 2).

No	Continents	Country	Latitude	Longitude	Generalist species	Rheophilic/riverine species	Eco-region	Type of interaction	Season	References
1	Africa	Nigeria	6.350006	5.650000	*Unspecified*	*Unspecified*	Ikpoba River	Community change	Spring, Summer	Victor and Tetteh (1988)
2	North America	United States	38.099791	−86.158582	*M. salmoides, Morone chrysops*	*Micropterus dolomieu, Esox americanus*	Central Indiana and Central Till Plain.	Community change	Spring	Guenther and Spacie (2006)
3	North America	United States	39.424294	−106.30112	*Unspecified*	*Unspecified*	White River	Community change	Spring	Martinez et al. (1994)
4	North America	United States	42.104124	−104.877552	*Unspecified*	*Unspecified*	Great Plains river	Community change	Spring, Summer	Quist et al. (2005)
5	Asia	India	27.590000	86.560000	*Unspecified*	*Schizothorax richardsonii, Labeo dero, Labeo dyocheilus*	Himalayas	Community change	Spring	Sugunan, (1995)
6	Asia	India	21.012094	84.040789	*Unspecified*	*Puntius sarana, Tor mahanadtcus, Tor mosal*	Mahanadi	Community change	Spring, Summer	Sugunan (1995)
7	Asia	India	12.528591	75.993629	*Unspecified*	*P. dobsoni, P. dubius, P. carnaticus* *C. drrhosa and Labeo kontius*	Cauvery	Community change	Spring, Summer	Sugunan (1995)
8	Asia	India	15.754239	80.89727	*Unspecified*	*P. kolus, P. dubius, P. sarana* *P. porcellus, L.fimbrtatus, L. calbasu, L. pangusia and Tor kudree*	Krishna River	Community change	Spring	Sugunan (1995)
9	Asia	China	28.900000	112.228777	*Unspecified*	*Unspecified*	Southeast Asia	Community change	Spring, Summer, fall	Li et al. (2021)
10	Asia	China	36.308176	115.783497	*Unspecified*	*Unspecified*	Huang He Plain	Community change	NA	Zhang et al. (2018)
11	South America	Brazil	−30.005117	−51.123734	*Unspecified*	*Unspecified*	Paraná	Community change	NA	Li et al. (2013)
12	Africa	South Africa	−24.58456	30.44019	*Oncorhynchus mykiss*	*Enteromius treurensis*	Zambezi	Competition	NA	Maimela et al. (2022)
13	Europe	Czech Republic	48.51219	13.55126	*Abramis brama*	*Salmo trutta*	Central and Western Europe	Competition	NA	Pfauserová et al. (2021)
14	South America	Brazil	−22.51000	−44.21000	*Cichla ocellaris*	*Rhamdia quelen, Hoplias malabaricus*	Paraná	Competition	NA	Franco et al. (2022a)
15	South America	Brazil	−27.396172	−56.516809	*Pterygoplichthys ambrosettii*	*Unspecified*	Upper Paraná	Competition	NA	Nobile et al. (2018)
16	Africa	South Africa	−33.652437	19.453672	*Oncorhynchus mykiss*	*Pseudobarbus, Burchelli, Sandelia capensis, Galaxias zebratus*	Zambezi	Predation	NA	Shelton et al. (2015)
17	Africa	South Africa	−33.820655	24.845112	*Clarias gariepinus*	*Pseudobarbus asper, Sandelia bainsii*	Zambezi	Predation	NA	Weyl et al. (2016)

(Continued on following page)

TABLE 1 (*Continued*) Examples of field-based evidence of the biotic interactions among generalist fish fauna of reservoir species and rheophilic fish with negative impacts on the remaining rheophilic fish populations based in reservoir tributaries. Number (No) indicates the geographical position of the study in the map (Figure 2).

No	Continents	Country	Latitude	Longitude	Generalist species	Rheophilic/riverine species	Eco-region	Type of interaction	Season	References
18	Africa	Zambia	−15.961329	23.14447	*Hydrocynus forskahlii*	*Hepsetus odoe*, Cyprinodontidae,Characidae	Upper Zambezi	Predation	NA	Winemiller and Kelso-Winemiller (1994)
19	North America	United States	33.7705278	−96.8194926	*Micropterus* sp., *Lepomis* sp.	*Cyprinella lutrensis*	US Southern Plains	Predation	NA	Matthews and Marsh-Matthews (2011)
20	North America	United States	61.41340	−150.18230	*Esox lucius*	*Oncorhynchus tshawytscha, O. kisutch, Lethenteron camtschaticum, Cottus cognatus*	Alaska and Canada Pacific Coastal	Predation	NA	Sepulveda et al. (2013)
21	Europe	France	44.06376	0.55333	*Silurus glanis*	*Salmo salar*	Cantrabic Coast - Languedoc	Predation	NA	Boulêtreau et al. (2018)
22	Europe	France	45.02458	0.364156	*Silurus glanis*	*Petromyzon marinus*	Cantrabic Coast - Languedoc	Predation	NA	Boulêtreau et al. (2020)
23	Europe	Denmark	55.87037	9.813089	*Esox lucius, Stizostedion lucioperca*	*Salmo trutta*	Central and Western Europe	Predation	NA	Jepsen et al. (2000)
24	Europe	Switzerland	47.5595986	7.5885761	*Neogobius melanostomus*	*Chondrostoma nasus*	Central and Western Europe	Predation	NA	Lutz et al. (2020)
25	Europe	Czech Republic	49.578497	15.251671	*Alburnus*	*Leuciscus aspius*	Central and Western Europe	Predation	NA	Šmejkal et al. (2017)
26	North America	Canada	46.600481	66.632079	*Morone saxatilis*	*Salmo salar*	Northeast US and Southeast Canada Atlantic Drainages	Predation	NA	Daniels et al. (2018)
27	North America	Canada	47.094277	65.837024	*Morone saxatilis*	*Salmo salar*	Northeast US and Southeast Canada Atlantic Drainages	Predation	NA	Blackwell and Juanes (1998)
28	South America	Brazil	−18.78962	−48.14334	*Cichla ocellaris*	*Gymnotus carapo, Psalinodon fasciatus*	Paraná	Predation	NA	Franco et al. (2022a)
29	South America	Brazil	−25.405789	−54.5862	*Cichla ocellaris*	*Gymnotus carapo, Psalinodon fasciatus*	Paraná	Predation	NA	Franco et al. (2022a)
30	South America	Brazil	−15.72000	−44.60000	*Cichla ocellaris*	*Gymnotus carapo, Psalinodon fasciatus*	Paraná	Predation	NA	Franco et al. (2022a)
31	South America	Brazil	−22.21000	−43.31000	*Cichla ocellaris*	*Astyanax bimaculatus, Oligosarcus hepsetus*	Paraíba do Sul river basin	Predation	NA	Franco et al. (2022a)
32	South America	Brazil	−27.396172	−56.516809	*Pterygoplichthys ambrosettii*	*Unspecified*	Upper Paraná	Predation	NA	Franco et al. (2022a)

Blackwell and Juanes, 1998; Daniels et al., 2018). Predation of eggs by non-native species can also be problematic for the recruitment of native fish (Table 1; Schaeffer and Margraf 1987; Silbernagel and Sorensen 2013; Karjalainen et al., 2015). Because of the spawning migrations of generalists in the spring into tributaries (Hladík and Kubečka, 2003), predation on eggs and juveniles may be an important issue. Another example of edge effects is predation of eggs by generalist bleaks, which reduced the reproductive success of rheophilic asp in a tributary of a reservoir (Šmejkal et al., 2017; Šmejkal et al., 2018).

Some rheophilic fish migrate to slower river sections and pools for overwintering (Näslund et al., 1998) and remain nearly inactive during the winter. However, if they use artificial impoundments as overwintering habitats, they may be at higher risk of mortality because many predators are still active when temperatures drop (Brönmark et al., 2008). Although little studied, this may be a very important hidden interaction in altered freshwater ecosystems (Jackson et al., 2001; Hurst, 2007).

6 Temporal habitat displacement of rheophilic species by generalists in tributaries: Competition for food and space

Competitive interactions among fish species may lead to habitat niche displacement or even extirpation of native species (Pfauserová et al., 2021; Tapkir et al., 2022). Strong seasonal migration patterns in generalists such as roach and bleak have been described for fragmented habitats (Slavík et al., 2009; Lothian et al., 2019; Mader et al., 2020). These result in community structure changes with seasonal patterns in tributaries: The ecological quality of fish stocks in the Vltava River, as classified by the European Fish Index (Breine et al. 2005), varied seasonally from good conditions in spring to moderate conditions in autumn, which reflected seasonal colonization by generalist species from the Lipno Reservoir (Pfauserová et al., 2021). Some populations of non-native species, including generalist bream, use this reservoir for overwintering during harsh conditions and tributaries for feeding and/or spawning during the rest of the year (Pfauserová et al., 2021). Such competition for food sources or habitats often results in displacement of native species from tributaries (Hoxmeier and Dieterman, 2016). Accordingly, the presence of non-native fish in tributaries forced native brown trout to relocate to small brook tributaries (Pfauserová et al., 2021). Spatial segregation is a known response of brown trout to increasing competition (Vehanen et al., 1999); however, it might have broader ecological consequences. For example, the critically endangered freshwater pearl mussel (*Margaritifera margaritifera*) utilizes brown trout as the primary host for its glochidia larvae (Bauer et al., 1991). Forced declines in the usage of the main river by brown trout during the summer when glochidia are released could be considered a threat to reproduction of this mussel, which is considered key to its conservation (Modesto et al., 2018). Seasonal colonization of tributaries by generalist species can thus alter habitats and available resources for native fishes but also affects interactions with other species.

Similar to the evidence from Europe, a study conducted in a reservoir located on the White River, United States showed increased competition of rheophilic fishes with non-native generalists. Generalist species proliferated in the reservoir and comprised up to 90% of the fish community, which also affected the remaining original fish community in the tributary (Martinez et al., 1994). The negative effects of competition with reservoir generalists may also be visible in the significant positive associations of certain species with increasing distances from reservoirs (Falke and Gido, 2006). Another example is the construction of the Three Gorges Reservoir, China, which led to a reduction in rheophilic fishes in the tributaries and increased competition with 18 non-native generalists that proliferated in the modified reservoir environment (Liao et al., 2018; Lin et al., 2018; Liu et al., 2019). Maimela et al. (2022) revealed that adverse impacts on community structure and function were observed due to competition for food and space between *O. mykiss* and indigenous species in the upper Blyde River Catchment, South Africa. *Psedudobarbus verloenii*, a tropical rheophilic species, is reported to decline in South Africa due to reservoir construction. This species spawns in clear water, moderate to fast flow throughout the year and rocky substratum. It was widespread throughout the Verlorenvlei and Langvlei River system, South Africa in the past, but the population declined during the last century due to competition with banded Mozambique tilapia (*Oreochromis mossambicus*), tilapia (*Tilapia sparrmanii*), and common carp (*Cyprinus carpio*) (Chakona et al., 2014; Shelton et al., 2015).

Competition for food and space in tributaries is not limited to adult fish. During spring spawning, reservoir generalists can outnumber native rheophilic species and deposit enormous numbers of eggs in tributaries (Hladík and Kubečka, 2004). This deposition of generalist offspring may affect the rheophilic species recruitment as they compete for very similar food sources as juveniles (Specziár and Rezsu, 2009); thus, there is the potential to investigate how rheophilic recruitment is affected by habitat edges with adjacent reservoir fauna. We are not aware of any studies that have quantified this effect.

7 Intentional fragmentation as a tool for reducing the spread of generalist species

Since generalist species usually occupy artificial, degraded habitats (Corbacho and Sánchez, 2001; MacDougall and Turkington, 2005), the simplest strategy to exclude them from uninvaded sites is to protect natural habitats or restore degraded environments and allow them to act as natural barriers against invasions of undesirable species (Rahel, 2007). This restoration measure has been used, e.g., by the removal of the Woolen Mills Dam, United States, and subsequent habitat improvement work, which reduced the dominance of non-native common carp (*Cyprinus carpio*) in favor of smallmouth bass (*Micropterus dolomieu*) (Kanehl et al., 1997). Although dam removal (reviewed in e.g. Bednarek, 2001; Tonitto and Riha, 2016; Ding et al., 2019) is optimal solution of strong interaction between generalist fishes and rheophilic fishes, the global trend is to increase proportions of rivers that will be affected by damming (Grill et al., 2015; Zarfl et al., 2015; Winemiller et al., 2016; Cutler et al., 2020). In cases where restoration of degraded environments are not possible, there is a possibility to disrupt the connection between the remaining unoccupied tributary to isolate the habitats that are already occupied by generalist species (Rahel, 2013). This approach, known as intentional fragmentation or isolation management, has been used worldwide and increasingly since the 1950's (Jones et al., 2021). This management measure significantly increases the eradication success of

TABLE 2 Examples of different types of barriers used to reduce the spread of generalists that were selected by using the criterion of estimated effectiveness.

Barrier type	Target species	Advantages	Disadvantages	Effectivity	Relevant citations
Mechanical—culvert	brook trout (*Salvelinus fontinalis*)	Easy construction	Association with road crossing	100%	
Gabions		Easy to build	Free interstitial spaces pervious	80%–100%	Thompson and Rahel (1998)
Electricall—small	Mediterranean trout (*Salmo cettii*) common carp (*Cyprinus carpio*)	Maintain hydrologic connectivity, flexible deployment	Size selectivity, chance of equipment or power outage	100%	Sabatini et al. (2018)
Large				>99%	Sparks et al. (2010)
Chemosensory alarm cue	Sea lamprey (*Petromyzon marinus*)	Maintain hydrologic connectivity, cheap, environmentally benign, potential species selectivity	High effort to produce sufficient bulk of cue, danger of habituation	97%[a]	Di Rocco et al. (2016); Imre et al. (2016)
Carbon dioxide	silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys* nobilis)	Maintain hydrologic connectivity, environmentally benign	Large investments in facility, danger of habituation	50%–66%	Schneider et al. (2018)
Light (600 FPS)	brown trout (*Salmo trutta*)	Less infrastructure, low costs	Species, life-history, ambient conditions dependent	88% (day); 67% (night) **	Jesus et al. (2019b)
Sound (sweep up mode)	brown trout (*Salmo trutta*)	Effective across wide range of environments	Variable effectiveness, species specific	16%	Jesus et al. (2019a)
	Douro nase (*Pseudochondrostoma duriense*)			91%	Jesus et al. (2019a)
	Iberian barbel (*Luciobarbus bocagei*)			96%	Jesus et al. (2019a)
Bubble curtain	common carp	Low cost	Low effectivity under certain conditions	74% (upstream); 28 (downstream)	Zielinski and Sorensen (2015)
	silver carp			80% **	Zielinski and Sorensen (2016)
	bigheaded carp			83% **	Zielinski and Sorensen (2016)
Hydraulic	Round goby (*Neogobius melanostomus*)	Selectively excludes nuisance species	Major modification to channel; few sites meet criteria	100% **	Wiegleb et al. (2021)

[a]The calculated effectiveness represents the proportion of directed individuals outside the treated stream; however, there was the possibility of migrating into the control (untreated) stream.** laboratory conditions.

targeted species in riverine sections, which has otherwise rarely been successful (Simberloff, 2013).

There are several ways to create intentional fragmentation in aquatic systems, and we present the most-often used methods. They consist of mechanical, electrical, chemical or other non-mechanical methods (Table 2). Most commonly, exclusion barriers are used to prevent upstream migration of undesirable species (Rahel 2013). Examples of mechanical barriers include constructing low head dams, gabion barriers, or culvert barriers to restrict common carp and other reservoir generalists from entering the upstream tributaries of the Roaring River, United States (Bulow et al., 1988), limit sea lamprey access to the spawning grounds in the Laurentian Great Lakes basin (McLaughlin et al., 2007; Miehls et al., 2020) and protect native salmonids in western North America (Novinger and Rahel, 2003; Kirk et al., 2018). Although creating new barriers increases fragmentation and can to some extent create new lentic habitats, this impact is exceeded by the benefits of preventing intrusion of unwanted taxa. Moreover, isolation management has been shown for a long time to support native trout populations in headwater streams, when strategically placed barriers isolate catchments that are large enough to allow seasonal movements and maintain metapopulation structures (Harig and Fausch, 2002) and the isolated population is large enough to avoid extinction due to loss of genetic variability or stochastic demographic or environmental events (Cook et al., 2010).

Isolation management using electric barriers has been successfully used to block non-native trout and protect reintroduced populations of native Mediterranean brown trout (*Salmo cetti*) (Sabatini et al., 2018) and a similar device is used seasonally to block the migration of sea lamprey (*Petromyzon marinus*) and limit its reproduction in the Black Mallard River, Michigan (Johnson et al., 2021). Electric barriers meet the conflicting demands of managers to disrupt biological connectivity while maintaining hydrologic connectivity. Despite this advantage, there is a possibility of power or equipment failure (Clarkson, 2004); these barriers could be overcome by jumping fish, or their effectiveness may decrease during the navigation of metal-hulled barges through these barriers (Parker et al., 2015). The world's largest and well-known electric barrier system was activated in the Chicago Sanitary and Ship Canal in 2002. Two additional barriers were added in 2009 and still function as the primary barrier to the spread of bigheaded carps (i.e., silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*) between the Mississippi River and the Great Lakes basin (Parker et al., 2016).

Various types of chemical barriers have been used worldwide, but their use is much less widespread compared to mechanical and electric barriers. Application of taxon-specific piscicides can be quite effective in preventing the invasion of non-native species in target areas (Araújo et al., 2018). Although their effects can be effectively neutralized by other substances (Weyl et al., 2014), they are potentially dangerous due to their possible negative effects on entire ecosystems (Birceanu et al., 2014). The use of chemosensory alarm cues (i.e., facilitating early warning for prey fish) could be a cheaper and safer alternative (Frisch, 1938; Ferrari et al., 2010; Imre et al., 2010). The effect of chemical alarm cues was demonstrated primarily under laboratory conditions (Wagner et al., 2011) and showed a significant reduction in the occurrence of non-native species in the field (Di Rocco et al., 2016); however, this effect is not absolute, and combinations with other measures are needed. Carbon dioxide and ozone are other options that can be used to block fish migration and prevent the further spread of non-native species, and they are relatively environmentally benign compared to other chemicals in aquatic systems (Buley et al., 2017; Suski, 2020). While the knowledge of fish behavior with respect to these substances is relatively well known, there are still many data gaps regarding the use of CO_2 and O_3 in the field, including determining how freshwater river systems will respond to the use of O_3 barriers.

Other types of non-mechanical devices that provide barriers to migrations of fish species, which are based on the behavioral responses of fish to physical stimuli (e.g., light, sound, and air bubbles; Bullen and Carlson 2003), are also being used more frequently. Some species are attracted to light (Stamplecoskie et al., 2012), while others are repelled (Hadderingh, 1982), but strobe lights repel most target species and are most effective at pulse rates greater than 300 flashes per minute (Kim and Mandrak, 2017). Experiments showed that acoustic signals influence fish behavior (Vetter et al., 2015), but the observed response was not sufficient to produce a strong deterrent effect in the field (Deleau et al., 2020) and is affected by strong species-specific variability that is likely caused by species differences in auditory sensitivity (Bullen and Carlson, 2003). The efficiency of this type of barrier could be increased in the future by using a sweep or modulated sound (Jesus et al., 2019a) or in combination with air-bubbles (ensonified bubble curtain), which helps to focus and enhance sound fields while often causing its bubbles to resonate (Dennis et al., 2019). The air-bubble curtains that are emitted from air diffusers located along the water bottom achieved over 80% efficiency in reducing passage for bigheaded and common carps (*Cyprinus carpio*) under laboratory conditions (Zielinski et al., 2014). Although the efficiency was lower in field experiments when fish were more motivated to migrate (Zielinski and Sorensen, 2016), the combination with sound (ensonified bubble curtain) increased its efficiency to 95% or more for bigheaded carps (Taylor et al., 2005). On the other hand, combination of ensonified bubble curtain with strobe light has been show unlikely to block upstream sea lamprey migration in laboratory (Miehls et al., 2017). A new approach to protect pristine upstream areas from invasion by non-native fish consists of hydraulic or velocity barriers (Wiegleb et al., 2021) and these have been tested under laboratory conditions. Based on knowledge of the differences in swimming performance under artificially elevated water flows (Kemp, 2016), environments can be created to prevent passage of the tested non-native species (e.g., round goby *Neogobius melanostomus*) and allow passage of desired species (e.g., gudgeon *Gobio gobio* and bullhead *Cottus gobio*). However, the performance of such barriers has yet to be tested in the field.

In summary, mechanical barriers, when properly operated and maintained, can achieve 100% fish exclusion. Other barrier types are either not 100% effective, are prone to fail in extreme or unexpected events or have not yet been properly tested under field conditions (Table 2). However, the resulting disruption of natural flows by mechanical barriers and blockage of non-target species pose significant challenges. The effectiveness of all behavioral and chemical barriers may continue to decrease over time due to the habituation process of target species (Imre et al., 2016). Nevertheless, they may significantly decrease the number of generalist fishes and potentially reduce the impacts on rheophilic species when combined with other management measures. A systematic review on barrier types and efficiencies along with proper identification of knowledge gaps may be beneficial in this field to achieve progress in the conservation of reservoir tributaries.

8 Conclusion and future directions

Here, we reviewed the impacts on generalists due to damming (which also applies to smaller impoundments) on rheophilic fish fauna based in tributaries and the potential solutions to mitigate their impacts through intentional fragmentation. We suggest that the observed changes in fish diversity and fish functional traits in reservoir tributaries following reservoir construction can be partly attributed to changes in the intensities of interactions among generalists and rheophilic species. We emphasize that the management of edge effects may be critical to maintaining viable populations of rheophilic fishes in lotic ecosystems that are modified to meet human needs. Although many studies have examined the effects of reservoirs on fish diversity (e.g. Esselman et al., 2013; Van Looy et al., 2014; Cooper et al., 2017), detailed data on the intensified interactions among generalists and rheophilic fish and ontogenetic bottlenecks due to competition or predation are generally lacking (Tamario et al., 2021). In particular, we call for detailed temporal telemetry, reproductive migration, and trophic interaction studies to move from descriptive and correlative science to a better understanding of the mechanisms behind the community changes that are caused by artificially enhanced fish fauna interactions. This knowledge may not only provide novel insights into the observed trends but also may lead to novel solutions for rheophilic species conservation efforts, which may be targeted to specific bottlenecks that emerge due to habitat degradation. An example of such conservation measures can consist of blocking the migration of generalists to enable year-round utilization of river channels by brown trout (Pfauserová et al., 2021).

One of the targets of future studies could be determining the habitat proportions that need to be maintained to sustain potamodromous rheophilic fish populations, e.g., (Fausch et al., 2002; Isaak et al., 2007; Perkin et al., 2015). In particular, an important issue is the magnitude of edge effects for protected rheophilic fish species that would prevent their long-term population stability in the face of competition and predation by generalists (e.g. Tamario et al., 2021). Since these patterns will often be species- and site-specific to some extent, considerable conservation efforts will need to be made to minimize local extinctions of rheophilic fishes in fragmented rivers. In case a barrier is important to human needs more than to protecting targeted species, what measures can be implemented to minimize the predation and competition pressures from generalists? Antimigration barriers that prevent generalists and other non-native species from entering tributaries can help preserve the remaining free-flowing segments, and much has been done in recent decades to make progress in this area. However, efficiency evaluations of particular barrier types need more research under comparable field conditions. Migrations of generalists from reservoirs to tributaries provide an opportunity to apply temporarily installed barriers and mitigate edge effects for conservation needs.

Author contributions

MŠ initiated a topical workshop on the manuscript concept and manuscript outline. All authors contributed by drafting manuscript chapters. All authors provided substantial feedback to the first and subsequent drafts.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Glossary

Anadromous species fish species spending part of their life cycles in marine environments and reproducing in freshwater

Edge effects interactions among modified and natural environments on their neighboring edges through changes in biotic and abiotic conditions

Generalist species species that can utilize a wide range of ecological conditions and various food sources

Lentic environment a body of standing water

Lotic environment fluvial freshwater environments such as streams and rivers

Potamodromous species fish species spending their whole life cycle in freshwater and typically undergoing only short-distance migration

Rheophilic species fish species that are specialized to live in fast flowing streams and rivers at least for some of their life cycles

River continuum concept continuously integrating series of abiotic and biotic parameters from river spring to its estuary