Toward a roadmap for diadromous fish conservation: the Big Five considerations

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Increasing habitat fragmentation is a major contributing factor to dramatic reductions in populations of migratory species worldwide. Diadromous fish species in particular are affected by this anthropogenic disturbance, resulting in historically low population abundances. Despite a plethora of management measures and considerable investment, desired results are often lacking. Here, we highlight five important considerations – the "Big Five" – for diadromous species management: removal of barriers to migration, installation of fish passages, habitat restoration, restocking, and fisheries management. We review current management measures and their effectiveness, and propose a way forward. Current management of diadromous fish populations largely focuses on mitigation of migration barriers, but management will likely fail if other fundamental aspects of diadromous species' life cycles are overlooked or disregarded. We therefore propose an integrated management strategy that takes into account the five major factors influencing diadromous fish species, with the ultimate goal of restoring their populations.

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Among the most fascinating aspects of animal behavior, migration evolved to maximize survival and reproductive success by stimulating movement between critical habitats (eg reproductive and feeding areas). Migration plays a crucial role in ecosystem functioning through, for instance, promotion of nutrient fluxes between habitats associated with the movement of large numbers of animals and maintenance of biodiversity (Dingle and Drake 2007). Increasingly, however, anthropogenic disturbances are fragmenting habitats, thereby constraining animal migrations. As a consequence, populations of numerous migratory species have declined drastically over the past century (Wilcove and Wikelski 2008).

In a nutshell:

- Diadromous fish species have declined globally due to habitat loss and fragmentation
- Any successful strategy to restore populations of diadromous fish needs to consider five main management measures: removal of migration barriers, installation of fish passages, habitat restoration, restocking, and fisheries management
- The interaction between those measures determines management success; for instance, removal of migration barriers may not lead to diadromous fish population restoration if the upstream habitat quality is insufficient
- Due to financial, logistic, and spatial limitations, management investments could focus on particular river stretches to develop so-called "diadromous species reserves"

Freshwater systems in particular have experienced substantial deterioration in habitat connectivity. Many waterways are now obstructed or embanked; have a highly regulated water flow and poorly developed riparian zone; and are subject to increased sediment loads, loss of downstream nutrient transport, eutrophication, and/or pollution (Sabater *et al*. 2018), causing deficits in growing and spawning habitats for fish (Figure 1). Over 1 million barriers exist in European river basins (Belletti *et al*. 2020), and there are nearly twice as many in the US (www.fisheries.noaa.gov/insight/barriers-fish-migration). Such impediments to migration greatly increase the extirpation risk of freshwater fish species in these regions (Collen *et al*. 2014); in Europe alone, 37% of species are currently threatened (IPBES 2019).

Diadromous fish migrate between freshwater and marine environments to complete their life cycle (Myers 1949) and are therefore particularly vulnerable to habitat fragmentation. Migration barriers impact their longitudinal (ie upstream/downstream movements) and lateral (ie between rivers and tributaries and their flood plains) movements (Drouineau *et al*. 2018a), blocking access to habitats crucial for feeding and/or reproduction. Barriers also influence habitat quality by altering water flow and transport of nutrients and sediment, changes that are facilitated by the increasing canalization of waterways (ie the straightening and fixation of waterways by, for instance, rock and gabion basket embankments). Barriers like hydropower plants and pumping stations can also cause injury to or even the death of passing fish (Winter *et al*. 2006; Buysse *et al*. 2014), and barriers and regulated water flows can delay migration. How these affect individual fitness and population viability of diadromous fish species remains unknown. Multiple passage

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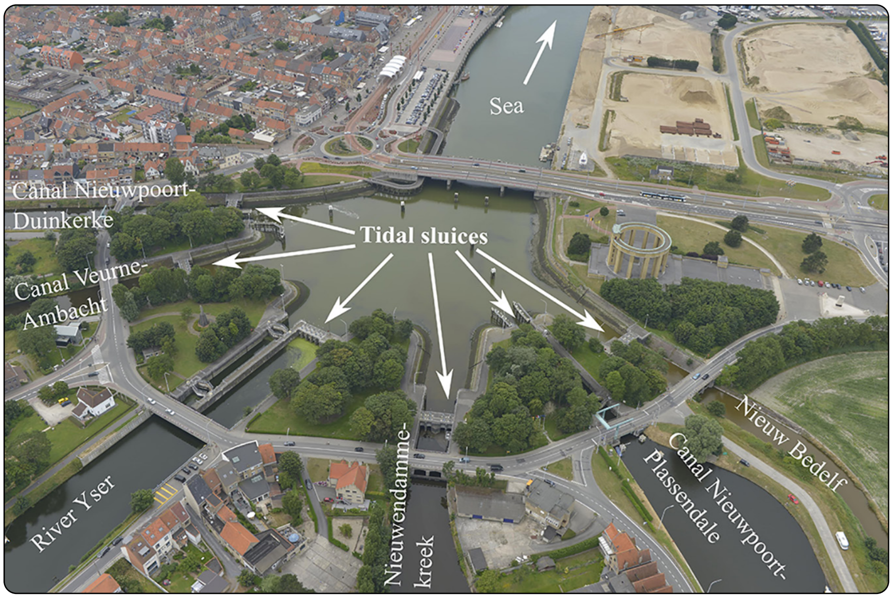

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Figure 1. The sluice complex near the Belgian coast at Nieuwpoort: water regulation structures such as tidal sluices impede the migration of diadromous fish species between the marine and freshwater environment of five artificial canals and the River Yser. In the River Yser and the Canal Veurne-Ambacht, water managers set the sluice doors ajar during high tide in spring to promote the colonization of juvenile European eels from the sea.

attempts can reduce fitness via energy depletion, increased predation risk, and failure to reach suitable habitat (Silva *et al.* 2018), especially given that many species do not feed during migration and are already in a weakened condition (eg Thorstad *et al.* 2008).

All 24 diadromous species native to the northern Atlantic Ocean have declined in abundance by at least 90% since the end of the 19th century, jeopardizing such ecosystem services as the provisioning of food and the exchange fluxes of nutrients between marine and freshwater environments (Limburg and Waldman 2009; Drouineau *et al.* 2018b). Moreover, global change may profoundly alter hydrological patterns in the future, for instance through increased winter and reduced summer runoff in several major European river catchments (Schröter *et al.* 2005). Hydrological management, including development related to navigation, drainage, and hydropower, will therefore need to be adapted, potentially impacting aquatic habitat connectivity (and consequently diadromous fish) to an even greater degree (Limburg and Waldman 2009; Drouineau *et al.* 2018a).

Various pieces of legislation have been enacted to restore populations of diadromous species in Europe, including the European Habitats Directive (Council Directive 92/43/EEC) and the EU Water Framework Directive (2000/60/EC). The latter imposes the restoration of river continuity and is similar to the US Revised Code of Washington (Title 77 "Fish and Wildlife"), which requires free flowing rivers and passability of migration barriers for fish. Although these and other legislative measures have triggered investment in an array of programs focusing on the restoration of diadromous fish populations, the desired results have yet to be attained. For instance, attempts to improve connectivity simply through construction of fishways may be insufficient for restoring diadromous fish populations because migration barriers have other impacts (eg migration-related delays, regulated water flows, and habitat deterioration) that interfere with management efforts to improve connectivity. Restocking is one widely applied strategy for restoring diadromous populations (Meffe 1992; Moriarty and Dekker 1997; Aprahamian *et al.* 2003), but this approach will be largely ineffective if stocked fish are unable to complete their full life cycle. Therefore, when sustainable fish populations are not attained due to environmental limitations, additional pressures (eg fishing) should be avoided. Due to the many bottlenecks in current diadromous species management, an evaluation of existing management practices is crucial for moving forward.

We contend that effective management of diadromous fish populations must address five basic considerations – the "Big Five" – for successful reestablishment of sustainable populations. These consist of (1) removing barriers to migration, (2) installation of fish passages, (3) habitat restoration, (4) restocking, and (5) fisheries management.

Removing barriers to migration

Migration barriers are major obstacles for diadromous fish, and the removal of non-operational or obsolete barriers is therefore a crucial management practice (Figure 2). This measure is both sustainable and cost-efficient in the long term, given that fishways, trap-and-transport, and other alternatives require maintenance and human intervention (see "Installation of fish passages" section below). Barrier removal can restore natural flow (and natural flow variability), which can facilitate the development of diverse habitats (eg pools and riffles with gravel beds) and allow for natural nutrient fluxes (Bednarek 2001; Mouton *et al.* 2007). Removal of dams, weirs, and other obsolete barriers is an increasingly common practice worldwide; in the US, for instance, 82 dams were removed in 2018 alone (www.americanrivers.org), while in Europe, almost 5,000 barriers have been removed since the 1990s (https://damremoval.eu).

However, removal of migration barriers is often infeasible due to economic and/or safety reasons (eg flood risk). For instance, water-pumping stations are necessary to drain low-lying areas and prevent flooding. Barrier removal may also have less obvious side effects, for example by facilitating the spread of invasive species (Kerby *et al.* 2005) or reducing water quality in cases where a barrier prevented runoff of polluted sediment into downstream river stretches (Shuman 1995;

Bednarek 2001). Barrier removal as a management measure should therefore be undertaken where possible if potential negative ecological side effects have been taken into consideration.

Installation of fish passages

When barrier removal is not possible, other measures should be taken to improve habitat connectivity. One common approach is the construction of fishways that provide alternate routes around a barrier, resulting in a gradual reduction of the differences in water level and energy of water flow between river stretches upstream and downstream of a barrier (Figure 2). Passages come in various types, ranging from fishways that emulate natural characteristics (eg nature-like and rock-ramp fishways) to more technical designs (eg pool-type fishways, vertical slots, Denil fishways, and eel ladders) (Clay 1994; Larinier and Marmulla 2004). Regardless of type, to be effective a fishway must have an entrance near the barrier that is easily detected and accessed by migrating fish. Although several studies have reported promising results (Franklin *et al.* 2012), the efficacy of many fishways remains low (Bunt *et al.* 2012). Improved understanding of movement ecology and behavior of the target species in relation to water flows (eg Piper *et al.* 2015) is urgently needed to optimize fishway design and management. Moreover, because most fishways were designed to aid salmonid upstream migration (Clay 1994), they may be inadequate for other species (Silva *et al.* 2018). To support the migration of multiple species and life stages, either a "multi-species" fishway (eg vertical slots and nature-like fishways) or several types of fishways may need to be constructed to allow different fish species to circumvent a barrier (Silva *et al.* 2018).

Fishways that facilitate upstream migration often do not do so for downstream migrating fish, which tend to follow the main current, thereby easily missing attraction flows near waterway margins (Jansen *et al.* 2007). When the only possible water flow and migration route runs through a hydropower or pumping station, fish experience injuries or even mortality (Buysse *et al.* 2014). Several supposedly fish-safe improvements for the passage of turbine stations have been designed (such as low-pressure turbines, Archimedes turbines, Alden turbines, Kaplan turbines with Minimum Gap Runner technology, DIVE turbines, Pentair turbines, and Very Low Head turbines; Hogan *et al.* 2014; Silva *et al.* 2018), yet success stories involving low-to-zero fish mortality rates are lacking; in some cases, mortality was in fact essentially the same following implementation of the "fish-safe" adaptations (Buysse *et al.* 2015). At a barrier, the exploration behavior by fish migrating downstream may expand opportunities for guiding those fish toward the inlet of a downstream fish pass, especially near turbine stations (Gosset *et al.* 2005). However, only a few applications have proven to be successful in aiding downstream migration, and these primarily allowed fish to pass small hydropower stations through vertical openings in gates instead of via fishways (Gosset *et al.* 2005; Egg *et al.* 2017). Development of truly effective solutions in the future will require substantial coordination between ecologists and engineers.

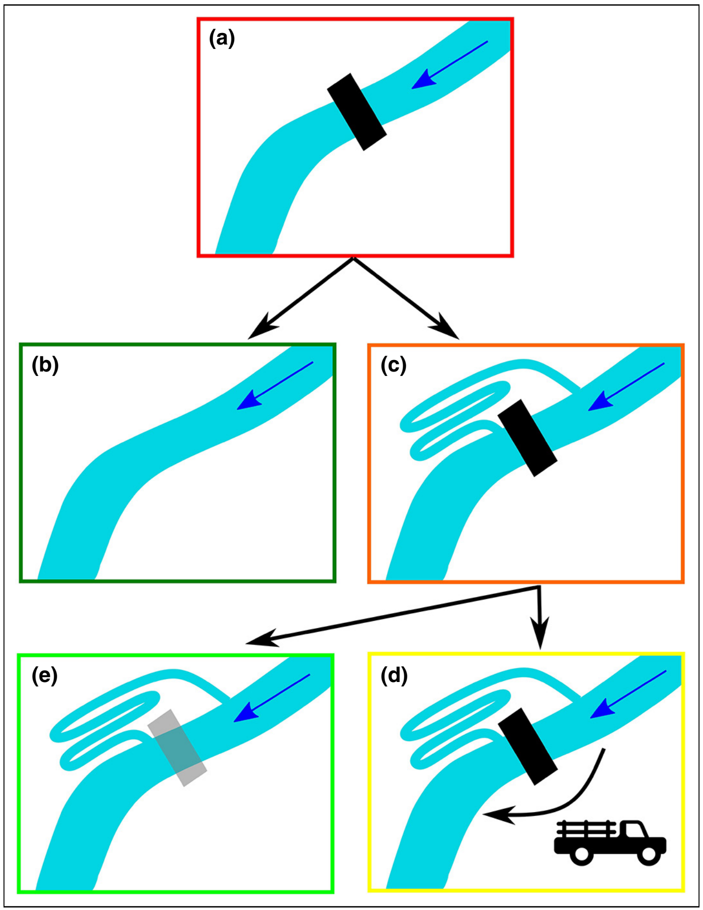

Figure 2. Hierarchical management scheme to improve habitat connectivity for diadromous fish species; red frame indicates worst scenario, followed by orange, yellow, light green, and dark green, which is the best measure. (a) When a migration barrier impedes habitat connectivity, (b) the most sustainable measure is to remove the obstacle and allow both up- and downstream migration. (c) When this is impossible, constructing fishways can be an alternative measure; because these are rarely effective in allowing downstream migration, however, additional measures must be undertaken. (d) Trap-and-transport can be applied to move fish downstream of a barrier, but this method is labor intensive, causes stress to the animals, and not all individuals may be caught and transported (image credit of vehicle icon: S Child/Noun Project). (e) Another approach is temporal opening of the barrier, for instance during specific migration periods. Blue arrows indicate the downstream current direction, and rectangles represent a migration barrier.

Alternative measures to overcome obstacles, such as fish lifts and trap-and-transport, can be implemented when there is a lack of space to construct fishways. Fish lifts are typically installed at tall obstacles (eg dams) and act as vertical moving reservoirs that attract and trap fish downstream of the obstacle, then transport and release them upstream. The efficiency of fish lifts varies greatly, however, and requires more research (Croze *et al.* 2008). Trap-and-transport involves human intervention, making it highly labor intensive, costly, and applicable only to species that are resistant to handling and stress (eg anguillid eels; Piper *et al.* 2020), but it can also be applied as a complementary measure, for instance when a fishway is not adequately aiding downstream migration (Figure 2).

Research on diadromous fish habitat connectivity has to date largely emphasized longitudinal connectivity, while lateral connectivity has seldom been addressed (Bolland *et al.* 2012). However, embankments make the hinterlands of rivers largely inaccessible for fish, thereby precluding their use as nurseries or sites for juvenile development (eg Shirakawa *et al.* 2013), or as refuges from unfavorable conditions such as the wake generated from waterborne vessels, high-flow conditions, dewatering, and backwash (Wolter and Arlinghaus 2003). Water regulation structures like inlet and outlet sluices are often constructed in side channels to control flooding, but are rarely the focus of research and seldom considered as potential migration barriers. An example of combined flood protection and restoration of lateral habitat connectivity can be found in the artificial Sigma Plan wetlands of the Scheldt Estuary, in Belgium (Cox *et al.* 2006). Improved understanding of fish migration into and out of such artificial floodplains could help to optimize connectivity with the main channel of the river and increase availability of key habitats (eg deep pools, shallow vegetated zones).

The fact that diadromous species migrate at certain times and under specific environmental conditions may facilitate formulation of management strategies that encompass economic, safety, and conservation considerations. Indeed, management can strive to stimulate fish passage during specific time windows when migration is most prominent; for instance, the decision could be made to channel more water through fishways or undershot sluice gates, or perhaps even to temporarily elevate barriers, during periods of peak migration (Figure 2). One recent example was the temporary opening of the gravitational discharge sluices of the Haringvliet barrier on the coast of the Netherlands (Griffioen *et al.* 2017). In 1970, when the barrier was built, estuarine habitats of the Rhine and Meuse rivers virtually disappeared and important migration routes were blocked for diadromous species, including Atlantic salmon (*Salmo salar*), twaite shad (*Alosa fallax*), allis shad (*Alosa alosa*), Atlantic sturgeon (*Acipenser sturio*), and European eel (*Anguilla anguilla*). Limited seawater intrusion through the sluices of the barrier has been allowed since autumn 2018, and the complete opening of this barrier is expected to facilitate the return of diadromous species to the system (Griffioen *et al.* 2017), given that the partial opening of the barrier has been accompanied by upstream management measures benefiting anadromous species (eg fishway construction, spawning habitat restoration). A second example comes from Belgium's Yser Estuary, where tidal barriers are left ajar during high tide in spring to promote colonization of the adjacent polder area (below sea level) by glass eels (an intermediary stage in the eel life cycle; Figure 1; Mouton *et al.* 2011).

Habitat restoration

River flow is one of the major hydromorphological drivers of habitat creation and diversity (eg pools and riffles; Brookes 1988); more simply, if natural river flow is disrupted, then habitats essential for diadromous fish may fail to form. Consequently, barriers can also affect fish migration through disruption of natural water flow (Sabater *et al.* 2018; Verhelst *et al.* 2018), a problem that cannot be addressed solely by the construction of fishways. Dams, for instance, transform a relatively narrow and shallow lotic system into the wide and deep lentic system of a reservoir. Thus, although a fishway may help fish migrating upstream to bypass a dam, the reservoir itself may serve as a bottleneck for downstream migrating fish, as well as for eggs and larvae that drift passively with the river current (Pelicice *et al.* 2015). Eggs, for example, face a higher risk of being buried due to higher levels of sedimentation, whereas migrating fish or larvae may be delayed or even prevented from continuing downstream due to the absence of a current that guides passage through hydropower turbines. Moreover, all life stages may be more susceptible to predation in a reservoir (Pelicice *et al.* 2015).

In addition to forming physical barriers, structures such as tidal sluices, shipping lock complexes, weirs, water-pumping stations, and hydropower plants can greatly affect fish migration simply by doing what they were designed to do: maintain a specific water level for agricultural or navigational purposes. A directional current to the sea may only be established when water management releases water from those systems, for instance by opening sluices or turning on water-pumping stations. In severe cases, this can lead to hydropeaking, which entails alternating moments of intense discharge and total standstill, leading to fish strandings, disorientation, and migration failures (Irvine *et al.* 2009). Moreover, in canalized rivers and shipping canals, the back-and-forth motion of water caused by the upstream and downstream movement of large ships through shipping locks can lead to disorientation and delayed migration (Verhelst *et al.* 2018; Vergeynst *et al.* 2019). Strategies to restore diadromous species populations must therefore include assessment of whether hydrological management of surface waters meets the requirements of the target species.

Although barrier removal can restore natural river flow, development of essential habitat variability may not always follow (eg when a river is embanked and unable to meander); in such cases, removal of barriers will result in limited water flow variability. In these situations, or when barriers can only be bypassed and not removed, other management measures are needed. One promising approach is the application of ecological flows (ie flow and water levels required to sustain the ecological function of the flora, fauna, and habitat processes within a water body and its margins; EU 2015). Maintaining ecological flow levels addresses not only the quality, quantity, and timing of discharges, but also variability in flow speed. "Ecological flow" differs from "environmental flow" primarily in that, in the former, ecological considerations are prioritized over economic ones (Dyson *et al*. 2003). Research on the effectiveness of ecological flow regimes has largely been based on predictive modeling (eg Bond *et al*. 2018); such models should in the future be complemented by empirical field tests, given that migration, time of spawning, flow requirements, and other factors often differ among diadromous species. Empirical studies have demonstrated the potential of this strategy; for example, both Australian grayling (*Prototroctes maraena*) and Australian bass (*Macquaria novemaculeata*) exhibited a migratory response upon release of excess water under an ecological flow management regime (Reinfelds *et al*. 2013; Amtstaetter *et al*. 2016).

Canalization of rivers and artificial canals used for shipping is not only characterized by strongly regulated water flows but also by very low structural variability. Typically, rivers are straightened and embanked with dikes and feature a more or less homogenous water depth and limited vegetation, resulting in loss of spawning and nursery habitats (Wolter and Arlinghaus 2003). Even though sections of a waterway could function merely as migratory "highways" for diadromous species, creation of resting and/or sheltering zones to allow migrating fish to recover is essential, as migration is not always continuous (eg anguillid eels migrate to the sea preferably at night and halt during daytime; Stein *et al*. 2016a).

Restocking

Restocking has been applied for over 150 years to compensate for species declines due to habitat loss and to improve fisheries (Levin and Williams 2002). Essentially, restocking involves artificial reproduction in hatcheries followed by the redistribution of reared juveniles (eg shads and salmonids; Mahnken *et al*. 1998; Hardy 1999) or the redistribution of natural recruits from locations where they are still abundant to areas where they are depleted (eg anguillid eels; Jellyman 2007; Dekker and Beaulaton 2016). However, the impact of restocking on diadromous species recovery is questionable because it tends to address symptoms rather than underlying causes, and also is labor intensive and expensive (Meffe 1992). Moreover, fish are often restocked in systems without concomitant consideration of issues of habitat connectivity and quality.

Part of the inefficiency of restocking can be attributed to genetic effects. Subpopulations of a species often exhibit considerable local adaptation, and their offspring may therefore be at a competitive disadvantage when transferred to an area with different environmental conditions. Hatchery reared fish are also more prone to accumulation of deleterious mutations (a phenomenon known as "hatchery selection"; Ford 2002), which can be reinforced when the brood stock is too small, resulting in inbreeding. In addition to inbreeding depression, outbreeding depression may occur when introduced fish reproduce with fitter natives, leading to offspring less well adapted to prevailing environmental conditions than the native population (Ward 2006).

Restocking of one population of a diadromous species may also negatively affect other, non-stocked species populations; for example, wild Chinook salmon (*Oncorhynchus tshawytscha*) survival declined in response to steelhead trout (*Oncorhynchus mykiss*) restocking (Levin and Williams 2002). Consequently, local management should instead focus primarily on improving habitat connectivity and quality. When these conditions are met and a relict population remains present in (or in the vicinity of) a waterway, natural recolonization can occur rapidly, leading to restoration of both the population and its genetic diversity (Grandjean *et al*. 2009). Given the limited success and potentially negative population consequences of artificial restocking, this approach should be considered only in areas where natural recolonization is unlikely. Finally, only fish from stocks closely related to the historical natural population should be introduced.

Fisheries management

Diadromous fish species are an important source of protein in many parts of the world. Examples include Pacific salmonids in western North America and East Asia (Mahnken *et al*. 1998), Atlantic salmon in Europe (Haapasaari *et al*. 2007) and eastern North America (Saunders *et al*. 2006), shads in North America (Hardy 1999), and anguillid eels in Europe (Dekker 2018) and Asia (Kuroki *et al*. 2014). The decline in diadromous fish populations has led to the imposition of fisheries restrictions for many species in many parts of the world, including limitations on total allowable catches as well as on export and import. Intensive (open-system) aquaculture can help meet demand for certain species (eg Atlantic salmon) and reduce pressure on wild populations, but may also negatively impact wild populations through disease and parasite transmission in addition to genetic contamination (Ford and Myers 2008; Merotto 2018).

Whether fisheries can become sustainable when populations are not recovering due to insufficient habitat connectivity and quality is questionable. The term "sustainable fisheries" implies that fishing does not negatively affect a given species or population, which can then be regarded as a renewable resource (Kolding and van Zwieten 2014). This requires a selective fishing approach involving numerous aspects, including fishing techniques employed, fish sizes, life stages, seasons, and habitats (Zhou *et al*. 2010). Cooperation and collaboration among fishermen, ecologists, and authorities is essential for attaining a sustainable fishery

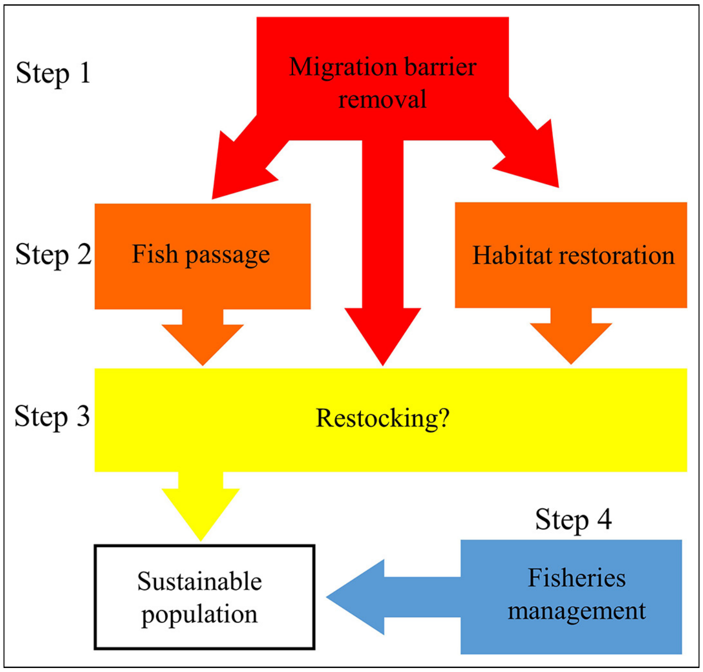

Figure 3. Hierarchical management scheme to restore diadromous fish populations in four steps. Step 1: removing barriers is given the highest priority, as barriers hinder migration and destroy essential habitat; their removal can aid fish passage and habitat restoration. Step 2: when a barrier cannot be removed, measures to ensure fish passage and habitat restoration must be implemented. Step 3: whether restocking is necessary to restore a population must be considered carefully; if recolonization does not occur naturally following implementation of steps 1 and 2, then restocking could be undertaken, preferably using brood stock from populations closely related to the population native to the system. Step 4: finally, when a sustainable population is reached, fisheries activities can be permitted. Colors indicate the necessity of the applied measures: red = high; orange = medium; yellow = low; blue = optional sustainable fishing.

(Stratoudakis *et al.* 2020) and reducing illegal fishing (Stein *et al.* 2016b).

The way forward

Reestablishing sustainable diadromous fish populations in many parts of the world will require management approaches that consider the Big Five factors described above. Isolated measures, such as habitat restoration or fishing limitations, will yield the desired results only if no other obstacle to population sustainability remains within the same system.

When developing an integrated management plan for the restoration of diadromous fish populations, initial steps must involve an assessment of existing migration barriers, flow regime, and qualitative habitat availability. Where possible, removing (eg non-operational) or overcoming (eg fishways, trap-and-transport) barriers and restoring more pristine conditions of flow and habitat diversity (ie free-flowing rivers, creation of backwaters and floodplains, establishment of well-developed and vegetated river banks, and so forth) should be the first measures instituted. Removal of migration barriers can promote fish passage and habitat restoration, especially when rivers have room to meander. This may, however, not be possible for rivers with concrete and straightened embankments or when barriers cannot be removed. Secondary steps encompassing water flow and habitat restoration may also involve restocking, but only when the target species no longer occurs in the catchment. Finally, when a sustainable population is reached, carefully monitored fisheries can be justified (Figure 3).

Despite the similarity of their life cycles, diadromous species differ greatly in migration intensity, swimming capacity, and habitat requirements. For instance, juvenile anguillid eels can grow and develop in various habitats and therefore mainly require access to productive habitats, and shads spawn in the midwater of rivers and are less demanding than salmonids in terms of streambed structure. To help promote positive conservation outcomes, resource managers must therefore prioritize the needs of target species and address the Big Five considerations.

Adequately addressing all five considerations will be challenging in many waterways due to funding constraints, limited space for meandering or fishway construction, and myriad other reasons. From a population perspective, it may therefore make more sense to focus efforts on improving a realistic number of river stretches in river basins in an integrated manner and address all major obstacles to successful population restoration as opposed to investing in isolated management measures in as many rivers as possible. Indeed, management should aim to prevent diadromous fish from inhabiting unsuitable systems or ones that act as biological traps (eg when fish are unable to leave a system; Verhelst *et al.* 2018). It may therefore be necessary to sacrifice a subset of waterways to function primarily for industrial services (eg shipping, hydropower) and forego restoration, provided that a sufficient proportion of other waterways are managed for diadromous fish. Identifying river basins and the minimum proportion of river stretches that could serve as "diadromous species reserves" will require extensive, and often multinational, cooperation between experts and stakeholders (eg scientists, water managers, industry representatives) to determine an acceptable balance between different aspects of sustainable development (Forio and Goethals 2020).

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