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River Damming Impacts on Fish Habitat and Associated Conservation Measures

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Key Points:

- Dam construction alters river hydro-geomorphological conditions and hence influences fish habitat quality and quantity
- Knowledge of river hydrogeomorphology and reservoir properties can inform which conservation measures may benefit fish conservation
- Long-term monitoring is needed to understand causal effects and synergies with climate change

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract River damming has brought great benefits to flood mitigation, energy and food production, and will continue to play a significant role in global energy supply, particularly in Asia, Africa, and South America. However, dams have extensively altered global river dynamics, including riverine connectivity, hydrological, thermal, sediment and solute regimes, and the channel morphology. These alterations have detrimental effects on the quality and quantity of fish habitat and associated impacts on aquatic life. Indeed, dams have been implicated in the decline of numerous fishes, emphasizing the need for effective conservation measures. Here, we present a global synthesis of critical issues concerning the impacts of river damming on physical fish habitats, with a particular focus on key fish species across continents. We also consider current fish conservation measures and their applicability in different contexts. Finally, we identify future research needs. The information presented herein will help support sustainable dam operation under the constraints of future climate change and human needs.

Plain Language Summary River damming yields great social-economic benefits, but also causes significant eco-environmental impacts, particularly on fish. Dams block fish migration routes, alter hydrological and water temperature regimes, and modify channel morphology. These changes impact fish physical habitats and associated communities. Here, we synthesize the impacts of river damming on fish physical habitats, and review potential conservation measures that could be used to off-set or mitigate the impacts of dams on fish habitats, populations and communities.

Box 1. Tutorial

This paper contains five sections. The "Introduction" briefly describes the background of the review. Section 2 is about river damming impact on fish physical habitat, including river connectivity, hydrological regime, sediment regime and morphology, water temperature regime, and dissolved gas. Section 3 is about river damming impact on key fish species across different continents, including salmonids, Chinese carps, sturgeon, eel and lamprey, and other typical fish species. Section 4 focuses on major conservation measures, which include fish passage facilities, artificial breeding and release, reservoir ecological operation, and habitat compensation in tributaries, for fish in dammed rivers. The last section highlights future research perspectives on impact assessments and mitigations, effect of climate and land cover changes, and long-term systematic observations.

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Box 2. Glossary

ATT: accumulated temperature threshold for fish gonad maturity.
ATU: accumulated thermal units.
CI: connectivity index. For each river basin, CI is quantified for each fish species by combining its occurrence range with a high-resolution hydrography and the locations of the dams (Barbarossa et al., 2020).
CSI: connectivity state index. CSI of river reaches is determined with four dimensions, including longitudinal connectivity between up- and downstream, lateral connectivity to floodplain and riparian areas, vertical connectivity to groundwater and atmosphere, and temporal connectivity based on seasonality of flows (Grill et al., 2019).
CTT: critical temperature threshold for fish spawning.
FMCCs: four major Chinese carps.
GBD: gas bubble disease.
IHA: indicators of hydrologic alteration.
LHPs: large hydropower plants.
MPUE: mass per unit effort.
NbS: nature-based solutions.
NFR: natural flow regime.
RVA: the range of variability approach.
SHPs: small hydropower plants.
TDG: total dissolved gas.
TGR: Three Gorges Reservoir.

1. Introduction

Since the first masonry dam was constructed around 3000 BCE on the Wadi Rajil at Jawa, Jordan, river damming has made significant positive contributions to the supply of water and energy, flood management, irrigation, and navigation worldwide, especially in the last century (Best, 2019). The first global boom of dam construction occurred after the Second World War, peaking in the 1960s and 1970s, mainly in Western Europe and North America (Figures 1a and 1b; Lehner et al., 2011). Following increasing concerns about the social and ecological impacts caused by river damming, the trend of global dam construction slowed in the 1990s (Moran et al., 2018). However, to meet the rapidly growing demands for energy and water for socio-economic development, there has been a second boom in dam construction, mainly in developing countries and emerging economies in Asia, Africa and South America (Figures 1c and 1d), and particularly in large river basins such as the Amazon, Congo, and Mekong (Winemiller et al., 2016; Zarfl et al., 2015). To date, approximately 3,700 major dams are either planned or under construction, and the number is predicted to increase further (Zarfl et al., 2015), although removal of aged dams has become an issue for engineering security and possible restoration of damaged river ecosystem in some countries (Habel et al., 2020; O'Connor et al., 2015). According to the International Commission on Large Dams (ICOLD, https://www.icold-cigb.org/), the number of registered large dams (dam height ≥15 m, or 5–15 m with reservoir capacity ≥0.03 km^3) worldwide reached 58,713 by April 2020. Dams can be categorized according to their height or the associated reservoir regulation capacity. Large dams usually convert the upstream lotic rivers into lentic reservoirs, and have an annual to seasonal regulation capacity that can significantly modify the hydrological regime downstream; small dams (dam height <15 m) and run-of-river dams typically have a small reservoir, or even no reservoir, and are associated with weekly to sub-daily regulation capacities that impose relatively low impacts on the hydrological regime downstream (D. Anderson et al., 2015; Timpe & Kaplan, 2017).

River damming disrupts free flows, and hence results in habitat fragmentation (Grill et al., 2015, 2019). Globally, 63% of the world's large rivers (>1,000 km) are no longer free flowing (Grill et al., 2019). The construction of over 3,700 expected hydropower dams is estimated to increase global river habitat fragmentation to 93% in the future, which has already reached 48% due to the 6,374 existing large dams (Grill et al., 2015; Zarfl et al., 2015).

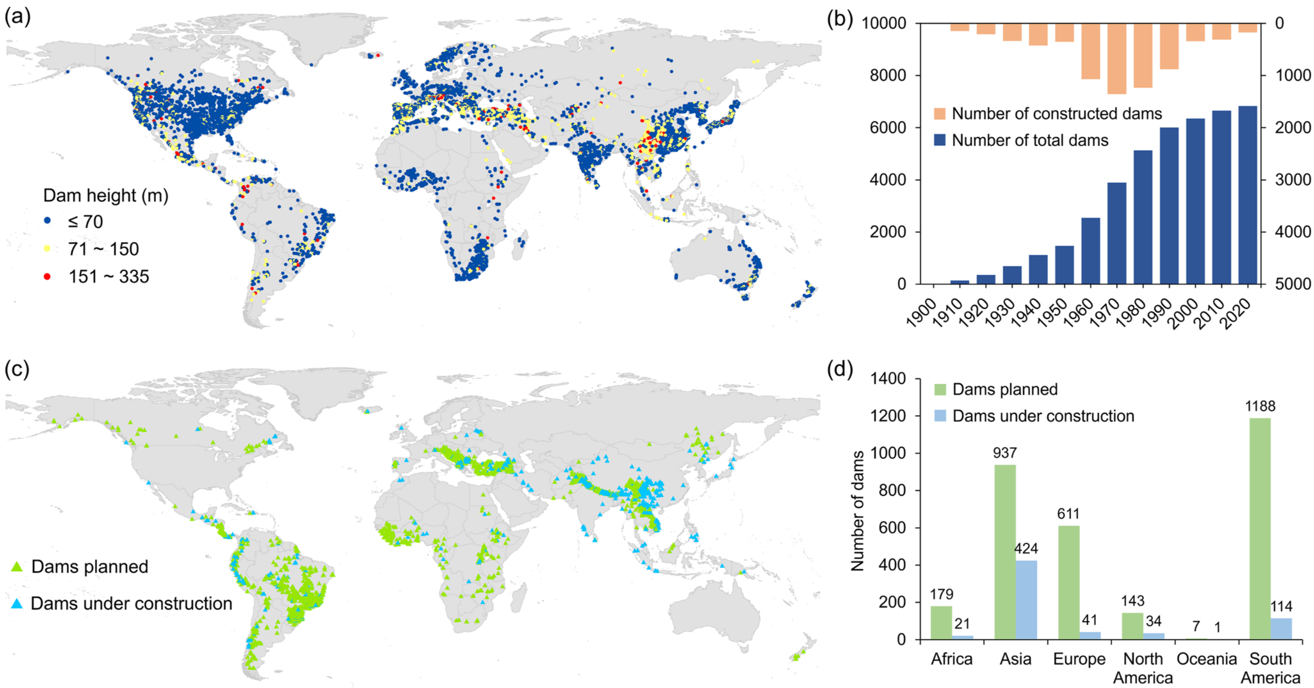

Figure 1. Global dam construction and distribution. (a) Distribution of global dams. (b) Number of global total dams and number of dams constructed in each decade from 1900 to 2017. (c) Distribution of global dams in planning and under construction. (d) Number of dams under planning and construction in each continent. Data of panel (a) and (b) are from Global Reservoir and Dam Database (Lehner et al., 2011). Data of panel (c) and (d) are from Future Hydropower Reservoir and Dams Database (Zarfl et al., 2015).

The seasonal and interannual dynamics of river flow and water temperature regimes have been greatly dampened by river dam operation (Poff et al., 2007). As the reservoir operating time increases, sediment is deposited in reservoirs, while the downstream riverbed tends to experience scour, eventually altering the river morphology (Kondolf et al., 2014, 2018; Schmitt et al., 2019). Moreover, the flood discharge and energy dissipation associated with high dams can result in supersaturation of total dissolved gas in the downstream waters (Q. Ma et al., 2018; Weitkamp & Katz, 1980).

The alterations of river geophysical conditions caused by dams have significant effects on river ecology, among which the impact on fish is of great concern because fish contribute to human welfare as key food resources. Inland fisheries provide the equivalent of all the dietary animal protein for 158 million people globally (McIntyre et al., 2016), particularly for poor and undernourished populations in food-insecure regions such as the Amazon (Winemiller et al., 2016) and Mekong (Orr et al., 2012; Ziv et al., 2012) basins, where river fish are a key source of protein. For example, in the Lower Mekong River basin, fisheries are the primary source of protein for 60 million residents (Ziv et al., 2012). Rivers also provide essential habitats for a diverse array of fishes. Alterations in river geophysical conditions arising from dams have considerably impaired fish biodiversity and resources worldwide (Reid et al., 2019; G. H. Su et al., 2021), as dams modify the natural flow, thermal and sediment regimes, and decrease fish access to spawning and nursery habitats (Freeman et al., 2007). These alterations cause dramatic reductions in fish productivity and lead to declines in fish populations, threatening global fishery production and regional food security. The effects of river damming on fish populations have received considerable attention (Fullerton et al., 2010), with many studies investigating impacts on globally important commercial and endangered fish species, such as salmonids (Hilborn, 2013), eels (Atkinson et al., 2020), Chinese carp (Q. Chen et al., 2021), and sturgeon (Z. Huang & Wang, 2018).

To mitigate the negative impacts of river damming on fish, a variety of conservation measures, spanning off-setting to mitigation, have been developed and applied. Reservoir operations have been optimized to mimic natural flow regimes (NFRs) to satisfy fish living conditions (W. Chen & Olden, 2017; Sabo et al., 2017), and fish passage facilities have been installed at river dams to maintain biological connectivity (Katopodis & Williams, 2012; Noonan et al., 2012). Some small dams and barriers have been removed in tributary channels to rehabilitate and

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compensate for fish habitats lost in the dammed mainstems (Marques et al., 2018; L. Tang et al., 2021). Artificial breeding programs have been implemented to restore fishery resources, which to some extent have succeeded by increasing the target fish populations (Holsman et al., 2012; J. Yang et al., 2013). However, the efficiency and effectiveness of these conservation measures have not been well investigated, leading to some controversial perceptions concerning fish conservation measures in dammed rivers. Therefore, assessing the efficiency and cost-effectiveness of different conservation measures could contribute significantly to identifying and promoting efficient practices.

The number of studies documenting the impacts of river damming on fish habitats, fisheries resources, regional food insecurity, and associated conservation measures has rapidly increased in the past decade. This review seeks to analyze and synthesize state-of-the-art studies concerning the impacts of river damming on fish physical habitats and associated conservation measures. Specifically, we focus on the geophysical aspects of hydrological and water temperature regimes, dissolved gas supersaturation, sediment dynamics and biogeomorphology in relation to fish habitats, with emphasis on several key fish species that occur on various continents. In addition, we assess the cost-effectiveness of existing fish conservation measures. Finally, we formulate future key research directions for fish conservation in dammed rivers, with the aim of helping foster sustainable hydropower development.

2. River Damming Impacts on Fish Physical Habitat

Dam construction alters river hydro-geophysical characteristics, including river connectivity, hydrological regime, sediment regime, and morphology, water temperature regime, and dissolved gas, which have essential impacts on fish physical habitat.

2.1. Impacts on River Connectivity

River longitudinal and lateral connectivity play a vital role in maintaining the structure and functioning of riverine ecosystems (Díaz et al., 2020). River systems are hierarchical tree-like networks, whose ecological function is highly dependent on physical connectivity (Fuller et al., 2016; Grant et al., 2007). The needs of fish for diverse habitats are strongly dependent on river connectivity and natural mobility (Arthington et al., 2016). Longitudinal connectivity is essential for fish migration (Figures 2a and 2b), and lateral connectivity provides fish the access to spawning and rearing grounds in floodplains, side channels, oxbows and floodplain lakes (Figure 2c).

With the increasing number of dams, the longitudinal connectivity of global rivers is significantly under threat. Currently, about half of global river reaches show diminished longitudinal connectivity, with the Connectivity State Index (CSI) below 100%; nearly 10% of global river reaches have CSI below 95%, which is the minimum value for a high level of connectivity (Grill et al., 2019). Large river networks with completely natural connectivity (CSI = 100%) exist only in remote regions of the Arctic, Amazon and Congo basins (Grill et al., 2019). During the second half of the 20th century, the impairment of river network connectivity became more severe and is now widespread throughout the entire pan-European continent. There are at least 1.2 million river barriers (an average density of 0.74 per km) in the 36 European countries (Belletti et al., 2020), and in general more than 50% of river length is affected (Duarte et al., 2021). The highest barrier densities are found in rivers in central Europe where river connectivity has been severely altered, whilst the lowest barrier densities are found in the most remote and less populated alpine areas. Relatively undisturbed rivers exist only in parts of the Balkans, Baltic States, and Scandinavia in Europe (Belletti et al., 2020). As far as large rivers (catchment area >10,000 km^2) are concerned, the Mediterranean and Western Atlantic regions are those most affected by fragmentation in terms of the number of basins, while the Black Sea and Caspian Sea regions are the most affected by fragmentation in terms of river length (Duarte et al., 2021). In the USA, large dams have increased river segmentation by 801% compared to free-flowing streams in the absence of dams, and 79% of stream length is disconnected from their outlet of oceans or Great Lakes (Cooper et al., 2017). In South America, more than a hundred hydropower dams have fragmented the rivers in the Amazon basin. For the eight major river systems in the Andean region of the Amazon headwaters, the 142 existing or under construction dams have fragmented the tributaries of six major river systems, and the 160 proposed dams could further result in a significant loss of river connectivity in the mainstreams of five major river systems (E. Anderson et al., 2018; Flecker et al., 2022; Latrubesse et al., 2017, 2020; Lees et al., 2016). In general, the Connectivity Index (CI) of rivers is the lowest in the Europe, United States, South Africa, India and China, and the completion of the dams currently under construction or planned will further reduce river

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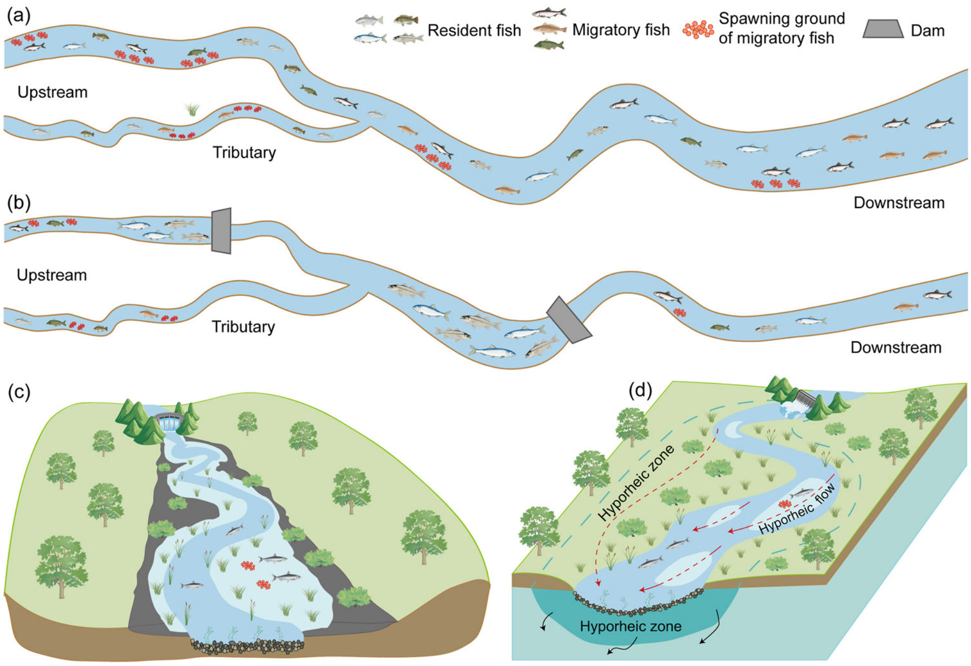

Figure 2. River connectivity and the impacts of dams. (a) Migration and spawning grounds of fish in free-flowing river. (b) Migration and spawning grounds of fish in dammed rivers, (c) Spawning and rearing grounds of fish in floodplain. (d) Hyporheic exchange and redd habitats.

connectivity, particularly in countries such as India and China that are facing a boom in dam construction. However, commensurate studies are insufficient in these developing countries (Barbarossa et al., 2020).

Dam construction also reduces lateral connectivity of rivers, which decreases the interactions between rivers and floodplains/wetlands in river basins (Latrubesse et al., 2017; Stoffels et al., 2022), and thereby affects the productivity of floodplain and wetland ecosystems (Palmer & Ruhi, 2019). In the Atreyee River basin in India, the active floodplain area was reduced by 66.2%, and 48.9% of total pre-dam wetland was completely obliterated, due to the reduction in lateral connectivity caused by the Mohanpur Dam (Saha et al., 2022). In the wet-dry tropics of Australia, dam construction reduces the average duration of the lateral connectivity between floodplain wetlands and their main river channels by 1% and 2% in the Flinders and Gilbert catchments, respectively (Karim et al., 2015). In the upper Paraguay River basin in South America, the Manso dam decreased the lateral connectivity between the Cuiaba River and Pantanal wetlands, one of the largest wetland systems in the world, which weakened the exchange of sediments and nutrients (Jardim et al., 2020). Regulated releases also impact on the vertical connectivity between surface and subsurface waters, which alters the exchange of solute, heat and nutrient between surface and sediment waters (Figure 2d) (Sawyer et al., 2009).

It is also necessary to emphasize river fragmentation caused by small dams, due to their large number and widespread distribution, which are usually neglected (E. Anderson et al., 2018; Castello & Macedo, 2016; Fuller et al., 2016; Rodeles et al., 2017). Couto & Olden (2018) estimate that 82,891 small hydropower plants (SHPs) are operating or under construction across 150 countries, which is more than the number (58,713 by April 2020) of large hydropower plants (LHPs) recorded by ICOLD. In addition, there are 181,976 SHPs planned, 10,569 of which are to be implemented in the coming decades, indicating that the number of SHPs will continue to increase rapidly. In developed countries, as the hydropower potential of large rivers has been mostly exploited, an increasing number of SHPs are under planning in some of these nations, such as Austria, to meet energy demands (Wagner et al., 2015). In water-rich countries in Asia, Africa, Latin America and southeastern Europe, the potential of SHPs has gained particular interest from policymakers and more SHPs will be constructed (Harlan et al., 2021). SHPs are conventionally considered as a type of clean energy resource with less environmental impact than LHPs (Dursun & Gokcol, 2011; Nautiyal et al., 2011). However, SHPs are usually set in high-gradient alpine streams and a river basin usually contains a large number of SHPs, which lead to cumulative, and hence more severe, impacts on river fragmentation than LHPs (Timpe & Kaplan, 2017). For instance, the average loss of connectivity due to SHPs is much higher than that due to LHPs in Brazil (Couto et al., 2021). Great concerns have been raised about the large expansion of SHPs in rivers feeding the Pantanal wetlands, as these SHPs have affected the lateral connectivity between rivers and wetlands (Figueiredo et al., 2021).

River fragmentation has significant impacts on freshwater fish (Barbarossa et al., 2020). Dams act as physical barriers in spawning or foraging routes and limit the expansion of fish populations (Figure 2b). Widely distributed dams have impeded fish migration and generated population isolation, leading to declines in fish populations and ultimately to local or total extinction, especially for migratory fish species (Duponchelle et al., 2021; Rodeles et al., 2017; van Puijenbroek et al., 2018). Over the past 50 years, freshwater migratory fishes have declined by 96% globally, becoming the vertebrate group suffering the most severe decline (Deinet et al., 2020). Studies concerning the impacts of river fragmentation on migratory fish have mainly analyzed the life history of certain migratory species, measured their habitat characteristics at different life stages, and assessed the potential impacts of damming on their habitats (Goodwin et al., 2014; Liermann et al., 2012; Wofford et al., 2005). River fragmentation also leads to fish populations becoming isolated and genetically fragmented, exposing them to severe effects of genetic drift and inbreeding (Brinker et al., 2018; Cheng et al., 2015). Moreover, river fragmentation changes the structure of riverine food webs, reducing the taxonomic diversity of fish (Freedman et al., 2014). The beta diversity of native fishes in pools and non-native fishes in riffles decreased with an increase in the ratio between the length of the longest non-fragmented sections in the river network and the total length of the river network (Díaz et al., 2020). The decreased lateral connectivity due to dam construction causes loss of access for some fish species to their spawning and rearing grounds in floodplain and wetlands (Figure 2c) (O'Mara et al., 2021). In the Amazon River, decreases in river-floodplain interactions due to dam construction have caused significant reduction in catch-per-unit-effort and shifts in the functional composition of fisheries in the Madeira River floodplain (C. C. Arantes et al., 2021). In addition to fragmentation effects of large dams, widespread small dams also impose significant, particularly cumulative, impacts on fish distribution and diversity (Consuegra et al., 2021). Studies show that two-thirds of 191 migratory fish species in Brazil would be affected by river fragmentation due to the increasing number of SHPs, which is greater than the connectivity loss caused by LHPs (Couto et al., 2021).

The impacts of river fragmentation on fish diversity and distributions at larger scales (e.g., continental and global scales) may differ from that at local scales (e.g., basin and sub-basin scales), as fish beta diversity shows significant differences among river networks with similar degrees of connectivity (Díaz et al., 2020). In recent years, the effects of dam-induced river fragmentation on fish, and the mechanisms by which fish diversity responds to river fragmentation at large scales, have become new areas of interest. Grill et al. (2015) assessed the effects of river fragmentation on fish habitat at high spatial resolution from sub-basin to watershed scales. Given current progress in river connectivity studies from watershed to continental scales (Belletti et al., 2020; Duarte et al., 2021; Grill et al., 2019), it is anticipated that research concerning the impacts of river fragmentation on fish diversity and distributions will quickly expand to global scales.

Most current studies concerning river fragmentation adopt physical connectivity indices (e.g., CSI, CI); however, the hydrological and hydraulic disconnections of dammed rivers should receive sufficient attention as they impose significant impacts on fish habitats. In addition, the impacts of cascade dams on river connectivity and their cumulative effects on fish are typically much greater than a single dam, and thus deserve more investigation. At present, indices of physical connectivity are mainly based on geo-spatial data, which may be insufficient in resolution or possess inadequate records for small dams. As such, the impacts of small dams on river connectivity worldwide are seriously underestimated, and demand urgent attention.

2.2. Alterations to River Hydrological Regimes

Hydrological regime, including variables such as discharge, flow velocity, water depth, and peak flow, plays an essential role in riverine bio-habitats and ecosystems (Y. Chen et al., 2016). Fish spawning, rearing and wintering are strongly related to hydrological conditions. For fish species spawning drifting eggs, continuous stimulation of flow velocity is required, and thus flooding processes can provide favorable conditions for their reproduction (Young et al., 2011). With sufficient flow velocity, drifting eggs are not susceptible to sinking, which improves their survival rate (George et al., 2017). River flow can mediate the dispersal of fish eggs, extending their survival range and promoting the stability of fish communities (Castello & Macedo, 2016). The annual rise and fall of river depth induces lateral exchange of materials between the river channel and floodplain, which extends fish physical habitat and increases baits for them (Castello & Macedo, 2016; Paillex et al., 2013). In cold regions, fish require water bodies with sufficient depth that have warm water in the deeper layers for overwintering (Cott et al., 2008).

River hydrological regime depends mainly on climatic conditions and possesses distinct features in different regions (Fiseha et al., 2014). In tropical regions, most rivers have a large annual runoff and their discharge possesses strong interannual fluctuations with little seasonality (J. P. Syvitski et al., 2014); some rivers have well-defined high and low discharges in correspondence to a unimodal rainy period, such as the Ganges River in south Asia and the Purus River in the Amazon basin; some rivers have two peak flows per year in correspondence to bimodal rainy periods, such as the Magdalena River in South America and the Congo River in Africa (Latrubesse et al., 2005; J. P. Syvitski et al., 2014). In subtropical and temperate regions, rivers usually have a relatively smaller annual runoff than those in tropical regions, and their discharges have distinct seasonality that is influenced by seasonal rainfall and snowmelt, such as the Yangtze River and Yellow River in eastern Asia (W. Yang et al., 2020). In cold regions, rivers are characterized by low flow in winter due to ice cover and high flow in spring due to ice-jam floods (Peters et al., 2014; Prowse, 2001), such as the Mackenzie River in the North America and Lena River in Russia. In some rivers, peak flows are dominated by snowmelt in spring (from March to May), and these rivers are mainly distributed in southern North America, eastern Europe and westernmost Asia; peak flows may appear near June due to relatively late snowmelt (Hansford et al., 2020), and these rivers are located mainly in regions of low altitude and mid-high latitude (Q. Liu et al., 2022). Peak flows can also be brief and intense as determined by monsoon rains, and these rivers are mainly distributed in eastern and southern Asia, and eastern Australia (Dettinger & Diaz, 2000). In some rivers, there are no significant peak flows due to stable rainfall or mixed climates, such as the St. Lawrence River in central-eastern North America and rivers in southern Finland (Haines et al., 1988).

Dam construction may significantly alter river hydrological regimes (Timpe & Kaplan, 2017). The conversion from lotic river to lentic reservoir upstream of a large dam fully modifies the original hydrological regime. Dams directly decrease river flow velocity (Y. Yang et al., 2017). Stevaux et al. (2009) reported that the annual mean flow velocity of the Paraná River in South America was 0.88 m/s in the pre-dam period, and decreased to 0.56 m/s after dam construction. Reservoirs impound water in wet seasons and release it in dry seasons, thus decreasing the seasonal variability of discharges in rivers (Figure 3a). The discharge of the Mekong River in the dry season is now 63% higher than that in the pre-dam period, while the discharge in the wet season has declined by 22% (Chong et al., 2021). Although run-of-river reservoirs do not alter the seasonal pattern of discharge (Figure 3b), they can significantly increase the variability of diel or daily discharge through hydropeaking operations (R. M. Almeida et al., 2020). River damming decreases the number and duration of peak flows, and alters the frequency of water level variability (Timpe & Kaplan, 2017). After the construction of the Gezhouba Dam and Three Gorges Dam, the number of flow pulses in the downstream Yangtze River decreased by 22%, and their maximum duration decreased from 16 days to 4–6 days (Y. Wang et al., 2016). River damming decreases the maximum discharge and increases the minimum discharge of river, resulting in reduced water level fluctuation zone (Poff et al., 2007). River damming may also reduce the extent of active floodplain, the period and duration of flooding, as well as the exchange of materials between main channel and floodplain (Jardim et al., 2020; Moi et al., 2020). Dam construction in the Balonne River in Australia has resulted in a 23% loss of active floodplain area and decreased the availability of nutrients from the floodplain (Thoms, 2003). To quantify alterations to river hydrological regime incurred by dam construction, Richter et al. (1996, 1998) have developed the Indicators of Hydrologic Alteration (IHA) method (Table 1), which is widely used to evaluate alterations to the hydrological regime of dammed rivers. Based on the IHA, the range of variability approach (RVA) has been developed to evaluate the degree of alteration within specific ranges (Richter et al., 1997).

Alterations to hydrological regime caused by river damming could detrimentally impact the spawning, migration and feeding behavior of fish (Mims & Olden, 2012). A decrease in flow velocity caused by river damming has been found to reduce the stimulation for fish spawning, resulting in declines of fish reproduction (Figures 3c and 3d). In dammed rivers, fish gamma diversity, which indicates the regional or total diversity of fish, is negatively correlated to magnitude in flow velocity (Jarzyna & Jetz, 2016; McGarvey & Terra, 2016; Timpe & Kaplan, 2017). For fish that fertilize in vitro, the decelerated flow of dammed rivers can reduce the success rate of fertilization (Campton, 2004). Decreases in flow velocity may lead to sinking of drifting eggs or failure to reach their destination for successful hatching (George et al., 2017). For fish species spawning sticky eggs, artificial hydropeaking incurred by reservoir operation can cause unsuitable conditions for their reproduction

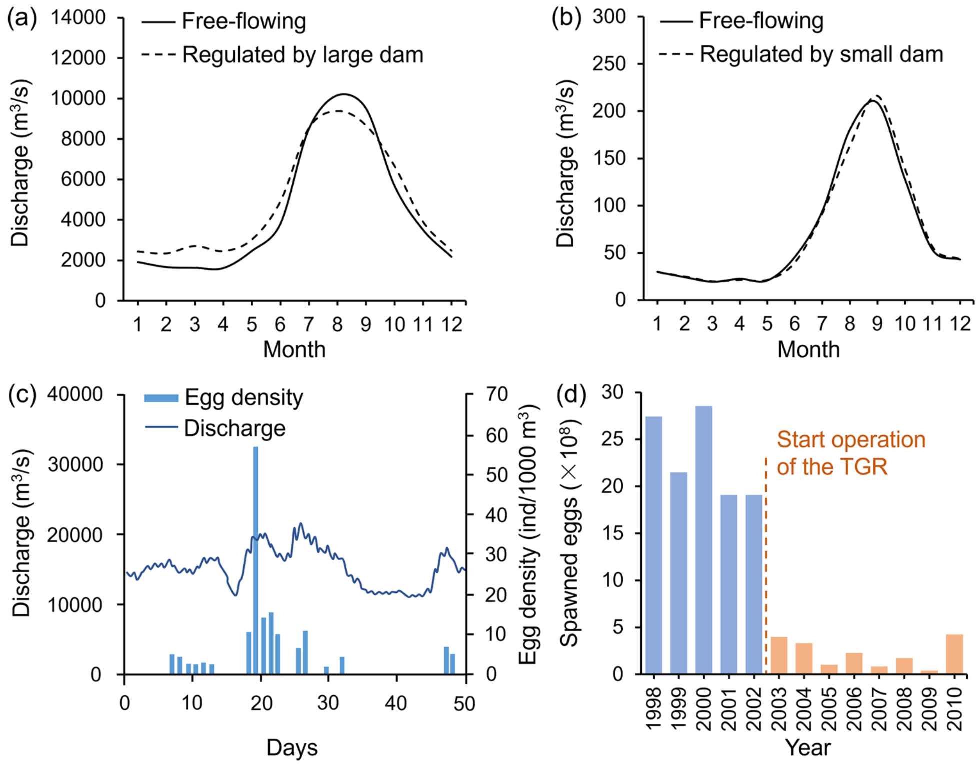

Figure 3. (a) Hydrograph of the Pingshan hydrological station (averaged monthly discharge during 2007–2010, free-flowing) and the Xiangjiaba hydrological station (replacement of Pingshan hydrological station, averaged monthly discharge during 2016–2020, regulated by a large reservoir) of the upper Yangtze River. (b) Hydrograph of the Ningnan hydrological station of the Heishui River, a tributary of the upper Yangtze River, before (2015) and after (2019) the removal of the Laomuhe Dam (a small hydropower dam with no reservoir regulation capacity). (c) Discharge from the Three Gorges Reservoir (TGR) and fish egg density of four major Chinese carps (FMCCs) measured at the Yidu cross-section of the Yangtze River during the ecological operation of the TGR in 2016. (d) The number of annual spawned eggs of FMCCs measured at the Yidu cross-section of the Yangtze River before and after the operation of the TGR. The data of panel (a) and (b) are available from Hydrological Data of Changjiang River Basin in Annual Hydrological Report P. R. China, and the data of panel (c) and (d) are from the authors.

(Vilizzi, 2012). The reduced seasonal variability of discharge in dammed rivers can decrease floodplain productivity, which leads to poor growth and low survival of the fry, resulting in reduction of fish populations (Ficke et al., 2007; Reinfelds et al., 2013; Terra et al., 2010). Meanwhile, the degradation of plants in floodplain areas reduces the matrix for sticky eggs to attach, leading to a decrease in the survival of the eggs (Perna et al., 2012). The decrease in high and low flow pulses and their duration due to river damming can eliminate the hydrological cues for fish migration, which reduces foraging opportunities and increase the risk of fish stranding (Bao et al., 2022; Reid et al., 2019). Rapid reductions of river water surface elevation due to dam operation may result in stranding of fish species (E. Bell et al., 2008; Irvine et al., 2015). Such fish stranding has been reported during flow reductions downstream of dams, leading to mortality of salmonids and sturgeon (Johnston et al., 2020; Nagrodski et al., 2012). Stranding is mainly caused by changes in flow magnitude, known as ramping rates in dam operations (Le Coarer et al., 2022; Poff et al., 1997). However, the potential for fish stranding also depends on factors such as fish species and their life stages, stream temperature, and the time of the day, and thus fish stranding may be site specific (Auer et al., 2022; Benjankar et al., 2023; Glowa et al., 2022). In newly constructed reservoirs, the decomposition of organic matter can provide more bait, and thus omnivorous fishes can increase in the short term (Bunn & Arthington, 2002; Junk et al., 2013). The increase in water depth and alteration of the substrate textures in reservoirs reduce the suitable habitat for periphytic algae and benthic macroinvertebrates (Holt et al., 2015; Taniwaki et al., 2013). This affects the fish feeding on periphytic algae and benthic macroinvertebrates, and increases the number of fish preferring phytoplankton and zooplankton, thereby altering the fish community structure in dammed rivers (W. Zhang et al., 2020). In winter, the rise of water depth in dammed rivers buffers the drop of water temperature, increasing the chances of fish survival during overwintering (Fuchs

Table 1
Summary of Hydrologic Indicators and Their Ecological Influences (Richter et al., 1998)

IHA statistics group	Regime characteristics	Hydrologic parameters	Examples of river ecosystem influences
Magnitude of monthly discharge conditions	Magnitude	Mean discharge for each calendar month	Habitat availability for fish
	Timing		Influences water temperature, oxygen levels, and photosynthesis in water
Magnitude and duration of annual extreme discharge conditions	Magnitude	Annual minima (1-day means; 3-day means; 7-day means; 30-day means; 90-day means)	Balance of competitive, ruderal, and stress-tolerant fish
			Structuring of river ecosystems by abiotic versus biotic factors
	Duration	Annual maxima (1-day means; 3-day means; 7-day means; 30-day means; 90-day means)	Structuring of river channel morphology and physical habitat conditions
		Number of zero-flow days	Volume of nutrient exchanges between rivers and floodplains
			Duration of stressful conditions (e.g., low oxygen, concentrated chemicals) in river ecosystem
		Seven-day minimum flow divided by mean flow for year (base flow)	Duration of high flows for aeration of spawning beds in river sediments
Timing of annual extreme discharge conditions	Timing	Julian date of each annual 1-day maximum discharge	Compatibility with life cycles of fish
			Predictability/avoid ability of stress for fish
			Access to special habitats during reproduction or to avoid predation
		Julian date of each annual 1-day minimum discharge	Spawning cues of migratory fish
			Evolution of life history strategies and behavioral mechanisms
Frequency and duration of high/low flow pulses	Magnitude	Number of high pulses each year	Availability of fish habitat in floodplain
			Nutrient and organic matter exchange between rivers and floodplains
	Frequency	Number of low pulses each year	Soil mineral availability
	Duration	Mean duration of high pulses within each year	Water birds enter foraging, resting, and breeding places
		Mean duration of low pulses within each year	Bed load transport, channel sediment structure, and substrate disturbance duration (high pulses)
Rate/frequency of hydrograph changes		Means of all positive differences between consecutive daily values	Entrapment of fish on islands and floodplains (rising levels)
	Frequency	Means of all negative differences between consecutive daily values	
	Rate of change	Number of flow reversals	Desiccation stress on low-mobility stream edge fish

et al., 2021; Keefer et al., 2008). In summary, alterations to river hydrological regime caused by dam construction impact significantly on fish habitats, further affecting the population and diversity of fish in dammed rivers.

Existing studies mainly focus on the impact of altered hydrological regime on the spawning aspects of fish reproductive biology. However, adequate attention should be paid to the impact of altered hydrological regime on the hatching processes of spawned eggs in dammed rivers, which also plays an essential role in early-stage fish resources. The reduced water levels during the flood season diminish material exchanges between channels and floodplain, which reduces feeding field and food abundance of fish. In addition, most available studies investigate the behavioral response of fish to hydrological alterations, and it is imperative to better understand the physiological mechanisms of fish reactions to dam-induced hydrological alterations.

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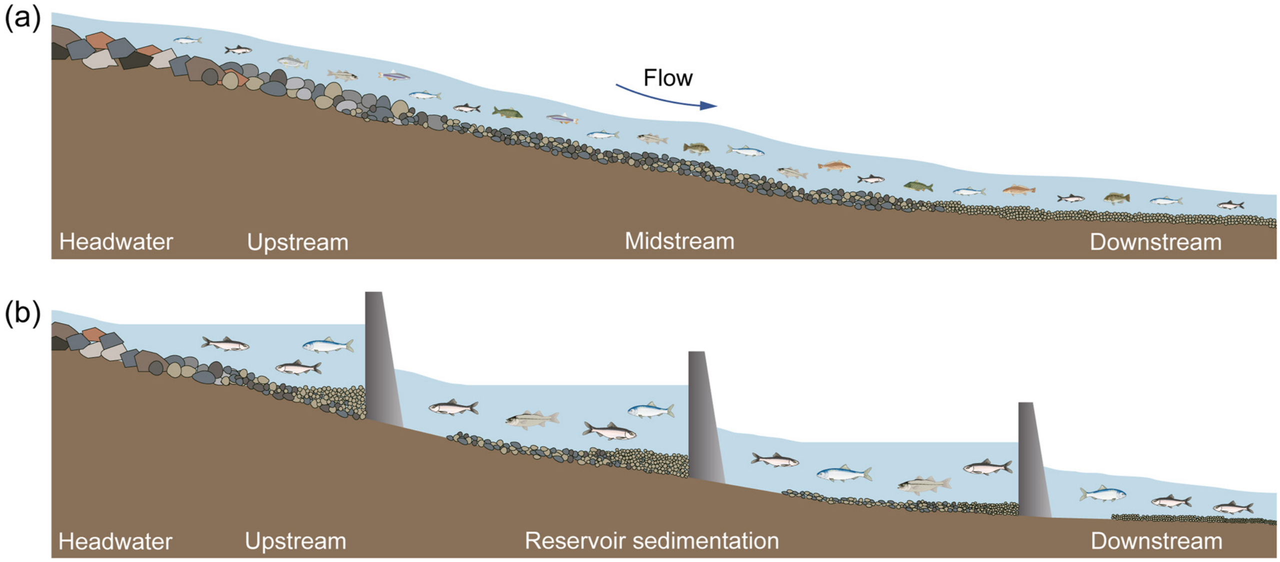

Figure 4. Impact of river damming on river bed sediment. (a) Bed sediment in free-flowing rivers. (b) Bed sediment in dammed rivers.

2.3. Changes to River Sediment Regimes and Morphology

Sediment is an essential component in rivers, and plays a pivotal role in maintaining the ecological status of global river systems (Chapman & Wang, 2001; Förstner et al., 2004, 2008; Netzband et al., 2007; Ralph et al., 2009). River sediment is entrained, transported and deposited, thus shaping river morphology and affecting fish habitat (Nichols, 2009). The balance between sediment supply and transport capacity of a river system is a fundamental driver for river geomorphology, which not only dictates the aggradational or degradational state of a system, but also controls channel morphology and substrate textures (Dietrich et al., 1989; Lisle et al., 1993; Pitlick & Wilcock, 2001). River planform can adopt a range types, form straight to sinuous, braided, anabranching or anastomosing shapes (Latrubesse, 2008; Leopold & Wolman, 1957). These different river planforms induce different hydrodynamic conditions, which in turn cause different patterns of sediment erosion and deposition, forming a variety of geomorphic units such as riffles, pools, barforms and bedforms, and flood plains, which thus increase the diversity of biological habitats, for example, those used for fish spawning and wintering grounds (Chapuis et al., 2015; Namour et al., 2015). Rivers also transport large quantities of organic matter, providing food sources for aquatic organisms (Karr, 1991). The content of organic matter in sediment is affected by sediment characteristics, including particle size and density, surface site density, and particle morphology (Y. Wu et al., 2020). In most rivers, bed sediments show an overall downstream-fining trend (Luo et al., 2012), as illustrated in Figure 4a.

Sediment from global rivers delivered to the oceans was estimated to be about 20 Bt/yr, prior to significant dam interception (Milliman & Syvitski, 1992). Dams alter the natural balance of sediment flux in rivers by trapping sediment in reservoirs, discharging waters often free of sediment downstream (Morris & Fan, 2010). Global dams decreased about 5 Gt/yr of sediment flux to the oceans by the 21st century (Milliman & Syvitski, 1992). Upstream of a dam, the reduction in flow velocity may facilitate sediment deposition in the river channel and floodplain (Fencl et al., 2015; X. Su et al., 2017; Walter & Merritts, 2008). As shown in Figure 4b, coarse particles, such as gravel and coarse sand, are the first to settle, forming a delta at the point where the backwater effect ends; fine sediment particles enter the reservoir and are transported by turbid density currents or non-stratified flow, and may be deposited near the dam (Fan & Morris, 1998; Garde & Raju, 1979). In addition, the peak sediment load in dammed rivers is separated in time from the maximum water flow (Dang et al., 2010; Topping et al., 2000), which also promotes the deposition of sediment. In the river downstream of a dam, the reduction in sediment content usually leads to channel incision, chronic erosion of the bed and banks, and even the loss of delta plain (Bittencourt et al., 2007; Graf, 2006; Magilligan & Nislow, 2005; Petts & Gurnell, 2005). Intensified scour and floodplain incision are often observed in sediment-starved rivers, as the flows entrain bed material equaling to their transport capacity (Csiki & Rhoads, 2010). In some cases, dams reduce the number of intense floods and lead to sedimentation downstream, which raises the river bed (Kotti et al., 2016; Słowik et al., 2018). After damming, pools may occur more frequently and individual pools are longer in the lower reach than that in the upper reach; in contrast, individual riffles in the upper reach are longer than that in the lower reach (Kobayashi et al., 2012). Low sediment loads downstream after dam construction also leads to reductions in associated nutrient transport, and thus affects fish feeding grounds (C. Guo et al., 2020). Moreover, the balance between inorganic and organic sediment is disrupted by damming, with mineral particles deposited predominately in the reservoirs, and the increased biological production causing the suspended load of the reservoir outflow to be largely composed of organic matter from aquatic organisms (Sokolov et al., 2020).

Alterations to sediment regimes due to river damming have potential impacts on fish habitat. The changes to erosion and deposition patterns, and hence the river morphology, may impede suitability for fish spawning and overwintering grounds (Kruk & Penczak, 2003; McLaughlin et al., 2006). For resident or potamodromous fish, river damming changes the number and distribution of fish habitats for spawning, feeding and overwintering downstream, leading to increases in competition for spawning and wintering sites as well as food resources (Cambray et al., 1997). The changes of mesoscale riverbed morphology, such as riffles and pools in the upstream and downstream, after river damming can indirectly lead to changes in the diversity and distribution of fish communities (Calderon & An, 2016; Langeani et al., 2005). In addition, different fish species may have a different preference for sediment properties. For example, larvae of white sturgeon (*Acipenser transmontanus*) prefer substrates of clean gravel and cobbles (Nguyen & Crocker, 2006), while larvae of *Schizothorax wangchiachii* change their preference for substrate at different life stages (Chai et al., 2019). Typically, lamprey spawn in riverbeds covered with a mixture of sand, gravel, and pebbles (N. S. Johnson et al., 2015). Fine sediment with relatively high organic matter is a primary source of food and energy for some species, and can even be an integral requirement within the lifecycles of species such as lamprey ammocete and psammophilous fish. Sediment coarsening downstream of a dam would result in less bait for these fish (Maitland, 2003). Moreover, complex habitat structure, such as pore space between coarse sediment, can increase predator-free space and thus reduce predation efficiency, an effect that is most pronounced at low prey densities (Barrios-O'Neill et al., 2015, 2016; Toscano & Griffen, 2013). Therefore, the altered river morphology and sediment gradation due to dam construction may seriously impact fish habitat. The alteration of suspended sediment content can also cause a variety of effects on fish habitat in dammed rivers. Some fish species prefer turbid over clear water, presumably benefiting from a reduced risk of predation and increased opportunity of feeding (Cyrus & Blaber, 1987, 1992). As reservoirs convert flowing water to relatively still water, the upstream water changes from turbid to limpid (C. Guo et al., 2020), and the increase in water clarity can directly affect the habitat of these fish species. In summary, the alterations of both suspended and bed load sediment regimes have important implications for the whole life history of fish in dammed rivers.

Despite extensive studies concerning the impacts of sediment regime alterations induced by river damming on fish, many challenges remain. The effects of changes in transparency and bed color on fish communities after river damming have not been explored sufficiently. Quantification of the contributions from direct effects, such as turbidity changes, and indirect effects such as predation behavior changes, also demand investigation. To date, most studies have focused on the response of fish to alterations in sediment regimes, but neglected the effects of alterations in fish activity on river sediment and morphology. It has been reported that spawning mucus of some fish species can modify substrate characteristics and thus affect sediment transport, which highlights the significance of spawning as a zoogeomorphic activity (Roberts et al., 2020). The effect of changes in spawning grounds of these fish species on river morphology after dam construction is a topic that demands further study.

2.4. Alterations in River Water Temperature Regimes

Water temperature is an important and highly sensitive factor in river ecosystems, and possesses distinct and regular seasonality. The natural rhythm of water temperature affects the phenological functioning of aquatic species, and the longitudinal variation of water temperature plays an essential role in generating spatial patterns of species communities (Isaak et al., 2012). Water temperature regime can affect the whole life cycle of fish (Servili et al., 2020), including migration timing, reproductive performance, embryo health, and growth rate (Figure 5c). For migratory fish, the change of water temperature within a suitable range is one of the key environmental cues for migration (Harvey et al., 2020; Rijnsdorp et al., 2009). The Atlantic salmon (*Salmo salar*) smolts in the three tributaries of the West River in Vermont, USA, begin migration when the water temperature rises to 5°C, and reach peak migration when water temperature rises to 8°C (Whalen et al., 1999). Fish have specific reproduction strategies, and a suitable temperature promotes healthy egg development and ensures

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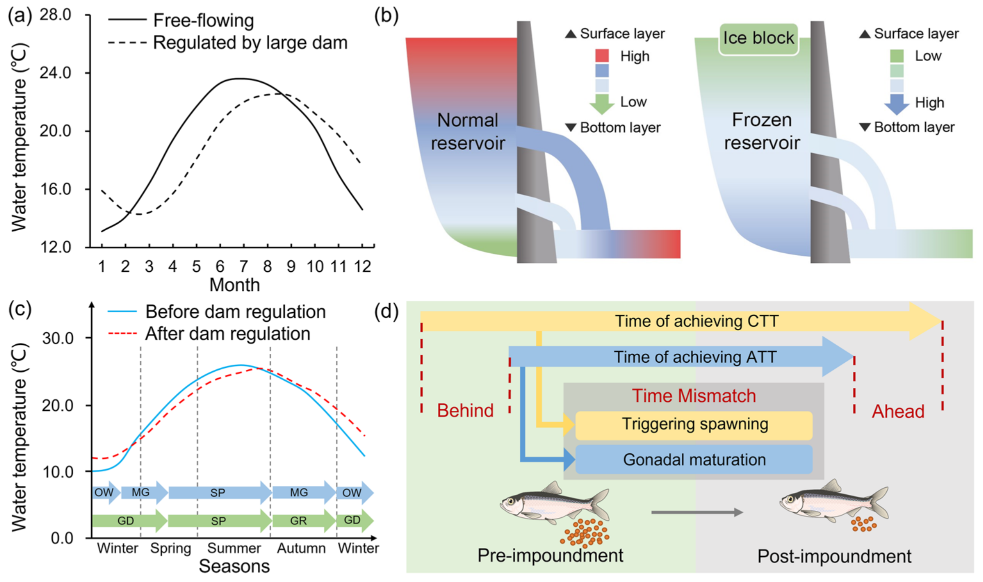

Figure 5. (a) Water temperature of the Pingshan hydrological station (averaged monthly water temperature during 2007–2010, free-flowing) and Xiangjiaba hydrological station (replacement of Pingshan hydrological station, averaged monthly water temperature during 2016–2020, regulated by the large Xiangjiaba Reservoir) of the upper Yangtze River. (b) Water temperature stratification in free-surface (left) and frozen-surface (right) reservoirs. (c) Water temperature in downstream of the Xiangjiaba Dam on the upper Yangtze River before and after the impoundment of Xiangjiaba Reservoir, and the phenological properties of fish (OW: overwintering, MG: migration, SP: spawning, GD: gonadal development, GR: gonadal recovery). Data are available from T. Li et al. (2021). (d) Impact of altered water temperature regime on fish spawning (CTT: critical temperature threshold for spawning, ATT: accumulated temperature threshold for gonad maturity). The data of panel (a) are available from Hydrological Data of Changjiang River Basin in Annual Hydrological Report P. R. China, and Figure 5d is adapted from T. Li et al. (2021).

successful spawning (Kurita et al., 2003; Sieiro et al., 2020). For temperate or tropical fishes that spawn in spring and summer, warm winters could affect the accumulation of nutrients during egg development, resulting in smaller eggs (Collingsworth et al., 2017; T. M. Farmer et al., 2015). For most cyprinids in temperate and tropical climates, temperature acts as a time clue for reproduction events, such as ovulation and oviposition (Pankhurst & King, 2010; N. Wang et al., 2010). In addition, changes in plankton and benthos in response to variations in water temperature directly affects fish food chains, and thus indirectly regulates the energy intake and growth of fish (Pörtner & Farrell, 2008; Prokešová et al., 2020).

The spatio-temporal variation of river water temperature is influenced by multiple factors, including water flux, climate, latitude and human activity (Caissie, 2006; Collins, 2009; Markovic et al., 2013; B. W. Webb et al., 2008). The study on a Cairngorm stream in northeast Scotland (Hannah et al., 2004) shows that in terms of average energy flux affecting water temperature, the main heat sources are sensible heat (38.7%), bed heat (37.0%) and friction at stream bed and banks (24.3%), while the main heat losses are latent heat (73.1%) and longwave radiation (26.9%). Typically, the water temperature of headwater streams is often lower than that of downstream reaches, because many rivers originate in plateaus or snow-covered mountains with water sourced from ice melting (Cai et al., 2018; Dugdale et al., 2017; Moors et al., 2011). At the global scale, regional trends of river water temperature are consistent with air temperature (J. Syvitski et al., 2019). In addition, river water temperature is increasingly affected by climate change (Dugdale et al., 2017; van Vliet, Franssen, et al., 2013; van Vliet, Ludwig, & Kabat, 2013). The response of river water temperature to climate change varies with latitude. Increases in water temperatures at low latitudes are generally greater than those in high and middle latitudes. However, water temperature changes in rivers in high-altitude regions, such as the Qinghai-Tibet Plateau (S. Liu et al., 2020), are different from this broad latitudinal pattern.

River damming can significantly alter water temperature regimes, as illustrated in Figure 5a (D. Cheng et al., 2015; Jung et al., 2022). The alteration of water temperature regime by reservoirs can be influenced by various factors, including the shape, storage and depth of the reservoir, the inflow water temperature, the hydraulic residence time, and the operation modes of the reservoir (Lessard & Hayes, 2003; Prats et al., 2010; Wotton, 1995). The essence of water temperature alteration by reservoirs is that the impounded water is thermally stratified seasonally and the outflow is mostly from deep layers. Although the impact of reservoirs on river water temperature regime is complex, the degree of alteration depends principally on dam height and regional climate characteristics (Maheu et al., 2016b), as summarized in Table S1 in Supporting Information S1. Reservoirs in different climatic regions have different effects on the water temperature regimes of dammed rivers (Pieters & Lawrence, 2012; D. Yang et al., 2005). In tropical, subtropical and temperate regions, large reservoirs usually form thermal stratification in the spring, summer and autumn, with high temperatures in the surface layer and low temperatures in the bottom layers (Figure 5b). In cold regions, large reservoirs have thermal stratification in freezing periods, mostly in winter and early spring, with low temperatures in surface layers but relatively high temperatures in the bottom layers (Figure 5b). The seasonal stratification of reservoir waters can, to some extent, alter the natural rhythm of water temperature downstream (Figure 5a), which are characterized by elevated water temperatures in winter, decreased water temperatures in spring and summer, and reduced amplitude of maximum water temperatures (Long et al., 2019; Soleimani et al., 2019). In particular, the largest alterations in downstream water temperature occur in dry seasons (Maheu et al., 2016a). Because of the surface layer discharge mode and non-stratification, the effects of small dams on river water temperature are different from that of large dams (Maheu et al., 2016b). The release of surface water from small dams in spring and summer tends to elevate downstream water temperature (B. W. Webb et al., 2008), which is opposite to water temperature alterations in the summer period caused by large dams (Skoglund et al., 2011). To quantify the alteration to water temperature in dammed rivers, a variety of indicators have been proposed, such as changes in suitable water temperature range of target species, and changes in maximum and minimum water temperatures (T. Li et al., 2021; Maheu et al., 2016a).

Alteration of water temperature regime by dams has serious impacts on river fish habitat (Ahmad et al., 2021; Couto et al., 2021; Grill et al., 2019; Kuczynski et al., 2017; Prats et al., 2010), which directly affect the spawning, migration and growth of fish (Figure 5c). Fish reproduction is the most vulnerable and sensitive to water temperature alterations. Due to the operation of the Xiluodu and Three Gorges dams on the upper Yangtze River in China, the elevated water temperatures in autumn inhibit the reproduction activities of Chinese sturgeon (*Acipenser sinensis*) that usually spawn in autumn, causing the effective breeding quantity to reduce to 0%–4.5% (Z. Huang & Wang, 2018). The warming of water during winter due to reservoir operation in northern Europe and North America leads to delayed timing of spawning and shortened time of egg incubation for winter-spawning Atlantic salmon and brown trout (*Salmo trutta*) (Bohlin et al., 1993; Heggenes et al., 2018; Jonsson & Jonsson, 2009). In addition, a phenological knock-on effect could emerge as a consequence of delays in spawning time (Elliott & Elliott, 2010; Skoglund et al., 2011), resulting in low survival rates of Atlantic salmon and brown trout larvae. In the upper Yangtze River, the ray-finned fish (*Coreius guichenoti*) spawns in late spring and early summer when the critical water temperature exceeds 20°C. The timing of the arrival of this critical temperature is delayed due to the operation of the Xiluodu Reservoir (T. Li et al., 2021). Meanwhile, the warming of water in winter accelerated the development of gonads and advances the time of egg maturity. The joint effects of warmed water in winter and cooled water in early summer thus cause ray-finned fish to miss the historical time window for spawning, resulting in the sharp decline of its population (T. Li et al., 2021; Z. Yang et al., 2021).

The critical temperature threshold (CTT) for fish spawning and the accumulated temperature threshold (ATT) for fish gonadal development have been used to quantify the impact of water temperature alteration on fish reproduction (Figure 5d). The ATT is the minimum accumulated temperature required for gonadal maturity, which is calculated by summing the temperatures higher than the ontogeny temperature in days during gonadal development (Chezik et al., 2014; Honsey et al., 2018). For example, the CTT and ATT thresholds for bronze gudgeon (*Coreius heterodon*) reproduction in the upper Yangtze River were about 18.4 and 1,324.9°C·day, respectively. Operation of large reservoirs results in cooling in spring and summer, and warming in autumn and winter (Long et al., 2019; Y. Tao et al., 2020), which delays the timing for reaching CTT and advances the timing for reaching the ATT (T. Li et al., 2021). It has been shown that elevated temperatures of 2–3°C in winter can have a significant impact on the development of fish gonads (T. M. Farmer et al., 2015; T. Li et al., 2022). When the time to reach the ATT is advanced, fish tend to consume energy in the yolk in order to maintain early exercise and strengthen metabolism (Mcqueen & Marshall, 2017; Wright et al., 2017). When the time to reach the CTT is delayed and becomes behind the time for reaching the ATT, temperature-sensitive fish cannot spawn in a timely manner, resulting in over-maturity of their gonads and thereby a decrease in reproduction (Kennedy et al., 2011; J. King et al., 1998). At present, most studies use the time to reach the CTT as the indicator for reservoir operation

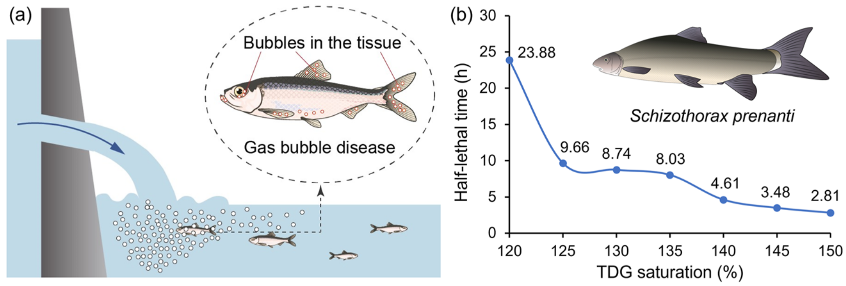

Figure 6. Impact of total dissolved gas (TDG) supersaturation on fish. (a) TDG supersaturation due to reservoir flood dispatch causes fish gas bubble disease. (b) Relation between TDG saturation and half-lethal time of Ya-fish (*Schizothorax prenanti*). The data are available from Y. Wang et al. (2015).

management (Y. Tao et al., 2020; Y. Wang et al., 2016); however, re-matching the time for reaching both the CTT and ATT is key to mitigate the impact of water temperature alterations on fish in dammed rivers.

Despite many studies addressing the effects of river damming on water temperature regimes, there is a great knowledge gap between alterations in water temperature and their impacts on fish, particularly on the whole life cycle of fish migration, growth and food chain. The limited number studies that document the impacts of water temperature alterations on fish physiology, such as sex determination and gonad development, have mostly been conducted at extreme temperature conditions (C. Li et al., 2014; Ribas et al., 2017) instead of natural temperature conditions (Dorts et al., 2012). In addition, understandings to the long-term impact of water temperature alterations on fish phylogeny are insufficient. In the future, climate change may increase the frequency of extreme weather events, which could intensify or offset the impacts of reservoir operations on water temperature. Therefore, the combined effects of river damming and climate change upon water temperature regimes and fish communities demand further investigations.

2.5. Dissolved Gas Supersaturation

Total dissolved gas (TDG) supersaturation refers to the physical condition that the sum of dissolved gas partial pressures in water exceeds the sum of gas partial pressures in the air under local atmospheric pressure (Weitkamp & Katz, 1980). In natural rivers, TDG supersaturation is often caused by a change of water temperature (Bouck, 1984) and water falling (Rowland & Jensen, 1988). Dammed rivers can occur severe TDG supersaturation caused by flood discharge during flooding seasons (Figure 6a), resulting in serious impacts on fish downstream (Ji et al., 2019; Pulg et al., 2016). For instance, the Chief Joseph Dam released flow in excess of the 110% TDG compliance criterion (EPA, 1987) in the Columbia River, causing the downstream Wells Dam to be unable to comply with water quality criteria for 125 of 133 compliance-mandated days in 2012 (Witt et al., 2017). During the flood discharge of the Xiluodu Reservoir in the upper Yangtze River in July 2014, the average TDG saturation of the downstream water was 135%, with a maximum value of 144%, resulting in massive fish mortality in the downstream reservoir (Q. Ma et al., 2018; Zeng et al., 2020). The release of TDG is slowed with increases in water depth and decreases in flow velocity. Thus, in a reservoir cascade system, water with supersaturated TDG from the upstream reservoir is transported to the downstream reservoir and can cause cumulative effects (Q. Ma et al., 2018). TDG supersaturation effects are thus particularly prominent in reservoir cascade systems.

The generation of TDG supersaturation is mainly affected by water pressure, water temperature, bubble pressure, bubble retention time, and aeration concentration. The saturation solubility of gas is positively related to water pressure (J. Feng et al., 2018). When a large volume of water with high head is released from a dam, the water jet entrains a large amount of air to form aerated water, and drops deeply into the energy dissipation pool near the dam (Bertola et al., 2018). Due to high water pressure in the pool, the air carried by the water jet dissolves rapidly, forming TDG supersaturation in the water (Pulg et al., 2016; H. Xue et al., 2018). The degree of TDG supersaturation in the stilling pool is positively correlated to the bubble retention time (Lu et al., 2019; Y. Peng, Lin, et al., 2022). The initial saturation of high dam release has little impact on the generation of TDG supersaturation in the stilling pool, as the water jet is largely saturated after undergoing the process of full gas mixing during the downward discharge (S. Xue et al., 2019). The influence of aeration on the stable saturation of the water body downstream of the dam is also marginal, since the amount of aeration carried by the water jet into the stilling pool is usually sufficient (Qu et al., 2011).

TDG supersaturated water gradually releases the dissolved gas during its flow downstream, with the release rate influenced principally by water depth, flow velocity, wind speed and water temperature (C. Cao et al., 2020; Ou et al., 2016). The release rate of TDG decreases with increase in water depth and decrease in flow velocity. Observations downstream of the Three Gorges, Ertan and Zipingpu dams, China, showed that the release rate downstream of the Zipingpu Dam is the highest, which corresponds to its lowest water depth (J. Feng et al., 2010). Compared to downstream, the upstream side of a dam has larger water depths and slower flow velocities, resulting in lower release rates, as observed in the Kootenay River, North America (Kamal et al., 2018). Increase in wind speed enhances gas transfer at the gas-liquid interface, which accelerates the release of TDG in the water (Chu & Jirka, 2003; J. Huang et al., 2016). Elevated water temperatures promote the thermodynamic movement of gas molecules, which can also increase the release of TDG (S. Liu, 2013; Ou et al., 2016). Suspended particles and water plants provide nucleation and aggregation sites for dissociative gas molecules, enhancing free gas molecules in the water to concentrate and escape in the form of bubbles, and thus promote the release of TDG (J. Feng et al., 2012; Y. Yuan, Huang, et al., 2018).

When TDG saturation exceeds the sum of atmospheric pressure and hydrostatic pressure, gases in the dissolved state in fish tissues and body fluids will precipitate and accumulate to form gas bubbles (Figure 6a). Gas bubbles often appear in the tissue of the head, mouth, fins, and gill arches of fish, or in the capillaries of the gill plates (Lemarie et al., 2011), resulting in gas bubble disease (GBD). GBD could affect the physiology and behavior of fish, such as loss of balance and abnormal buoyancy, leading to fish death in severe cases (Bouck, 1980; J. Huang et al., 2021). Several fish abnormalities caused by GBD have been reported, such as fast swimming, rapid breathing, back and forth movement, and mouth breathing with sticky bubbles (C. Feng et al., 2019; Y. Yuan, Wang, et al., 2018). Bleeding may also appear in tissues of gills, fins, muscles, gonads, and intestinal epithelium (Meyers et al., 2008). These symptoms may impose potential damage on fish, such as tissue necrosis, abnormal growth (Geist et al., 2013), decreased immunity (Schisler et al., 2000), reduced swimming ability (Y. Wang et al., 2017), increased risk of predation and increased buoyancy (Shrimpton et al., 1990a, 1990b), as well as changes in physiological characteristics (Yuan et al., 2021).

The impact of TDG supersaturation on fish is determined by TDG saturation, exposure time, age and species of fish, swimming depth, and behavioral habits. High TDG saturation and long exposure time increases the mortality of fish. The half-lethal time of Ya-fish (*Schizothorax prenanti*) at 150% TDG saturation is 8.5 times shorter than that at 120% TDG saturation (Figure 6b). Repeated exposure of fish to TDG supersaturated water can lead to reduced feeding ability and increased susceptibility to fungal and bacterial infections, thereby further reducing fish tolerance to TDG supersaturated water and affecting fish survival (Brosnan et al., 2016; Huchzermeyer, 2003; Schisler et al., 2000). Fish tolerance to supersaturated TDG also varies between species and growth stages. During the incubation phase of eggs, increased TDG saturation causes a gradual decrease in the hatching rate (N. Li et al., 2019; R. Liang et al., 2013). The tolerance threshold of TDG saturation for the juvenile fish of Ya-fish (Y. Wang et al., 2015), silver carp (*Hypophthalmichthys molitrix*) (Deng et al., 2020), and Chinese sucker (*Myxocyprinus asiaticus*) (L. Cao et al., 2016) is higher than that for the juvenile fish of rock carp (*Procypris rabaudi Tchang*) (X. Huang et al., 2010) and grass carp (*Ctenopharyngodon idella*) (F. Wu et al., 2020). However, when TDG saturation exceeds 135%, the tolerance threshold of TDG saturation for fish is not significantly different between species and body sizes (S. Xue et al., 2019).

With an increase in water depth, the saturation solubility of TDG increases, and the relative saturation of TDG decreases. The release of TDG is also related to turbulence, and thus TDG supersaturation is unevenly distributed vertically (P. Li et al., 2022). Therefore, the tolerance of fish to TDG supersaturation is improved with greater water depths, which is known as the effect of depth compensation (Yuan et al., 2020). Some fish species can avoid TDG supersaturation stress using the effect of depth compensation. For instance, when TDG saturation exceeds 120%, Ya-fish, Chinese sucker and elongate loach (*Leptobotia elongata*) have the ability to detect and avoid TDG supersaturated water in horizontal and vertical directions (Deng et al., 2020). Rainbow trout (*Oncorhynchus mykiss*) has a significantly higher TDG exposure risk than mountain whitefish (*Prosopium williamsoni*), but refuge habitats with sufficient water depth can mitigate exposure risk and GBD. To alleviate the stress of TDG supersaturation, rainbow trout uses depth compensation, with each 1.0 m increase in swimming depth offsetting

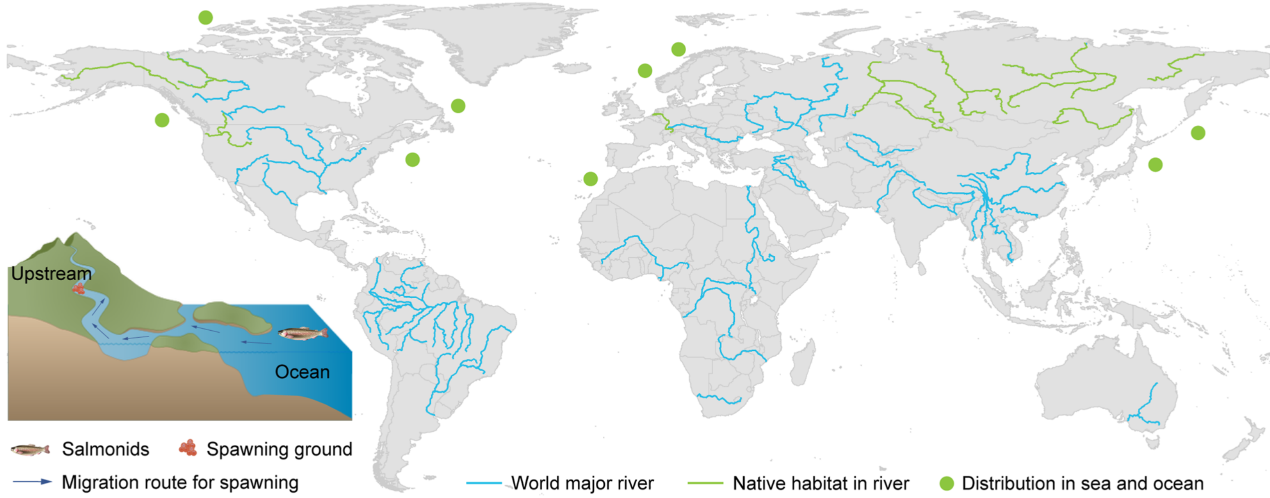

Figure 7. Distribution of salmonids around the world and their migration route for spawning.

9.7% TDG saturation (Pleizier et al., 2020). Therefore, TDG exposure risk and actual risk depend on the interplay between species-specific ecology and dam-induced TDG patterns (Algera et al., 2022).

TDG supersaturation only occurs occasionally during the discharge of floodwaters, when it is usually risky and difficult to conduct field surveys (Bertola et al., 2018; Pulg et al., 2016). Therefore, field observation data of TDG supersaturation are relatively scarce. Also, limited by monitoring technologies, TDG concentration in the near-field of large dams is difficult to measure well (Algera et al., 2022). Scale models in laboratories possess substantial difficulties in simulating the processes involved in generation and release of supersaturated TDG in the field, due to insufficient consideration of the Reynolds and Weber numbers as well as water pressures (P. Li et al., 2022). Therefore, it remains challenging to model the mass transfer process accurately, and predict bubble size as well as size distribution in order to support the development of effective mitigation measures. In addition, the threshold of TDG saturation for fish injury in different tissues requires further investigation. Moreover, fish adopt an avoidance behavior when TDG saturation exceeds their tolerance threshold, and the tolerance of fish to TDG supersaturation is enhanced with an increase in water depth. Previous laboratory studies investigating the response of fish to TDG only consider different TDG concentrations, lacking investigations on depth compensation effects. Therefore, it is essential to further study the effect of depth compensation, as well as fish physiological and behavioral response, in the assessment of TDG supersaturation impacts on fish.

3. River Damming Impacts on Key Fish Species

The interests in the key fish species impacted by river damming vary between different continents. Herein, we focus on salmonids, Chinese carps, sturgeon, eel and lamprey, which have been intensively studied.

3.1. Impact on Salmonids

Salmonids (family Salmonidae) are one of the most popular commercial fishes, providing high-quality protein to people around the world, particularly in Europe and the United States (Phillips & Rab, 2001). They mainly include the genera Salmo and Oncorhynchus, which have received most research concerns (Klemetsen et al., 2003). The genera *Salmo* contains two typical anadromous species, which are the Atlantic salmon and brown trout. Atlantic salmon are mainly distributed along both the east and west coasts of the North Atlantic Ocean, while brown trout is indigenous to Europe, North Africa and western Asia (MacCrimmon et al., 1970; MacCrimmon and Gots, 1979). The genera Oncorhynchus contains the Pacific salmon (*Oncorhynchus tshawytscha*, named Chinook salmon; *Oncorhynchus keta*, named Chum salmon) and Pacific trout (*Oncorhynchus mykiss*, including rainbow trout and steelhead trout subspecies), which mainly inhabit the north Pacific and the coastal rivers of both America and Asia (Figure 7). The Chinook salmon and Atlantic salmon have received most research attentions due to the threats of river dams (Harnish et al., 2014; Hilborn, 2013; Potter & Crozier, 2000).

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The anadromous salmonids migrate to freshwater rivers for spawning and juvenile rearing, and to saltwater oceans for feeding, growing and maturing (Crozier et al., 2021; Groot, 1991). The main life cycle of anadromous salmonids includes a spawning stage (egg, alevin), juvenile stage (fry, fingerling, parr), smolt stage, and adult stage. In the autumn, female salmonids excavate nest pits (called redds) in river bed gravels and spawn eggs into them. The optimal spawning temperature for salmonids is in the range of 6–14°C, and the spawning timing is especially sensitive to temperature changes. Over the winter, the eggs develop into very small salmonids (alevins). In the spring, the alevins swim out of the redds and become fry, with the fry growing into parr that can protect themselves from predators. The parr grows in freshwater for 2–3 years, and transforms into smolts. In the early spring, silvery smolts swim to the ocean and spend 1–2 years maturing into adults. Atlantic salmon is a cool-water species, and the downstream migrating smolts must swim to the ocean before river temperature becomes too warm. River discharge plays an important role once migration is under way, and influences the onset, duration and termination of smolting (Sykes et al., 2009). During the adult stage, salmonids feed in the open ocean for a certain period of time, which differs between different species. In the summer, adult salmonids migrate back to the freshwater, strongly following the migratory route they adopted when leaving the river as smolts (Rivinoja et al., 2001). Increasing flows can facilitate downstream migration of smolts, and flow augmentation during the upstream migration period can improve the survival of migrating salmonids (Connor et al., 2003). The upstream swimming capability of salmonids would be reduced at low (below 10°C) and high (>20°C) temperatures (Alabaster, 1990; Johnsen & Jensen, 1994). Therefore, the connectivity between freshwater and ocean, water temperature, and river discharge are key factors affecting the physiological behaviors of anadromous salmonid across their life cycle (Caudill, et al., 2013).

Dams impede both the downstream and upstream migration of salmonids, resulting in the decline of salmonid populations around the world (Lawrence et al., 2016; Limburg & Waldman, 2009). In North America, dams have been one of the most important factors blamed for the decline of Chinook salmon populations in the Pacific coast of Oregon and British Columbia (P. H. Wilson, 2003). Dams in the upper Columbia River have caused a decline in the abundance, survival and population of Chinook salmon (Levin & Tolimieri, 2001). In South America, both the catch rate and body size of introduced salmonids decreased in several dammed large rivers in Chile and Argentina (Arismendi et al., 2019).

Budy et al. (2002) demonstrated that the survival rates of salmonids in dammed rivers decreased mostly in the smolt-to-adult life stage, rather than in the spawner-to-smolt life stage. When smolts migrate downstream from the dammed river to the ocean, most of them pass the dams through the spillway, the juvenile bypass system, or the hydropower turbines. Physiological or behavioral stresses caused by this passage experience on smolts would result in direct death or a chronic influence, including injury, trauma, diminished physical abilities, and increased susceptibility to predation and disease, which may eventually lead to death at a later life stage (Budy et al., 2002). Compared to rivers with a single dam, rivers with cascade dams make juvenile salmonids experience multiple dam passages, and these cumulative stresses can result in significantly higher mortality (Molina-Moctezuma et al., 2021). For instance, in rivers with three or four dams, the decline of fish populations can increase to exceed 30% (Lawrence et al., 2016).

When adult salmonids migrate upstream to their natal spawning and rearing habitat, their instinct and imprint of the downstream passage experience during their juvenile stage leads them to the bypass channel or the turbines, which increases mortality or results in the situation that they cannot find the correct route, and delays their migration until they determine the correct route (Rivinoja et al., 2001). On average, there is a 70% loss of potential Atlantic salmon spawners during their upstream passage at dams in Sweden (Lundqvist et al., 2008). In Europe, many rivers of the Baltic Sea have lost the natural juvenile reproduction of Atlantic salmon, because river damming has blocked or reduced the access of adult salmon to their spawning grounds (Rivinoja et al., 2001). Over several generations, some of the white-spotted charr (*Salvelinus leucomaenis*) in Japan in dammed-off areas no longer migrate to the sea and become resident fish due to habitat fragmentation, which leads to a decrease in their spawning and populations (Morita et al., 2009). Therefore, river fragmentation caused by dams can lead to the increasingly direct or delayed mortality of salmonids, and thus may severely reduce their population.

Hydrological alterations caused by dam operations may lead to the decline of salmon populations (E. J. Ward et al., 2015). During the spawning period, the female and male Chum salmon that remain on their redds would increase swimming activity, reduce digging activity and leave their redds when flow velocities are above a threshold of 0.8 m/s. Therefore, artificial hydro-peaks would lead to a decline in spawning rates (Tiffan et al., 2010).

A significant reduction in discharge under the dam could lead to the stranding of salmonid fry and increase their mortality (E. Bell et al., 2008). For example, dam operations result in dewatering of Chinook salmon redds, causing the mortality of eggs and larval fishes (Harnish et al., 2014; Ostberg & Chase, 2022; Young et al., 2011). Regulated flows, even if they do not dewater the redds, can still impact on redd habitats for embryos survival and development by altering hyporheic exchange of heat and dissolved oxygen (Figure 2d) (Bhattarai et al., 2023; Martin et al., 2020). The upstream migration of adult salmonids may be disrupted by the seasonal and weak variation in spillway discharge from the dam (Rivinoja et al., 2001). Therefore, alterations to hydrological regime caused by dams may result in declines in spawning rate, survival of fish eggs and juveniles, and migration of adult salmonids, thus decreasing the populations of salmonids.

Dam construction can cause the historical spawning grounds of salmonids to become warmer, which makes the hatchery juveniles progress their life history at an earlier time and thus swim to areas with relatively cool water temperatures and lower growth opportunities, leading to a decline in their survival and populations (Connor et al., 2002). However, rising water temperatures in springtime caused by dam operation can negatively affect the rate of salmonid egg incubation, such as Chinook salmon (Dusek Jennings & Hendrix, 2020). Compared to the daily mean temperature or threshold temperature, temperature experience (accumulated thermal units, ATU) has more effects on the onset, duration and termination of downstream migration of Chinook salmon smolts (Sykes et al., 2009). Stich et al. (2015) found that dams decreased the ATU for smolts, thus delaying the time to initiate their downstream migration. In addition, dams as barriers along migration routes can delay or prolong the migration of smolts, which may result in a mismatch with migration-timing adaptations. For instance, water temperatures in downstream reaches become warmer in the spring due to dam operations, which delays the downstream migration of smolts of Atlantic salmon. Consequently, the delayed smolts may face a situation that the water temperature further increases to a lethal or near-lethal level for smolts (Marschall et al., 2011). Compared to fish in free-flowing rivers, upstream-migrating fish in impounded systems could encounter potential thermal barriers in fishways. For instance, fishways offer opportunities for upstream migration of adult Chinook salmon, but the unfavorable water temperature gradient in the fishway caused by thermal stratification in reservoirs presents an obstacle to the upstream migration of individuals (Caudill et al., 2013). Therefore, the altered water temperature regime caused by dams negatively affects egg hatching, the downstream migration of smolts, and the upstream migration of adult salmonids in fish passages.

The TDG supersaturation caused by flood discharge of dams has little impact on juvenile and adult salmonids (Geist et al., 2013; Muir et al., 2001). There is little potential of negative effects of TDG supersaturation on populations of adult Chinook salmon, although fish tissues are probably damaged by the dissolved gases (E. L. Johnson et al., 2005, 2007). Among the fish that pass through dam spillways, the survival of juvenile salmonids is the highest (Beeman & Maule, 2006; Muir et al., 2001).

Overall, most studies focus on the impact of dam construction on the spawning process and migration of salmonid smolts. However, sufficient attention should also be devoted to investigating the direct impact of altered flow regimes and water temperatures on the upstream migration of adult salmonids, which can provide specific evidence to improve conservation measures for adult salmonids during upstream migration. Meanwhile, natural factors such as climate and oceanic conditions also affect the physiological behavior of salmonids. Dam-induced and natural factors could interact with each other, resulting in nonlinear interdependence (Goodwell & Bassiouni, 2022; Ye et al., 2015). This complex interaction highlights the necessity to better understand how co-varying dam-induced and natural factors influence the physiological behavior of salmonids across their whole life cycle. Engineering mitigation measures have been used to reduce the adverse influence of dams on salmonids. However, it is controversial whether these mitigation efforts are effective if differential mortality rates of salmonids occur for reasons unrelated to river damming (Rechisky et al., 2013; Welch et al., 2008). In the future, long-term observations of upstream and downstream salmonid are needed to determine whether dams are the major cause for the decline of salmonids in impounded rivers.

3.2. Impact on Chinese Carps

The four major Chinese carps (FMCCs) are grass carp (*C. idellus*), black carp (*Mylopharyngodon piceus*), silver carp (*H. molitrix*) and bighead carp (*Aristichthys nobilis*). FMCCs are freshwater fish whose adults migrate upstream to spawning sites during flood seasons and spawn semi-buoyant drifting eggs (Figure 8). The fertilized eggs drift a long distance for development, and then juvenile fish swim into riparian lakes, which serve as nursery

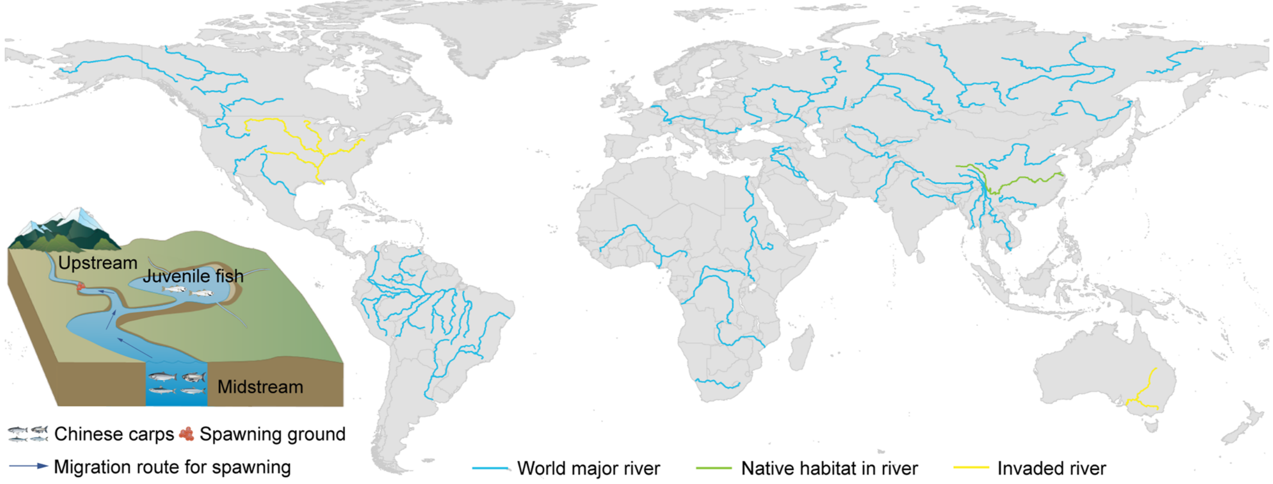

Figure 8. Native and invading distribution of Chinese carps around the world and their migration route for spawning.

habitats (Q. Chen et al., 2021; W. Xu et al., 2020; B. Yi et al., 1988). The spawning activity of FMCCs requires a minimum flow velocity to trigger the release of eggs (Q. Chen et al., 2021), and the drifting eggs require a suitable flow velocity to keep them suspended (Garcia et al., 2013; M. Li et al., 2013; Q. H. Yang et al., 2014; P. Zhang et al., 2021). High flow events are the most visible physical phenomena associated with the reproductive success of FMCCs (Coulter et al., 2018; Embke et al., 2016). Under natural conditions, adult fish usually initiate spawning activity when the water level continues to rise for 0.5–2 days, and reduce or even cease spawning when water levels begin to recede (B. Yi et al., 1988). In China, the Yangtze River basin provides the principal habitats and spawning sites for the FMCCs, although they are widely distributed across many parts of China. The FMCCs in the Yangtze River are the dominant natural germplasm resource, which sustains the gene diversity and maintains freshwater fish aquaculture (J. Wang, Li, Duan, Chen, et al., 2014). Prior to the construction of the Three Gorges Dam, there were 30 spawning sites for FMCCs in the mainstream Yangtze River (C. Tang et al., 2022), with the middle reach of Yangtze River being the main reproduction area. There are 12 spawning sites scattered along the 380 km long reach from Yichang to Chenglingji, producing about 43% of the total eggs in the Yangtze River (Y. Yi et al., 2010).

FMCCs play a vital role in providing high-quality animal protein, ensuring national food security, as well as promoting rural economic development in China (Ban et al., 2019; D. Li, Prinyawiwatkul et al., 2021). However, FMCCs are an aggressive invasive species in other countries (D. Li, Prinyawiwatkul, et al., 2021), as shown in Figure 8. The silver carp and bighead carp, jointly known as Asian carp, were first imported to North America in the 1970s as aquaculture fishes. Due to their rapid growth rates and lack of natural predators, they have established dense populations in the Mississippi, Ohio, Missouri and Illinois Rivers, and may pose a threat to the Great Lakes (Heer et al., 2019; Wittmann et al., 2014; Zhu et al., 2018). In Europe, bighead carp are found to have been widely recruited in northeastern Italy, demanding serious efforts to limit the spread and establishment of reproducing populations (Milardi et al., 2017). In Australia, Asian carp impose significant impacts throughout the Murray-Darling basin and other freshwater systems (Marshall et al., 2018).

River damming can block or delay reproductive migration, affect fish assemblages, impair spawning habitat conditions, and thus reduce the recruitment of FMCCs. After the impoundment of the Three Gorges Reservoir (TGR) in 2003, the larval abundance of FMCCs in the middle reach of the Yangtze River declined sharply to less than 20% of the pre-dam abundance (P. Zhang et al., 2021), and the eggs and larvae in the lower reaches of the Yangtze River declined to 0.34 billion, accounting for only 13% of the pre-dam amount (M. Li et al., 2016). The Three Gorges Dam reduces river connectivity, preventing FMCCs migration (P. Zhang et al., 2021). Loss of connectivity in dammed rivers also restricts the gene flow between fish populations located upstream and downstream of a dam, affecting population genetic structure. Since the construction of the Gezhouba Dam and Three Gorges Dam, significant genetic differentiations have appeared in the grass carp populations between the upper and middle reaches of the Yangtze River, which might stimulate population divergence (Zhao et al., 2011). Although spawning grounds for FMCCs downstream of the dam remain after impoundment, eight spawning grounds in the reservoir have been lost due to establishment of the lentic ecosystem (Y. Yi et al., 2010). Reservoir operations cause direct changes in the annual hydrograph and thus water depth and flow velocity, which affect the spawning activity of FMCCs (Duan et al., 2009; W. Jiang et al., 2010; Z. Wang et al., 2013). Downstream of the Three Gorges Dam, the suitable flows required for the reproduction of FMCCs are suggested to start from 12,500 m^3/s on the day when a spawning event begins, and gradually increase to 18,600 m^3/s at day 4 when spawning actions reach their peak, and then quickly drop to support hatching and larvae survival (Q. Chen et al., 2021). However, this flow process is mostly not met during the spawning period of FMCCs.

Water temperature has strong impacts on the reproduction of FMCCs. Laboratory studies and field measurements have shown that the minimum water temperature threshold for gonad development of FMCCs is 18°C, and the ideal water temperature range for spawning is between 21 and 24°C (Embke et al., 2016; M. Li et al., 2013; Y. Yi et al., 2010). There is also a significant correlation between spawning time and the arrival date of the cumulative temperature needed for gonad development. The initial date of FMCCs spawning in the Yangtze River has been delayed from early May to middle June since operation of the TGR in 2003. The main reason for this delay is that the water temperature downstream of the dam drops by 2–4°C from March to May, which is the critical period for gonad development of FMCCs (J. Wang, Li, Duan, Luo, et al., 2014), and thus postpones the arrival date of their gonad maturity. In addition, flood release could cause the TDG saturation to exceed 120% in the downstream reach of the Three Gorges Dam during the spawning periods of FMCCs, resulting in the dispersing larvae being highly vulnerable to the effect of TDG supersaturation. Dead larvae were found due to GBD during the early operation stage of the Gezhouba Dam between 1981 and 1984 (L. Liu et al., 1986).

However, as invasive species in some regions such as the North America, a viable strategy to prevent the spread of FMCCs and reduce their population is to manage the existing dams and barriers to limit their dispersion (Fritts et al., 2021; Whitledge et al., 2019). In the upper Illinois River, reducing gate openings of the locks and dams during the late spring and summer could provide opportunities to avoid the upstream migration of bighead carp, and thus limit their recruitment into the upper section of the river (Lubejko et al., 2017). Rather than attempting to directly block the migration route through dams, another option would be to encourage adult carp to spawn in the reaches that have suitable spawning sites but lack adequate hydrological conditions to further support embryo development. Such action could be implemented by adaptive management of hydraulic engineering structures in rivers (Coulter et al., 2018; Cupp et al., 2021; Prada et al., 2020).

Previous studies attribute the primary cause of decreases in the population of FMCCs in the Yangtze River to the construction of dams. However, it has also been argued that intensive fishing contributes greatly to their decline (D. Chen et al., 2009). However, there are few published data on long-term trends in FMCCs catches, making it difficult to assess whether dam construction or overfishing plays the major role in the degradation of natural FMCCs resources. Meanwhile, a series of physical barriers, including dams, behavioral deterrents and electric dispersal barriers, have been applied to block migratory pathways of FMCCs in the rivers in which they have become invasive, although in practice the effectiveness of this approach is limited. There remains a knowledge gap in understanding the associated hydrological mechanisms that affect the spawning behavior and early life development of FMCCs. Studies have indicated that a warm winter-spring period advances the expansion of Asian carp by altering thermal characteristics to be more favorable for their growth and lessening the time for competitive interaction with invasive mussels (Alsip et al., 2020; M. Li et al., 2013). It has been observed that the surface water temperature of the Great Lakes is warming faster than the global rate (Collingsworth et al., 2017; O'Reilly et al., 2015), and there is thus a great value to investigate whether climate change will increase the risk of invasion by Asian carp in this region.

3.3. Impact on Sturgeon

Sturgeons are one of the earliest extant vertebrates, and play an important role in the evolution of fishes and even all vertebrates (Shen et al., 2020). There are 27 species of sturgeons that belong to the Acipenseridae and Polyodontidae families. The family Acipenseridae mainly includes Chinese sturgeon (*A. sinensis*), Russian sturgeon (*Acipenser gueldenstaedtii*), Dabry's sturgeon (*Acipenser dabryanus*), Atlantic sturgeon (*Acipenser oxyrinchus*), ship sturgeon (*Acipenser nudiventris*), sterlet (*Acipenser ruthenus*), and starry sturgeon (*Acipenser stellatus*). The family Polyodontidae, which is commonly called paddlefish, includes the American paddlefish (*Polyodon spathula*) and Chinese paddlefish (*Psephurus gladius*). The number of wild sturgeons in the world has decreased significantly in recent years, due to the degradation of natural habitats, dam construction, and overfishing (Billard

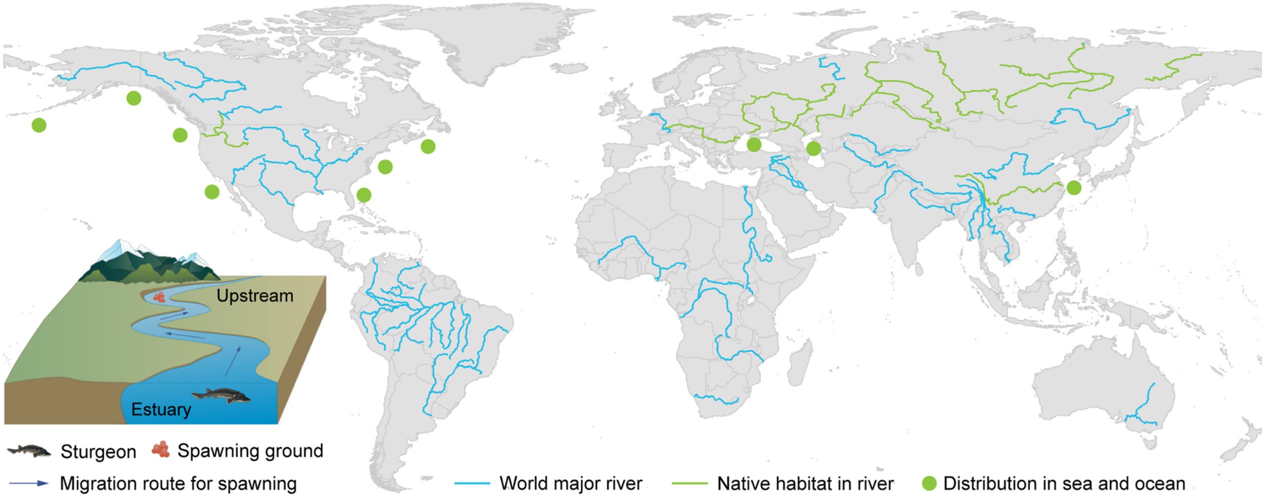

Figure 9. Distribution of sturgeon around the world and their migration route for spawning.

& Lecointre, 2000; T. Webb & Meyer, 2019). Sturgeons are typically anadromous fish that spend most of their lives in the ocean and return to freshwater to spawn (Figure 9). They lay adhesive eggs in rivers with fast currents and gravel beds. They are subcooled fishes, which prefer to live in water with relatively low temperature (Billard & Lecointre, 2000; McDowall, 1997; Siddique et al., 2016), and are mainly found in Eurasia and North America (Du et al., 2020). According to the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species, Dabry's sturgeon has been considered extinct in the wild, Chinese paddlefish has been considered completely extinct, and 85% of the extant 25 species, such as Chinese sturgeon, Russian sturgeon, starry sturgeon and sterlet, are endangered (Brevé et al., 2022; IUCN, 2022; Lenhardt et al., 2006; H. Zhang, Jarić, et al., 2020).

Chinese sturgeon has lived in the Yangtze River for about 140 million years, and is often considered a living fossil. It is a demersal fish species that usually breeds in river reaches with fast currents and gravel beds (Z. Huang & Wang, 2018). Every year, this migratory fish travels 2,000 miles from the East China Sea to its spawning grounds in the Yangtze River (D. Cheng et al., 2015). The spawning season of Chinese sturgeon is from October to November, and spawning occurs at water temperatures between 15.3 and 20.0°C, with the optimal water temperature for spawning being 18.0–20.0°C (Y. Wang et al., 2020). Atlantic sturgeon is one of the seven sturgeon species found in North America, and extends from New Brunswick, Canada, to the eastern coast of Florida, USA. Atlantic sturgeon spawns in the spring, and the water temperature requirement for spawning is 13.3–23.0°C (Hager et al., 2014). It spawns in running waters with rocks, pebbles and other hard objects on the bed, or in pits and pools under waterfalls (Popov, 2017). Russian sturgeon is widely distributed in the Caspian Sea, the Sea of Azov and the Black Sea, as well as in the rivers flowing into these waters (H. Song et al., 2022). The water temperature requirement for the spawning of Russian sturgeon is 12–14°C (Elhetawy et al., 2020). Most of the spawning activity of Russian sturgeon takes place in the sloughs of main channels, with a few individuals spawning in the high tide zone. Sterlet is distributed in the Black Sea, Caspian Sea, Yenisei River and Ob River in Russia. The optimal water temperature range for sterlet spawning is 13–16°C (Ponomareva et al., 2020), and the typical spawning grounds of sterlet include riverbed and roaming beach formed by spring water (Lenhardt et al., 2006). Juvenile sterlets are often found in groups in shallow water, while individual adults are scattered in deeper water for feeding. White sturgeon is the largest of the eight sturgeon species found in North America. White sturgeon inhabits the Pacific Ocean from northern Baja California of Mexico to the Aleutian Islands in Alaska, and the large rivers flowing into the Pacific Ocean between Monterey, California and Alaska. White sturgeon exhibits freshwater amphidromy, although evidence suggests that only small proportions of their populations live in marine environments. White sturgeon is an iteroparous broadcast spawner, spawning in the spring and early summer when water temperatures are between 7 and 18°C (Counihan & Chapman, 2018). Therefore, water temperature and riverbed substrate are major factors that affect sturgeon life cycles, including spawning migration and reproductive processes.

Global dam construction has blocked the migration routes and damaged the spawning habitats of sturgeons, leading to a significant reduction in their populations. The completion of Gezhouba Dam in 1981 and the Three Gorges Dam in 2003 on the Yangtze River blocked the migration routes, cut off the spawning grounds and affected the spawning time, spawning size as well as spawning frequency of the Chinese sturgeon, Dabry's sturgeon and Chinese paddlefish, leading to significant reductions in their populations (Boscari et al., 2022; H. Zhang, Jarić, et al., 2020). The Gezhouba Dam shortened the migration distance and reduced the capacity of new spawning grounds of Chinese sturgeon, resulting in the number of hatched larvae being only 25% of that before dam construction (Z. Huang, 2019; J. Tao et al., 2009). The construction of the Volgograd Dam on the Volga River, Russia, has destroyed the natural spawning area of the Russian sturgeon, starry sturgeon and Beluga sturgeon, which caused mass mortality of these species. The Volgograd Dam has reduced the area of Russian sturgeon spawning grounds by 80% (Secor et al., 2000), and the limited spawning area led to high spawning densities, resulting in egg mortality rates of up to 60% (Popov, 2017). In the Don River, Russia, dams cut off the main path of Russian sturgeon migrating to their spawning grounds, resulting in a sharp reduction in their spawning areas that are only located downstream of the dam (Boldyrev, 2018). At present, Russian sturgeon with natural reproduction only exists in the undammed Ural River in Russia and Kazakhstan. In North America, the Eddyville Dam on the Hudson River has blocked the migratory routes of shortnose sturgeon (*Acipenser brevirostrum*), leading to a significant reduction in its population and hence its inclusion in the Endangered Species Act (T. Webb & Meyer, 2019). In the Great Lakes region, dam induced sedimentation in many tributaries has led to a reduction in spawning grounds and juvenile habitats of lake sturgeon (*Acipenser fulvescens*), posing great challenges to the restoration of their population (C. C. Wilson et al., 2022). In Europe, the construction of the Djerdap I and Djerdap II dams blocked the migration of sturgeon in the Danube River, which seriously reduced populations of the ship sturgeon and Atlantic sturgeon (Lenhardt et al., 2006). Therefore, river damming seriously compromises the connectivity of sturgeon habitats worldwide, leading to significant declines in successful spawning and egg hatching rates, and thus severely decreasing the population of sturgeons.

Water temperature is a primary factor affecting the migration of sturgeons, and determines their spawning time. However, reservoir operations can alter water temperature regimes and thus affect the migration and spawning of sturgeon (Y. Wang et al., 2020; H. Zhang et al., 2019). In the Yangtze River, the patterns of water temperature have been temporally and spatially altered by reservoir operation, which leads to the degradation of gonad development and delays the spawning of the Chinese sturgeon (Z. Huang & Wang, 2018; H. Zhang et al., 2019). The TGR and Xiluodu Reservoir in the upper Yangtze River have reduced the effective breeding quantity down to below 4.5% by elevating the water temperature that inhibits breeding activity during the spawning season. The cumulative effect of the cascade dams, including Wudongde, Baihetan, Xiluodu, Xiangjiaba, Three Gorges and Gezhouba, has led to an ongoing decline in the abundance of adult Chinese sturgeon in the Yangtze River and the sea (Chang et al., 2017; Z. Huang & Wang, 2018). In the Sacramento River, USA, the optimal water temperature for Chinook salmon spawning is 12°C, while the optimal water temperature for green sturgeon (*Acipenser medirostris*) growth is 19°C. At present, the Keswick Dam regulates the water temperature of the river in winter to match the suitable spawning temperature for the endangered Chinook salmon, causing the cold water to extend to the habitat of the green sturgeon, whose growth is thereby greatly affected (Zarri et al., 2019). In the Columbia River, cascade dams have fragmented the spawning habitat of white sturgeon in the mainstream into short sections connected by long-distance impoundments. Due to differences in dam operation and geographically local environments, the water temperature in different river reaches varies greatly, which in turn leads to differences in the spawning temperature and time of white sturgeon in different river sections. In the lower Columbia River, the spawning of white sturgeon downstream of the Bonneville Dam begins at a water temperature of 8°C, but spawning in the three furthest downstream dam tailraces begins when water temperature reaches at least 10°C. In addition, spawning occurs earlier downstream than upstream in the Columbia River during the spring season (Counihan & Chapman, 2018; Péril, 2004).

Dam construction alters the natural hydrological regimes of rivers, and thus affects the growth and reproduction of sturgeons. The reduced downstream flow results in limited lateral connectivity to the floodplain, which adversely affects habitat availability and reproduction of sturgeons (F. He et al., 2021). In the Kootenai River, the demand discharge during the spawning period of the white sturgeon is 1,416–2,832 m^3/s; however, the peak flow is reduced usually to 250–450 m^3/s due to operation of the Libby Dam, which has seriously affected the reproduction of white sturgeon (Paragamian et al., 2001). River impoundment reduces flow velocity and possibly causes hypoxia in the transition zone of the reservoir upstream, which exposes the pallid sturgeon (*Scaphirhynchus*

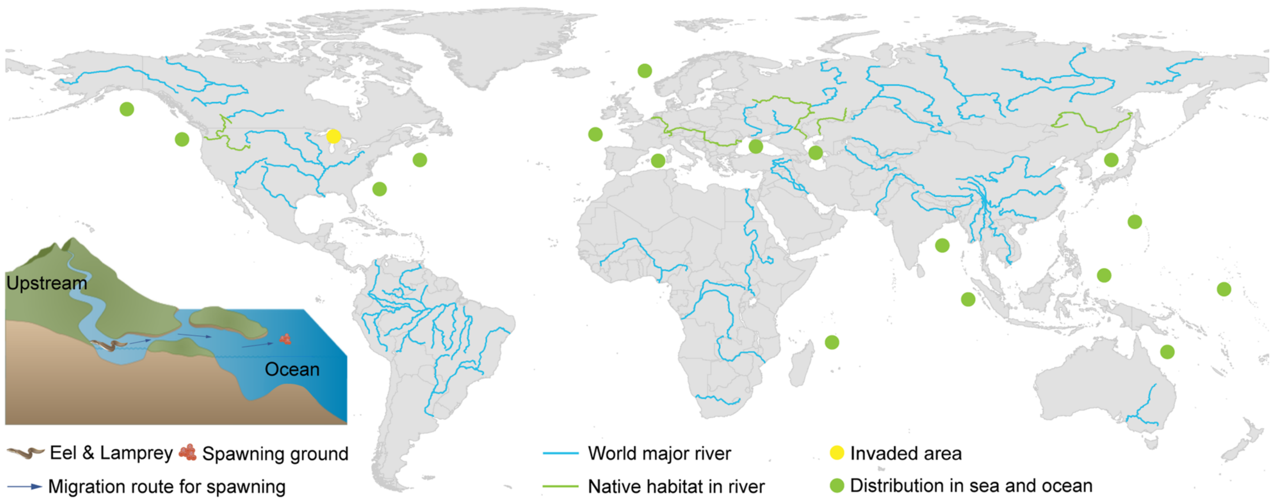

Figure 10. Native and invading distribution of eel and lamprey around the world and their migration route for spawning.

albus) to low oxygen conditions and thus results in their high mortality (Guy et al., 2015). However, dedicated flow regulations can in some cases provide suitable condition for migration and spawning of sturgeon. For example, intermittent flood pulsing through dam operation to achieve key water temperature thresholds may have better facilitated the upstream migration and spawning of shortnose sturgeon adults (Vine et al., 2019).

Previous studies claim that the barrier effect of dams is the primary cause for the decrease in Chinese sturgeon populations. However, new spawning grounds for Chinese sturgeon may have formed downstream of the Gezhouba Dam (P. Zhuang et al., 2016), indicating that blockage by the dam has not completely hindered the natural reproduction of this species. Therefore, it is essential to investigate the impacts of other factors, such as altered water temperature regimes, in addition to the blockage of migration routes, on the spawning of Chinese sturgeon. To date, most studies focus on the impacts of river damming on the migration and spawning of sturgeon, but it is also important to understand the impact on other life stages, such as foraging and overwintering.

3.4. Impact on Eel and Lamprey

Eels (genus *Anguilla*) and lamprey (genus *Lampetra*) are among the most valuable fishery species around the world (P. R. Almeida et al., 2021; FAO, 2015). There are 19 species or subspecies of eels being identified globally (Righton et al., 2021), of which 17 are scattered throughout the Indo-Pacific and the other two species are distributed in the Atlantic Ocean (Figure 10). At present, several species of eel have been listed as "endangered" or "critically endangered" in the wild (Jacoby et al., 2015; Vié et al., 2009), including the European eel (*Anguilla anguilla* L.), American eel (*Anguilla rostrata*) and Japanese eel (*Anguilla japonica*). Lampreys are often misidentified as eels because of their similar appearance; however, lampreys belong to the Order Petromyzontiformes whilst eels belong to the Order Anguillifomes (Renaud, 2011). Most lampreys, such as the sea lamprey (*Petromyzon marinus*), European river lamprey (*Lampetra fluviatilis*), Pacific lamprey (*Entosphenus tridentatus*), and Caspian lamprey (*Caspiomyzon wagneri*), are anadromous parasitic fish. The sea lamprey is a notorious invasive species in the Laurentian Great Lakes (Figure 10), and has devastated the fisheries of whitefish and lake trout (McDonald & Kolar, 2007; Zielinski et al., 2019).

The life stages of eels comprise eggs, leptocephalus (larva), glass eel (post-larva), elver (juvenile), yellow eel (non-mature adult), and silver eel (migratory adult). At each life stage, eels exhibit distinct morphologies (Tsukamoto et al., 2011). The larva of eels is notably larger than that of almost all the other fish species, and their morphology is well equipped for both passive and active swimming in their oceanic migration (Righton et al., 2021). Eels usually form their sex at the silver stage (Miller & Tsukamoto, 2016). Unlike salmonid and sturgeon, eels have reverse migration and spawning behaviors, as they grow up in freshwater and return to the ocean for reproduction (Figure 10). They typically dwell in seawater during the life stages of eggs, leptocephalus and glass eel, and in brackish and freshwater during the life stages of elver, yellow eel, and silver eel (Haro, 2014). The spawning of temperate eels, such as European eel and American eel, occurs in the Sargasso Sea (Béguer-Pon et al., 2015; Schmidt, 1923; Tucker, 1959), which has been recently reconfirmed by genetic analyses (Barth et al., 2020). The eggs and spawning adults of Japanese eel have only been discovered within a restricted area along the seamount chain of the Pacific West Mariana Ridge (Tsukamoto et al., 2011). In contrast to the distribution of spawning zones, the habitats of eels during the entire growth stage are flexible, encompassing all saltwater and freshwater areas, because eels can adapt to diverse environmental conditions and different dietary niches (Tesch, 2003). Lampreys have an anadromous migration habit and a wide habitat range (Moser et al., 2021). Some lampreys are life-long freshwater dwellers, whilst others are seawater dwellers that migrate to freshwater to spawn (Renaud, 2011). The sea lamprey breeds anadromously in basins of Western Europe and eastern North America, and swims into the North Atlantic and Western Mediterranean. The Korean lamprey (*Eudontomyzon morii*) is a small freshwater species that is mostly distributed in the Yalu River as well as some mountain rivers in northeast China, North Korea and the Russian Far East (Renaud, 2011).

Although eels and lampreys have strong acceleration and high mobility (Tytell & Lauder, 2004), they cannot jump over obstacles and their burst swimming speed is relatively low (Kemp et al., 2011). The barrier effect caused by dams is thus the most immediate impact on eels and lampreys, impeding their migration between spawning and rearing grounds. The downstream passage through turbines and dams leads to the high disorientation and mortality of breeding silver eels, which results in significant declines in spawning rates and populations. It has been reported that 75% of eels are delayed in their downstream migration, and up to 65% are definitively halted by dams (Besson et al., 2016). Eels are especially vulnerable to screens and turbines due to their anguilliform morphotype (Kerr et al., 2015), and thus hydroelectric facilities in dams can cause sublethal injury and direct mortality to migrating adult eels (Bruijs & Durif, 2009). In rivers with cascade dams, the cumulative effect may result in the level of overall escape of eels not reaching the required conservation criteria, which is 40% for silver eel in European countries (Pedersen et al., 2012). Habitat fragmentation caused by dams also impedes the upstream migration of eels (Jellyman, 2022). More than 15,000 dams have been constructed in the coastal drainages of the North Atlantic, obstructing direct access to 87% of rivers and streams flowing into the Atlantic, and hence drastically reducing the inland extension of American eels (Jellyman, 2022; Miller & Casselman, 2014). The decline of the European eel (Bevacqua et al., 2015), American eel (Kwak et al., 2019) and Japanese eel (J. Z. Chen et al., 2014) in turn affects the ontogenetic stage and physiological traits of eels (Righton et al., 2021). The barrier effect of dams is also the main reason for the decline in the global population of most lampreys, such as about 80% loss of sea lamprey in the Iberian Peninsula and Caspian lamprey in the Volga River, leading to the collapse of associated commercial fisheries (Atkinson et al., 2020; Jellyman, 2022), and strong decline of Pacific lamprey in the Columbia and Snake Rivers (Moser & Close, 2003).

Eels have specific habitat preferences and requirements, with their habitat selection involving water temperature, water depth, substrate, salinity, flow velocity, oxygen concentration, vegetation cover, prey availability, and predation threat (Jellyman, 2022; Righton et al., 2021). Water temperature appears to be an important factor throughout the whole lifespan of eels, as they grow faster and mature earlier in warm waters (Tesch, 2003). Water depth can affect the habitat quality of eels, since small eels tend to favor shallow waters and large eels prefer deep waters (Jellyman, 2022; Jellyman & Arai, 2016). In particular, large eels spend the daytime in deep waters and night time in shallower waters (Righton et al., 2021). Eels choose different types of substrates in different seasons, preferring soft substrates with abundant organics or silts in the spring, muddy substrates in the summer, and rubble substrates in the autumn (Tomie et al., 2016). Their substrate preference varies with body size, with smaller eels preferring coarse substrates (gravels, cobbles, and boulders) and larger eels preferring fine substrates. These habitat variations are likely due to the combined effects of changes in physical space requirements and prey preference with the increasing body size of eels (Lloyst et al., 2015).

Alterations of water temperature regime, flow velocity and riverbed substrate due to river damming can have dramatic effects on the living conditions of eels (Righton et al., 2021). The release of hypolimnetic water from reservoirs has a cooling effect on water temperature in summer and thus degrades the growth of eels downstream of dams (Maheu et al., 2016a). The migration speed and route selection of eels are affected by flow velocity, and thus decreases in flow velocity due to dams may cause failure of their migration (Jansen et al., 2007). During downstream migration, eels usually swim actively with a speed of 0.3–1.2 m/s (Behrmann-Godel & Eckmann, 2003), and those that manage to migrate downstream pass over the dam crest only when the flow velocity is high (Besson et al., 2016). Artificial fluctuations in water depth due to dam operations inevitably affect the living environment of eels (Righton et al., 2021). Dams are known to cause substrate-sorting effects and thus result in local habitat homogeneity, which limits the diverse substrate requirements of eels (Naganna

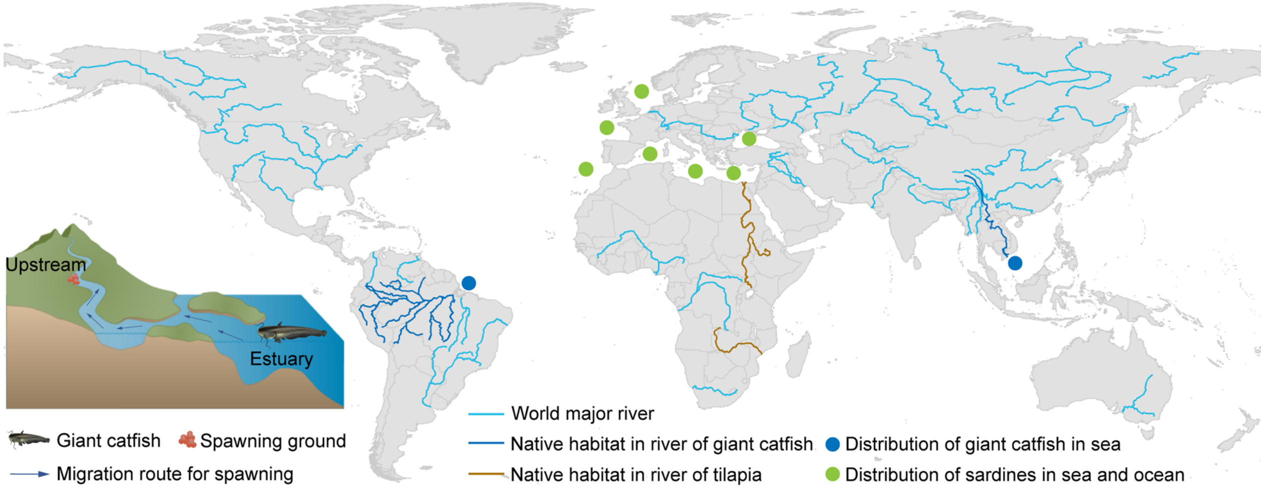

Figure 11. Distribution of giant catfish, tilapia, and sardines around the world, as well as migration route for spawning of giant catfish.

& Deka, 2018). Dams intercept sediment and reduce downstream substrate availability for the critical life stages such as nesting and refuge of eels (Černý et al., 2003). The decreased sediment flux can also cause delta recession (Baisre & Arboleya, 2006), which increases the susceptibility of eels to natural disturbances (Day et al., 2007; O'Connor et al., 2015). The introduction of non-native species due to river damming squeezes the habitat and even leads to extinction of native eels and lampreys (Marohn et al., 2014). Nonetheless, there are also some marginal benefits of river damming for eels. Reservoir eutrophication has been reported to increase chironomid populations, which comprises the major food of eels (Aprahamian et al., 2021). The increase in plant and zooplankton production caused by reservoir eutrophication is considered to provide an additional benefit to the populations of eels (Bunting et al., 2007). In some cases, the isolation created by dams can be beneficial to eels by preventing the introduction of contaminants, parasites and diseases into their habitats (Liermann et al., 2012; Righton et al., 2021).

Limited by monitoring technology, comprehensive and reliable data on the migration routes and spawning grounds of eels are sparse, which hinders accurate assessments of the impact of river damming on eels. To date, relevant studies outside of Europe, the Americas and Japan are scarce, and the lack of information across Africa is a severe barrier to the appropriate assessment of the conservation status of eels on a global scale (Righton et al., 2021). In addition, when compared to intensive studies concerning the impacts of river damming on eels, similar research on lampreys needs to be enhanced. Although an individual small dam has much less impact on eels and lampreys than a large dam, the cumulative impact of many small dams requires adequate attention, given their widespread and intensive distribution (Lehner et al., 2011). Climate change could alter water temperature regime and thereby induce impacts on the habitat of eels and lampreys, and is regarded as one of the least understood risks to the species worldwide (Jacoby et al., 2015).

3.5. Impact on Other Fish Species

River damming also impacts on other fish species, which have less socioeconomic and cultural value, such as giant catfish, tilapia and sardines (Figure 11).

Giant catfishes are widely known for their giant bodies and mysterious trails in deep water areas, and they can grow to more than two m in length (Boulêtreau & Santoul, 2016). Giant catfish species mainly include the Mekong catfish (*Pangasianodon gigas*, *Pangasius krempfi*, *Pangasius sanitwongsei*, and *Pangasius mekongensis*), Amazonian catfish (*Brachyplatystoma rousseauxii* and *Brachyplatystoma filamentous*), and European catfish (*Silurus glanis*). Megafaunal species have disproportionate per capita effects on community structure and ecological processes, and any shift in their abundance is likely to affect food webs and ecosystem functions (Malhi et al., 2016). Giant catfishes generally spawn in freshwater rivers and live in estuaries with long-distance migration (Figure 11). The Mekong catfish migrates long distances to spawn, spending much of their lives in the brackish waters of the Mekong Delta and in the South China Sea near Vietnam before returning to spawn in the Mekong River in Laos and Thailand (Hogan et al., 2007). Amazonian catfish adopt a basin-wide migratory life cycle between the Andean piedmont and the Amazon estuary, which makes them possess the longest river migration that may total up to 12,000 km in the case of *Brachyplatystoma rousseauxii* (Duponchelle et al., 2021). Amazonian catfish are of high commercial importance to fisheries of the Amazon River basin, forming a major ecosystem service provided by this river system (Fraser, 2018). Due to the impact of dam construction, giant catfish, and especially long-distance migratory species such as the Mekong and Amazonian catfish, have become endangered in the wild, threatening the stability of ecosystem structure due to their top-tier status in the food web (Duponchelle et al., 2021; Fraser, 2018; Hermann et al., 2016; Hogan, 2011). Dams on the Mekong River have disrupted the migration and spawning of giant catfish, and the situation may become worse as Laos plans to build more dams on the mainstream of the Mekong River (Soukhaphon et al., 2021). The migration route and access to a substantial portion of the spawning grounds of the Amazonian catfish in the Madeira River are blocked by two dams built a decade ago, which profoundly affects the populations and fisheries of the Amazonian catfish and further alters the food web of the river ecosystem controlled by this apex predator (Duponchelle et al., 2016; Fearnside, 2013; Fraser, 2018). It has also been reported that the body size and trophic level of Amazonian catfish have declined in the reservoir and downstream reach of the Belo Monte Dam on the Xingu River after large hydropower development (Keppeler et al., 2022). Dams intercept sediment and nutrients that nourish the Amazon River and its floodplain, and damage fish physical habitats with a cascade of ecological effects (Fraser, 2018). The disruption of nutrient connectivity is more pronounced by dams in the Andean-Amazonian transition, whose rivers provide most of the sediment and nutrients to the Amazon (Lees et al., 2016).

Tilapia is the third most-cultured finfish in inland aquaculture, with its production reaching 4.41 million tons in 2020, and accounting for 9% of world inland aquaculture (FAO, 2022). Tilapia mainly includes the Nile tilapia (*Oreochromis niloticus*) and Mozambique tilapia (*Oreochromis mossambicus*). The Nile tilapia is indigenous in the Nile River; however, it is highly invasive elsewhere and has invaded many ecosystems worldwide (Faunce & Paperno, 1999). The Mozambique tilapia is indigenous in South Africa, Zimbabwe, Mozambique, and Eswatini (Moyo & Rapatsa, 2021). Tilapia possess a strong survivability and are physiologically tolerant to a wide range of salinities, dissolved oxygen content and water temperature, and are characterized by multiple spawning, parental care, and extreme feeding plasticity (Avella et al., 1993; G. Farmer & Beamish, 1969; Vitule et al., 2009). Tilapia inhabits the middle and bottom layers of water bodies, and can survive in waters of 16–40°C, with the optimal temperature being 28°C. Tilapia is a warm-water fish, which will hibernate or even die when water temperature is lower than 15°C. Tilapia feeds on the base of the food web at the bottom layer of a water body, most often on sediment resources such as nematodes, rotifers, bryozoans and hydrozoans, and is well adapted to surviving and growing in non-native environments (Peterson et al., 2006). Tilapia is widely cultured in reservoirs using cages in tropical and subtropical regions (Hishamunda, 2007), which can alleviate pressures from water scarcity and also help tilapia to overwinter safely (Moyo & Rapatsa, 2021). However, due to the strong environmental adaptation ability of tilapia, non-native tilapia that escapes accidently from aquaculture in reservoirs could rapidly become the dominant population. This increases the risk of invasive species to the original ecosystem of reservoirs, resulting in the loss of genetic integrity of native species, damage to the native biodiversity, and further affecting the stability of the native river ecosystem (Bernery et al., 2022; Canonico et al., 2005; Cucherousset & Olden, 2011). Therefore, it is critical to quantify the impact of cultivated tilapia on the native fish species in reservoirs, and conduct actions to control their habitat range and prevent their escape into the wild, in order to protect the ecosystem stability of dammed rivers.

River damming also affects non-migratory offshore marine fishes such as sardines (*Sardina pilchardus*), which are mainly distributed in the Atlantic and Mediterranean (Figure 11). Sardines are a small pelagic fish that typically feeds on plankton, and plays an important role in global fisheries (FAO, 2019). The availability of food such as phytoplankton and zooplankton depend on the nutrient inflows from rivers, and thus river damming indirectly affects sardine populations (Biswas & Tortajada, 2012). For example, the autumn flooding of the Nile River irrigates and fertilizes the floodplain annually, and supplies sufficient nutrients to the Mediterranean Sea. Before 1965, the flood of Nile River delivered about 7×10^3 tons year^{-1} of nitrogen and $7–11 \times 10^3$ tons year^{-1} of phosphorous to the Mediterranean coast (Nixon, 2003). The nutrients in the Nile floodwater support a massive diatom bloom and a productive fishery, particularly for sardines (Halim, 1960; Halim et al., 1964). However, completion of the Aswan High Dam in 1965 decreased the fall flood by about 90% (Dorozynski, 1975) and reduced the fertility of the southeastern Mediterranean waters, leading to a sharp decline in the marine fisheries (Milliman, 1997; Mohamed, 2019; Rzóska, 1976). It has been reported that sardine catches along the Egyptian coast declined from 18,000 tons in 1962 to a mere 460 tons in 1968 (Abul-Atta, 1978). Since the late 1980s, the total fish catch, including sardines, of the Nile and its estuaries have recovered back to the level before construction of the Aswan High Dam (General Authority for Fish Resources Development, 2012). The cause for this recovery may be attributed to the increasing discharge of sewage from urban expansion stimulated by damming in the Nile (Nixon, 2003; A. J. Oczkowski et al., 2009; Richards, 1982). However, the long-term fertilizing effects of sewage require further investigation, as the persistent discharge of highly poor-quality water could damage the coastal ecosystem and lead to an unsustainable increase, or even decline, of the fishery (A. Oczkowski & Nixon, 2008).

In many cases, the time of dam construction coincides with adjustment of fishery policies that aim at increasing fish catch and consequently results in overfishing. The contribution of overfishing and river damming to the decline of fish catches demands quantification, in order to investigate and reveal the extent of fishery decline attributed to dam construction (Biswas & Tortajada, 2012). Meanwhile, due to rapid urbanization and industrialization, nutrient supply to downstream river reaches and estuaries has largely increased (A. J. Oczkowski et al., 2009), leading to rebounds of estuarine fisheries after river damming. It is essential to understand whether this effect is sustainable or brings new challenges. Most current studies have focused on endangered or major commercial fish species in order to prevent extinction or sustain fishery economies. However, fish diversity plays an irreplaceable role in the aquatic food web and its integrity, as well as the stability of river ecosystems. Therefore, we highlight the necessity for future investigations on the impacts of river damming on more fish species and fish communities.

4. Fish Conservation Measures in Dammed Rivers

To offset or mitigate the impacts of river damming on fish, a variety of conservation measures, including fish passage facilities, artificial breeding and release, ecological reservoir operation, and habitat compensation in tributaries, have been proposed and implemented. Each measure has its own advantages and limitations, application conditions, efficiency, and cost-effectiveness, and thus should be selected according to the specific situations of a given dammed river. Of course, policies concerning fishery conservation play an essential role, but are outside the scope of the present review. These policies include, but are not limited to, setting up nature reserves and germplasm resources reserves, implementing policies and laws for no-catch measures, and navigation restrictions during fish-sensitive seasons such as the spawning season (S. Huang & He, 2019; Maxwell et al., 2020; H. Zhang, Kang, et al., 2020).

4.1. River Connectivity Restoration and Fish Passage Facilities

Restoring longitudinal and lateral connectivity, such as river-floodplain reconnection and fish passage facilities, could be the most direct approach to rehabilitate physical habitat and migration routes of fish in dammed rivers.

In recent decades, there have been increasing efforts to restore fish floodplain habitats in riverine rehabilitation practices, as floodplain channels that are lost or disconnected from the main river have demonstrated visible impacts on river ecosystems. Establishing the connectivity of floodplain channels to the main channel and restoring lateral connectivity of river can provide essential nursery areas for fish and mitigate the loss of fish diversity (Stoffers et al., 2022). The restored floodplain channels in the Rhine River, Netherlands, have served as suitable nursery areas for rheophilic fish species (Stoffers et al., 2021). The restoration of hydrologic linkages between the main channel and floodplain in the Kissimmee River, USA, has demonstrated positive effects on food web structure and ecosystem functioning (Jordan & Arrington, 2014). In the upper Danube River, a secondary floodplain channel has been artificially created following a nature-based construction scheme, which has provided additional habitats and restored migration routes, thereby making an important contribution to restoring the population of endangered fishes (Pander et al., 2015). The restoration on a tributary of the upper South Esk River, Scotland, has reconstructed a natural meandering channel guided by historical maps, which reinstates floodplain connectivity and habitat for Atlantic salmon and trout (Addy et al., 2016).

Fish passage is potentially an effective engineering approach to reconnect fragmented ecological corridor due to river damming and restore river longitudinal connectivity. It is the earliest, and also the most widely used, measure to conserve migratory fish in dammed rivers (Schilt, 2007). Fish passage mainly includes fishway, fish lift, fish collection, and transportation, turbine passage, juvenile bypass, and other engineering transport measures (Figure 12). The earliest fishway can be dated to the mid-18th century in Europe (Clay, 1995). In the early

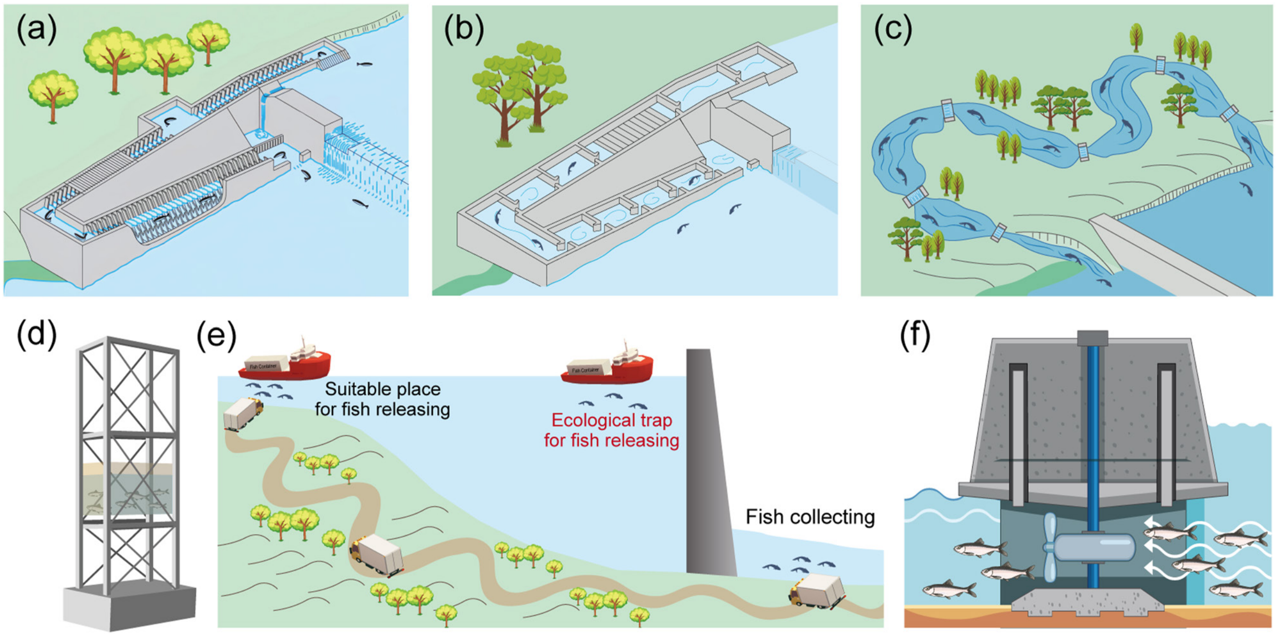

Figure 12. Different types of fish passage facilities. (a) Denil fishway. (b) Vertical-slot fishway. (c) Nature-based bypass system. (d) Fish lift. (e) Fish collection and transport system. (f) Fish-friendly turbine. Panel (a)–(c) are redrawn from Thorncraft & Harris (2000).

20th century, field and laboratory experiments on different fishway designs were performed. Denil (1909, 1938) created the unique Denil fishway to reduce the flow velocity inside the path (Figures 12a and 13a). In 1946, a vertical slot fishway (Figures 12b and 13b) was constructed on both sides of Hells Gate in the Fraser River, Canada, to allow salmonids to successfully cross the channel barrier caused by a landslide (Jackson, 1950). Monk et al. (1989) proposed a fishway configuration of pool and weir, in which nearly 100% of shad and almost all

Figure 13. Different types of fishways. (a) Denil fishway for Arctic grayling in the Big Hole River watershed in Montana, Canada (source: Montana State University, photo by Matt Blank, 2015; https://www.montana.edu/ecohydraulics/research/). (b) Vertical-slot fishway in the Mosel River in Koblenz, Germany (source: The Federal Waterways Engineering and Research Institute (BAW); https://www.baw.de/en/die_baw/wasserbau/umwelt/umwelt.html). (c) Pool-weir fishway for migrating pink and coho salmon to spawning grounds in Anderson Creek, Canada (source: McElhanney Company; https://www.mcelhanney.com/project/anderson-creek-fishway/). (d) Nature-based bypass fishway beside the Se San River of Cambodia (source: the Xinhua News Agency; https://new.qq.com/rain/a/20191026A099LC00).

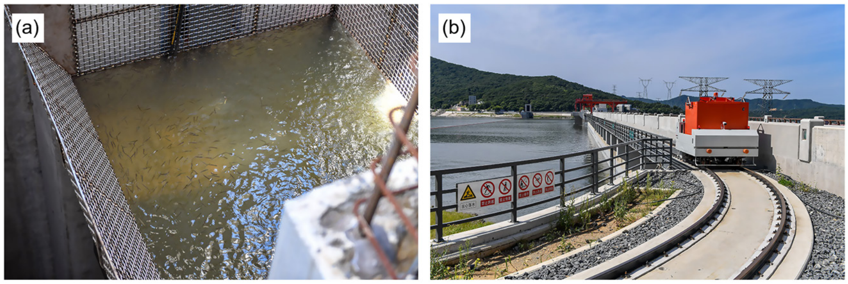

Figure 14. Fish collection and transportation system in Fengman hydropower station in Jilin, China (source: the Xinhua News Agency; https://www.gov.cn/xinwen/2021-08/31/content_5634534.htm#10). (a) Fish collection from the box of fish lift. (b) Transportation of collected fish to upstream.

other species could successfully pass through (Figure 13c). These early efforts were mostly oriented at salmon species, with only a small number of studies aiming at shad. Recent legislation for endangered species in the United States, Canada, and Europe has re-emphasized the importance of fishways for migratory species other than salmonids and shad; meanwhile, some successful initiatives have been taken for migratory species in other parts of the world (Katopodis & Williams, 2012).

With the rapid growth of large dams, the applicability of fishway has been facing great challenges due to high cost, low efficiency and engineering complexity, which promotes the exploration of other types of fish passage. Fish lift has a design principle similar to an elevator, which can actively move and release fish from the downstream reach of the dam to the upstream reservoir (Figure 12d). These lifts induce fishes into a hopper that is raised from the bottom to the upstream side of the dam (Santos et al., 2021). Barry and Kynard (1986) found that the tailrace lift was more efficient than the early fish lift for American shad. It has been reported that the combination of an Archimedes screw and fish lift can significantly improve the efficiency of fish lift (McNabb et al., 2003; Zielinski et al., 2022). In some cases of high dams, where the construction of fishway and fish lift is unfeasible, a fish collection and transportation system could be an appropriate alternative (Figure 12e). Fish collection and transportation is a special form of fish passage facility, which is mainly adopted in high dams or in projects where fish need to climb several steps continuously. It attracts fishes into cabins or other boxes, and then transports the fish over the dam by ships or vehicles (Figure 14). In 1981, massive collection and transportation was implemented as an operational program by the United States Army Corps of Engineers (USACE) to reduce losses of juvenile salmonids during their seaward migration. Fish collection and transportation systems can improve the survival rate of fish passing through dams and has proved to be more effective than other fish passage facilities in some contexts (D. L. Ward et al., 1997).

Traditional turbines are extremely harmful for fish to pass through, thus fish-friendly turbines such as Archimedes screw turbines and blunt blade turbines have been gradually used (Figure 12f). Fish-friendly turbines have slowed rotational speeds and large openings, which can allow safe passage of small objects (Bracken & Lucas, 2013; YoosefDoost & Lubitz, 2020). Bypass systems (Figures 12c and 13d), such as the curved-bar rack bypass and the horizontal rod rack bypass, can guide downstream-moving fish toward a reasonably safe corridor around water intakes, and thus effectively reduce the mortality of fish passing through dams (Beck et al., 2020; Meister et al., 2022). In the eight dams of the lower Snake River and lower Columbia River, USA, most of the fish entering the powerhouse are diverted to a juvenile bypass system, providing safe and efficient passage for juvenile salmon to migrate downstream (Faulkner et al., 2019). River-like side channels are constructed in some dammed rivers, which serve as a bypass for fish migration and even as a supplementary habitat for fish reproduction (L. Zhang et al., 2023). In the Don River, Russia, a natural-type channel has been constructed to allow sturgeon to bypass the Konstantinovskiy Dam. Stellate sturgeon (*Acipenser stellatus*) eggs are found in the bypass channel, indicating that the bypass channel has been used as a spawning habitat (Pavlov & Skorobogatov, 2014).

Overall, fish passage facilities can assist fish to pass through the barrier of dams and mitigate the impact of habitat fragmentation. The efficiency of fish passages differs significantly between different types of fish passages. On average, the efficiency of downward passage is slightly higher than that of upward passage; pool-weir, vertical slot and naturalized fish passages have higher efficiency than Denil fishways and fish lifts (Noonan et al., 2012).

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Fishways are used mostly in low dams, which are usually built in low gradient rivers, to improve river longitudinal connectivity. The Denil and nature-based fishways are the most efficient fish passages (Baumgartner et al., 2018; Bunt et al., 2001). These fish passages can remain effective even when significant fluctuations in upstream or downstream water level occur (Quaranta et al., 2019). The Vianney-Legendre vertical slot fishway in the Richelieu River, Canada, has shown to be successful for passing a variety of fish species, including lake sturgeon (Marriner et al., 2016). The Denil fishways of the 63 diversion dams in the Big Hole River basin in southwestern Montana provide opportunities for Arctic grayling (*Thymallus arcticus*) and other fish for year-round access to critical habitats (Triano et al., 2022). The nature-based fishway installed at a low dam in Indian Creek, Canada, has proven effective for multiple fish species to traverse the dam (Steffensen et al., 2013). However, fishways may have a poor effectiveness for some fish. The effectiveness of a fish weir at Foster Dam in the Santiam River, USA, is low to moderate for the downward passage of juvenile Chinook salmon, while it is consistently high for steelhead trout, indicating that fish weirs may not be a suitable solution for all species (J. S. Hughes et al., 2021). Overall, the passage efficiency of fishway is dependent on the slope, baffle and other characteristics affecting the flow field inside the pools, the water head drop between the pools, as well as the turbulence levels and flow velocities (Quaranta et al., 2019).

Fish lifts, fish collection and transportation systems are regarded as the most cost-effective fish passage facilities for high dams. The fish lift of large hydropower dams on the Lima River, Portugal, effectively prevented fragmentation of potamodromous populations between different reaches (Mameri et al., 2019). Fish collection and transportation systems have the advantages of high flexibility, no interference to the structural layout of the dam, suitability to large variations in reservoir water level, and small occupation of space for fish to cross the dam. In the 1940s, a temporary collection and transportation system successfully transferred thousands of adult salmonids at the Rock Island Dam on the lower Columbia River. Fish collection and transportation systems have also been used to transport shad successfully at the Mactaquac Dam on the St. John River, Canada, and Essex Dam on the Merrimack River, USA (Clay, 1995). D. L. Ward et al. (1997) reviewed studies conducted by the US National Marine Fisheries Service from 1968 to 1989 concerning the efficiency of using trucks and barges to transport migrating juvenile Chinook salmon from the Snake River around dams to reservoirs in the lower Snake and Columbia rivers, and suggested that the use of barges to transport juvenile Chinook salmon could improve their survival rate. However, only 47% of Atlantic salmon succeeded in passing through the fish lift of the Golfech-Malause hydroelectric complex on the Garonne River, France. In the Gezhouba dam, it has proven successful to lure the bottom fishes by releasing jet flow during the collecting procedure (Y. Liang et al., 2014). The main difficulty specific to fish lifts involves fish trapping, as the V-shaped entrance of fish lift may inhibit salmonids entering the holding pool and cannot guarantee that the entered fishes will not return back to the river (Croze et al., 2008).

The passage efficiency of different fish species under different hydraulic conditions in passage facilities varies greatly from case to case (Bunt et al., 2016; Nieminen et al., 2016; Williams & Katopodis, 2016). Salmonids and clupeids have been found to efficiently pass through the vertical slot, pool-weir fishway, and Denil fishway, with an efficiency of 63%, 45%, and 51%, respectively (Castro et al., 2016; Mallen-Cooper & Stuart, 2007; Noonan et al., 2012). Brown bullhead (*Ameiurus nebulosus*) and striped bass (*Morone saxatilis*), which have a smaller body size than adult carp, prefer nature-based fishways, and have a passage efficiency of up to 70% (Bunt et al., 2012). Fish lifts are the most effective up-migration measure for lamprey and brown trout, but the difficulty is to capture small-sized individuals (Castro et al., 2016; Pompeu & Martinez, 2007). Tummers et al. (2016) highlighted that the physical characteristics of baffles and high turbulence may inhibit lamprey ascending the passage, and Moser et al. (2019) proposed a novel modification of fishway entrance for Pacific lamprey. The passage efficiency of fishways is also related to the behavior of fishes (Shahabi et al., 2021), as their swimming direction in fishways is dependent on their experience with the flow field (Goodwin et al., 2014). Inadequate attractiveness for fish is recognized to be a major factor limiting the efficiency of fish passages (David et al., 2022). According to Laine (1995), fish often need to become acquainted with the passage entrances before they start to climb the passage facilities. Mensinger et al. (2021) suggested that fish may segregate at barriers based on their personality and sizes, and this could be alleviated by increasing fishway attraction and maximizing passage opportunity, leading to more exploratory eels passing through successfully. Generally, the functionality of fish passages in alleviating dam barrier effects on fish is limited, and requires both good design of the facilities and good swimming ability of fishes (Noonan et al., 2012).

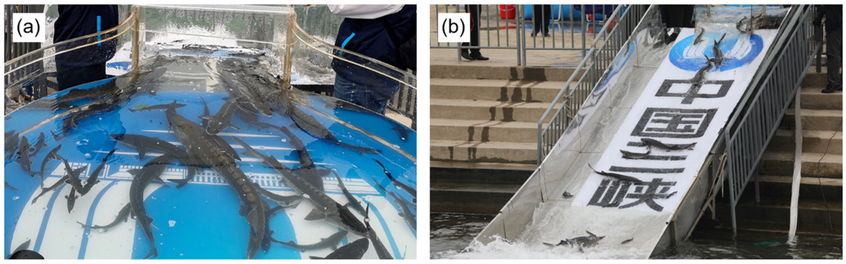

Figure 15. Artificial breeding and releasing of Chinese sturgeon. (a) Artificially bred fry and juveniles of Chinese sturgeon. (b) Release of artificially bred fry and juveniles of Chinese sturgeon into the Yangtze River. Photos are provided by China Three Gorges Corporation.

Fish passage has demonstrated to be an effective way in many cases to reconnect fragmented fish habitats in dammed rivers. However, it is argued that moving fish preferring a lotic environment from downstream reaches to reservoirs could cause further damage to these fish species, as the lentic environment of reservoirs may form an ecological trap that makes the transferred fish unable to find their migration path or suitable habitats. Fishways are mostly favorable to the fish species with strong swimming ability, which could potentially change the structure of fish communities both upstream and downstream of a dam, and hence further impair fish biodiversity in the dammed river. There are also plenty of fish passages that have not achieved their expected functionality. Their low effectiveness could be attributed to insufficient considerations of fish swimming ability and hydraulic characteristics in the design of the facilities. This demands renewed efforts to develop innovative solutions, at the core of which is the need for engineers and biologists to work together and design passages based on the preferred hydraulic conditions of multiple fish species. In addition, nature-based solutions and application of natural materials, instead of concrete and metal, in fish passage constructions are an important aspect. The lack of long-term monitoring and prompt assessment of the effectiveness of the operational fish passages also restricts the modification and improvement of such facilities.

4.2. Artificial Breeding and Release

Artificial breeding and release of target fish species in dammed rivers is a viable conservation measure to replenish the populations of endangered fish species in the wild and restore fishery resources (Molony et al., 2003; Naish et al., 2007; J. Yang et al., 2013), although the evidence base for effectiveness is incomplete (Rytwinski et al., 2021). Artificial breeding and release can be categorized into two main types: "ecological restoration" and "resource restoration." "Ecological restoration" aims to conserve the endangered native fish populations and prevent extinction by releasing hatchery-reared fish into the original habitats of dammed rivers. "Resource restoration" aims to recover fishery resources and improve the economic fishery in dammed rivers by artificial breeding and release (L. Wang, 2016).

This measure has been adopted as an essential conservation strategy for more than 20 vulnerable fish species in China (J. Yang et al., 2013). For instance, Chinese sturgeon are preferentially distributed in the lower reaches of the Yangtze River; however, their spawning migration route is blocked and spawning grounds are damaged by hydropower dams on the upper Yangtze River, which reduces the length of natural spawning ground from 600 to 7 km and causes their gonads to degenerate (L. Wang & Huang, 2020; Xie, 2003; Y. Zheng et al., 2022). Since 1984, artificial breeding and release of larvae and juveniles (Figure 15) into the natural environment has become an important approach to conservation efforts of the Chinese sturgeon (Chang et al., 2021; Gao et al., 2009; Qin et al., 2020; Stone, 2008; Wei et al., 2004). From 1983 to 1998, approximately 6 million Chinese sturgeon fry and juveniles were released into the Yangtze River (H. Wang et al., 2019). About 500 to 1,500 adult sturgeons were released each year into the spawning ground of the Yichang section of the Yangtze River from 1997 to 2003 (J. Li et al., 2021; P. Zhuang et al., 1997). In addition, a breakthrough in artificial breeding technology for the two sturgeon species has been made, so that the artificially bred Yangtze sturgeons can be developed to a third generation in the laboratory (D. Li, Prinyawiwatkul, et al., 2021).

The first stock enhancement program by breeding and release in Brazil was carried out for non-native fishes in the northwest region, which improved fishery yields significantly (Paiva et al., 1994). Nowadays, stock enhancement

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has become a mandatory management action, which is considered a primary measure to mitigate the impacts of reservoirs on fish populations and protect ichthyofauna in Brazil (F. P. Arantes et al., 2011; Casimiro et al., 2022). In China, dam construction in the Yangtze River basin has significantly affected natural reproduction processes and decreased the fishery resources of FMCCs (Q. Peng et al., 2012). After impoundment of the TGR, the resources of FMCCs have decreased by more than 90%, compared to that in the 1960s (Y. Yi & Wang, 2009). The development of artificial breeding techniques and large-scale implementations of stock enhancement have significantly recovered the FMCCs resources in the Yangtze River basin. The annual release of over 10,000 kg of bloodstock of FMCCs has been carried out in the Shishou and Jianli sections of the middle Yangtze River since 2010, which has brought substantial economic, social, and ecological benefits (H. J. Chen, 2019). The improved FMCCs fishery has alleviated limitations depending only on the catches of natural FMCCs resources (H. J. Chen, 2019; J. Yang et al., 2013). In the Lancang River, China, fish breeding and release has been introduced for almost all the dams, which has proven effective in recovering fish resources (H. Xu & Pittock, 2018).

Overall, artificial breeding and release of target fish species is an important measure to recover endangered fish species, maintain genetic diversity, support population expansion, and further preserve the ecosystem integrity of dammed rivers (Le Luyer et al., 2017; Leinonen et al., 2020). However, monitoring data shows that the number of juvenile Chinese sturgeon in the estuary of the Yangtze River has not shown a visible increase (Wei et al., 2004), as there are only small-scale natural breeding activities in the spawning grounds below the Gezhouba Dam (P. Zhuang et al., 2016). Thus, artificial breeding and release has not recovered the natural reproductive processes of wild Chinese sturgeon, but only maintains their populations to some extent and prevents them from extinction.

In the artificial breeding process, the selection and renewal of breeding fishes are sometimes overlooked during artificial reproduction, leading to parent fishes with inferior genetic characteristics arising from inbreeding. The genetic introgression of the released populations has the potential to reduce the genetic diversity and impair the performance of wild populations due to genetic drift (Lin et al., 2022). For instance, artificially bred FMCCs with inferior genetic characteristics escaping from tributaries and connected lakes, have affected the natural high-quality germplasm resource of FMCCs in the mainstream Yangtze River, further leading to a decrease in the quality of the germplasm resource and adaptation ability to the wild environment of the wild FMCCs (H. J. Chen, 2019). Fish stocking activities can introduce exotic diseases and parasites into the water body, which is potentially harmful to the endangered populations (J. Yang et al., 2013). Therefore, the genetic admixture between artificially bred fishes and wild fishes could cause genetic contamination and affect the genetic structure as well as the stability of wild populations, leading to genetic and ecological risks (Abdolhay et al., 2011). In addition, there is competition between large-scale released hatchery fish and wild recipient fish, squeezing the population of wild species (J. D. Bell et al., 2008). It is necessary to understand the carrying capacity of the receptor environment and the size of the wild population before conducting artificial stocking and release, in order to reduce the negative impacts and maximize the benefits (Agostinho et al., 2016). In particular, artificial breeding and release of non-native species can lead to biological invasions, which will result in changes and declines in native fish diversity (Bernery et al., 2022). For instance, tilapia, which possess a wide environmental adaptive ability, have become the dominant species in reservoirs and lakes due to artificial enhancement of stocking, threatening the survival of native fish species (Cucherousset & Olden, 2011).

Long-term field monitoring has shown that most artificially bred fishes cannot reproduce naturally in the wild, but merely maintain the size of the target fish population. Failure to reproduce a second generation naturally leads to the challenge that the wild population of the fish species cannot increase, and thus the stability of the wild population is vulnerable in the long-term. Therefore, it is important to investigate the mechanisms of natural reproduction of the target fish species in dammed rivers, including both artificially bred and wild individuals, for restoring populations. Moreover, due to the lack of long-term and continuous monitoring data, the quantitative impacts of artificial breeding and release on river ecosystems remain unclear. It is essential to establish a risk assessment system on genetic admixture and species invasion to evaluate quantitatively the negative effects of artificial breeding and release. This could help improve conservation measures to increase the target fish population and protect river biodiversity.

4.3. Nature-Based Solutions and Reservoir Ecological Operation

Nature-based Solutions (NbS) have been recognized as an umbrella concept to capture eco-friendly strategies that mimic nature with broad public acceptance (Cohen-Shacham et al., 2016; Y. A. Song et al., 2019). NbS follows the laws of nature to protect and restore degraded ecosystems as a whole, which can be applied in various domains (Maes & Jacobs, 2017; Nesshöver et al., 2017; Raymond et al., 2017). After the first appearance in the official report from the World Bank (2008), the idea has gained increasing attention in scientific communities, governmental agencies and non-governmental organizations worldwide (Cohen-Shacham et al., 2016; Griscom et al., 2017; Krull et al., 2015). NbS is particularly suitable for watershed ecosystem protection and river ecosystem remediation so as to preserve and restore the functions and valuable services that nature provides.

Conventional reservoir operations aim predominantly to maximize social-economic benefits, which may cause severe damage to the ecological structure and functioning of river ecosystems. By contrast, ecological reservoir operations follow the idea of NbS, which aims to balance social-economic benefits and river ecosystem requirements (X. Xia et al., 2009). Studies on reservoir ecological operation have spanned several decades, since Schlueter (1971) proposed that reservoir operation schemes should take the habitat diversity of river ecosystems into account when meeting the social-economic water demand. Many studies have been dedicated to developing optimization models for reservoir ecological operation (D. A. Hughes & Ziervogel, 1998; C. Liu et al., 2019; Suen & Eheart, 2006). The United States and Australia are two countries that have undertaken relatively early implementations of reservoir ecological operation (Higgins & Brock, 1999; A. J. King et al., 2010). In recent years, China has made great efforts in reservoir ecological operations, which have made visible contributions to restoring fish resources in dammed rivers (Q. Chen et al., 2021; C. Ma et al., 2020).

Flow regulation can create suitable hydrological conditions for fish to acquire their demand environment at critical life stages, especially during spawning periods (Yin et al., 2011). The NFR, which shapes river species community and ecosystem structure and function (Poff, 2018), is crucial to riverine biodiversity and healthy (Bower et al., 2022; Poff et al., 1997). Releasing ecological flow (Maavara et al., 2020; Poff, 2018) is an important measure of reservoir ecological operation (Y. Miao et al., 2020; X. Xia et al., 2009; Y. Xia et al., 2019). Q. Chen et al. (2012), D. Chen, Chen, et al. (2016) proposed an operation scheme for the Qingshitan Reservoir in the Lijiang River, China, to maintain a quasi-NFR in the downstream reach for fish conservation when meeting the demands of irrigation, cruise navigation and water supply. Creating artificial floods through reservoir operation has been used to stimulate spawning of drifting eggs in dammed rivers (C. Ma et al., 2020; Zhou et al., 2019). In the Colorado River, artificial flood experiments have been conducted at the Glen Canyon Dam for many years, which have successfully restored the endangered humpback chub (*Gila cypha*) and maintained populations of other native fish species (Jacobson & Galat, 2008; Melis et al., 2015; Yao et al., 2015). The Hume Reservoir in the Murray River, Australia, rebuilds some small-to-medium floods, which modifies the timing of peaks to trigger the spawning of native golden and silver perch, and increase the duration of floods to extend the recruitment of species from mid-October to mid-December 2005 (A. J. King et al., 2010). In China, ecological operation of the TGR has substantially increased the spawning of the FMCCs (Figure 16). During the 4-day experiment of ecological operation of TGR conducted in mid-June 2018, an initial outflow of 11,000 m^3/s and a flow increment in the range of 1,000 to 1,500 $m^3/(s\ d)$ was implemented, which formed a concentrated egg spawning activity of FMCCs in the Yichang section of the Yangtze River (C. Ma et al., 2020). In Brazil, reservoir operators have recently proposed a flow regime that could restore flooding for 32 fish breeding sites in the Xingu River (Moutinho, 2023).

Discharge regulation alone is sometimes insufficient to meet the demand of fish reproduction, since fish spawning also requires suitable water temperature. Controlling the selective withdrawal device to adjust the water temperature of the outflow from temperature-stratified reservoirs can improve the water temperature rhythm to some extent for fish reproduction downstream of dammed rivers (Saadatpour et al., 2021). A selective-withdrawal device was installed at the Shasta Dam in 1997 to manage the water temperature regime in the downstream reach of the dam to meet the year-round thermal requirements of salmonid while fulfilling the obligation on water delivery, power generation and flood control. Its use resulted in a significant increase in the salmonid fish population (Bartholow et al., 2001; Hanna et al., 1999). A water temperature regulation experiment was conducted in the Xiluodu-Xiangjiaba cascade reservoirs in the Yangtze River in May 2017, which increased outflow temperature and thereby facilitated fish spawning in the reaches downstream of the Xiangjiaba dam. About 10 million and 100 million fish eggs were monitored in the Yibin and Jiangjin section of the Yangtze River, respectively. In particular, the annual peak in fish spawning occurred during the period of the experiment (Ren et al., 2020).

Sediment regulation of reservoirs can change the morphology of the downstream reaches, and this potentially affects the location and quality of fish habitats (W. Wang et al., 2012; H. Zhang, Jarić, et al., 2021). Sediment

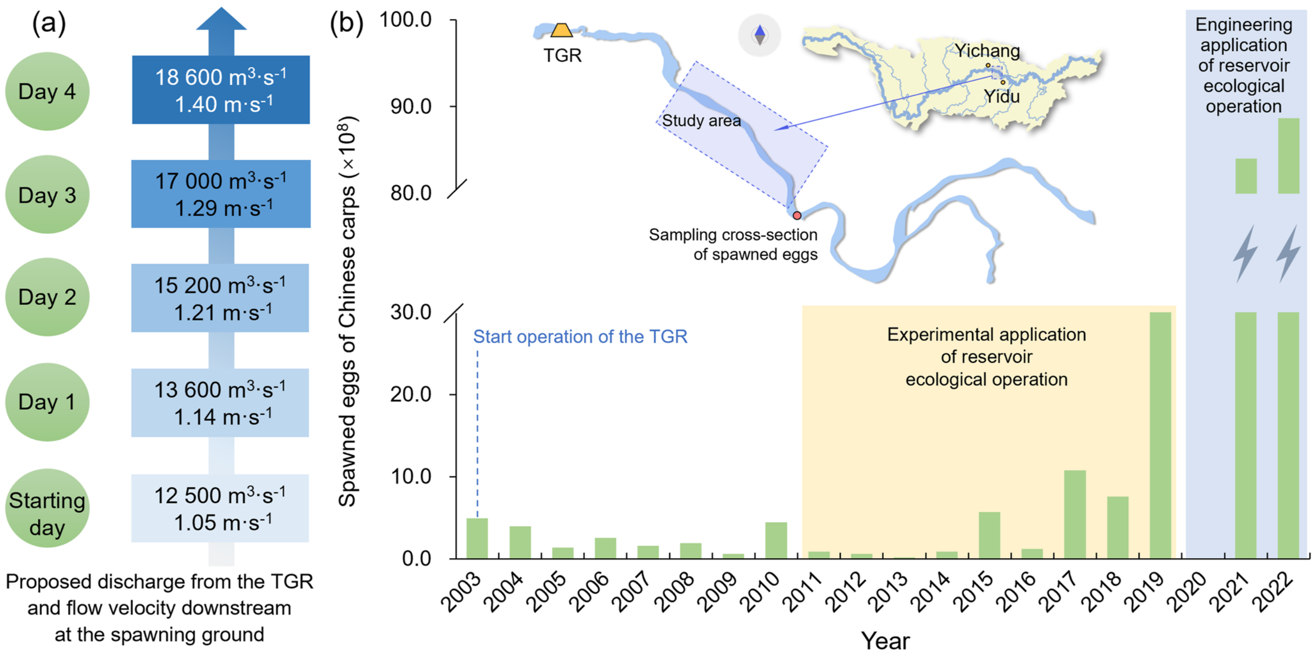

Figure 16. Effect of reservoir ecological operation on fish spawning in dammed river. Adapted from Q. Chen et al. (2021). (a) The proposed ecological operation of the Three Gorges Reservoir (TGR) for improving the spawning of four major Chinese carps (FMCCs) in the downstream river of the TGR. (b) The changes of spawned eggs of FMCCs in the downstream river of the TGR before and after the proposed ecological operation. Data are available from China Three Gorges Corporation and China National Environmental Monitoring Center. There was no measurement of spawned eggs during the TGR ecological operation in 2020 due to COVID-19.

regulation has been implemented at the Xiaolangdi Reservoir in the Yellow River since 2002, resulting in the main channel of the lower reach of the dam being fully scoured (C. Miao et al., 2016). The regulation also brings abundant nutrients and hence plankton blooms downstream, providing suitable feeding sites for pelagic and epipelagic fish that congregate in the Yellow River estuary (L. Zheng et al., 2014). Some studies show that sediment flushing could erode the areas of spawning and feeding grounds of fish, and even lead to fish mortality (Kong et al., 2017). However, proper design of sediment flushing could control suspended sediment concentration and reduce adverse effects on fish in the downstream reaches (Cattaneo et al., 2021). In addition, fish can possess a certain resistance to the negative impacts caused by sediment flushing operations (Grimardias et al., 2017). The three-year field investigation conducted from 2009 to 2011 concerning the controlled sediment flushing of a small reservoir on the Adda River in Italy showed that fish resources in the downstream reach were not affected significantly (Espa et al., 2015). Similarly, fish density showed no significant impairment during controlled sediment flushing operations conducted in 2016 at the Verbois Reservoir in Switzerland (Cattaneo et al., 2021).

Control of intermittent reservoir discharges is possible to reduce the damage of TDG supersaturation on fish. Modeling results illustrate that intermittent discharges from the Bala Reservoir could diminish TDG supersaturation and reduce the negative effects on fish in the Zumuzu River, China (J. Feng et al., 2014). Based on numerical modeling of TDG, Wan et al. (2021) found that a proper discharge scheme for the Xiluodu Reservoir on the Yangtze River could reduce the level and maximum residence time of TDG in downstream waters, thereby alleviating negative impacts on fish. The mixing of tail water and spill discharge can create areas of low TDG level, providing shelter zones for fish to avoid damage from high TDG levels (Wan et al., 2020).

Reservoir ecological operation has developed from single factors to the coupling of multiple factors of fish physical habitat. W. He et al. (2020) proposed an operation model for the Sanbanxi Reservoir in the Yuanjiang River, China, to meet the demand of outflow water temperature and downstream ecological flow. Z. Xu et al. (2017) proposed an eco-friendly operation scheme considering flow velocity and water temperature demands of target fish, which significantly facilitated the spawning of this fish species. In South Africa, an experiment has been conducted at the Clanwilliam Dam on the Olifants River by creating small pulses of high flow and making the water temperature at the spawning site reach above 19°C, which has resulted in a visible increase of successful spawning activities of yellowfish (*Barbus capensis*) downstream of the dam (J. King et al., 1998). In the USA, a flow pulse has been released from the Gavins Point Dam, together with the improvement of water temperature, to promote spawning of pallid sturgeon in the lower Missouri River (Jacobson & Galat, 2008).

The effect of ecological operation of a single reservoir is sometimes limited. Joint operations of multiple reservoirs, which can be in a cascade along one river or are distributed on multiple rivers within the same watershed, can better coordinate the social-economic interests and ecological requirements. Dalcin et al. (2022) reported a methodological framework to guide operations of cascade reservoirs for rebuilding expected flow regimes. The application to the reach between Porto Primavera Reservoir and the Itaipu Reservoir in the upper Paraná River basin in Brazil provided suitable conditions for the successful recruitment of migratory fish species. Q. Chen et al. (2013), D. Chen et al. (2015) proposed an adaptive operation scheme for two cascade reservoirs, Jinping-I and Jinping-II, in the Yalong River, China, to meet the requirements of daily ecological flow and water temperature for the conservation of the indigenous fish species *Schizothorax chongi* in the dewatered river reach between the two dams. D. Chen, Leon, et al. (2016), D. Chen, Leon, Engle, et al. (2017), and D. Chen, Leon, Hosseini, et al. (2017) optimized the operation of 10 reservoirs in the Columbia River to maximize total power revenue and fulfill the ecological flow requirements of fish, providing an important reference to ecological operation of multiple reservoirs. Z. Jiang et al. (2019) developed a multi-objective optimization model to balance flood control, power production, and ecological flow requirement of a large-scaled cluster of reservoirs with mixed types in the Pearl River basin, China. The model results played a significant role in the operations to improve both social-economic benefits and fish conservation.

Although there are studies and engineering practices of reservoir ecological operation concerning multiple factors, such as flow and water temperature, the spatiotemporal matching of different factors with regards to habitat requirements of different fish species and their life cycles remain challenging. In the joint operation of cascade reservoirs, available studies mostly use water balance methods to link the reservoirs. In future, it is better to adopt hydrodynamic models, which can simulate the distribution of flow fields, water temperature, and TDG to achieve refined operation strategies for more effective conservation of fish. In addition, climate change could bring large uncertainties to the inflow of reservoirs (Y. Wang et al., 2019), which implies that current reservoir ecological operations based on historical data and deterministic models must be updated to incorporate inflow uncertainties under future climate changes.

4.4. Habitat Compensation and Dam Removal in Tributaries

The shift from a lotic to a lentic environment of the reservoir after river damming leads to a permanent loss of habitats for the maturation and spawning of fish species (Antonio et al., 2007; Liermann et al., 2012), and such loss cannot mostly be remediated through reservoir ecological operations. The situation is more severe in rivers with cascade dams, for instance the Lancang River, where an upstream dam is located in the backwater zone of the nearest downstream reservoir, and the lentic section stretches for over one thousand kilometers. Under such circumstances, relatively unaltered tributaries can provide possible alterative places to conserve indigenous species of the dammed mainstream by serving as high-value natural surrogates or supplements that can restore some function of the mainstem ecosystems (Neely et al., 2009; Nunes et al., 2015; Pracheil et al., 2009, 2013). The elements of natural flow fluctuations and the availability of food resources and shelter areas could be maintained in these tributaries. Moreover, diverse hydraulic conditions exist in the upper, middle, and lower tributary reaches, giving the migratory or rheophilic fish species chances to colonize new habitats. In addition, for some native fish species, their survival and life history requirements are directly related to intact longitudinal pathways, including the possibility of migration into tributaries for reproduction and rearing (Da Silva et al., 2015). Therefore, the use of unregulated tributaries to alleviate the adverse impact of impoundments in the mainstream has recently been forwarded as a key alternative for fish conservation in dammed rivers (Figure 17).

Successful spawning of humpback chub is found to be related to the migration of adult individuals from the highly altered Colorado River to a relatively unregulated tributary, which offers necessary spawning habitat and hydrological variability (Gorman & Stone, 1999). Adults of American paddlefish prefer to migrate up the unaltered Yellowstone River rather than the regulated Missouri River when they move above the confluence of the two rivers, probably because the more natural flow pattern in the Yellowstone River tributary provides better spawning conditions than the Missouri River (Firehammer & Scarnecchia, 2006). In South America, recent findings indicate that at least eight long-distance migratory species utilize alternative spawning and nursery habitat in four tributaries of the upper Paraná River, after the construction of Porto Primavera Reservoir (Da Silva

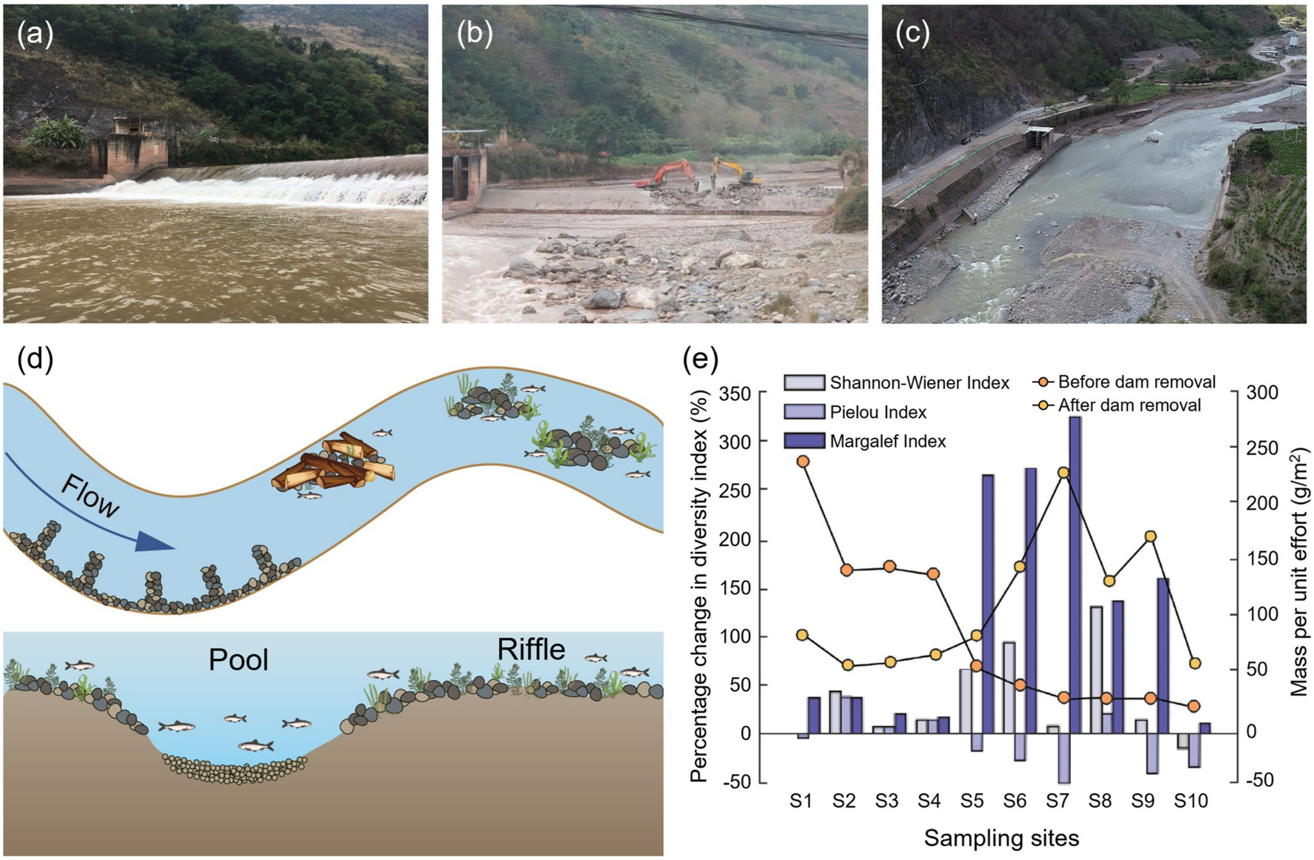

Figure 17. Habitat compensation and rehabilitation in dammed river. (a) Laomuhe Dam on the Heishui River, a tributary of upper Yangtze River. (b) The removal of the Laomuhe Dam. (c) The Heishui River after the removal of the Laomuhe Dam. Photo by Lei Tang. (d) Habitat restoration measures in dammed river, including ecological spur dike construction, creating diverse habitats with large woody debris, big rocks, pool and riffle. (e) Changes of fish diversity and mass per unit effort in the Heishui River before and after the removal of Laomuhe Dam. Adapted from S. He et al. (2021).

et al., 2015, 2019). The Congonhas River in Brazil provides possible reproductive routes and feeding sites for six important rheophilic and migratory species, *Piaractus mesopotamicus*, *Megaleporinus obtusidens*, *Prochilodus lineatus*, *Salminus brasiliensis*, *Pinirampus pirinampu*, and *Pseudoplatystoma corruscans*, after the construction of Capivara Dam. These species are long-distance migrators and represent about 29% of all migratory species inhabiting the upper Paraná River basin (Garcia et al., 2019). In China, indigenous fish species in the upper Yangtze River and Lancang River are facing great threats incurred by the cascade dams. Conservations of the indigenous fish in these severely impounded rivers often focus on their large tributaries, which remain natural or are lightly dammed and have been recognized as alternative habitats for spawning and larvae development (L. Tang et al., 2021). W. Cao (2000) and Park et al. (2003) suggested that three tributaries, the Jialing, Chishui and Tuo rivers, in the upper Yangtze River can be a potential refuge for 22 endemic species, including Dabry's sturgeon that is listed as a first-class protected animal in China. In the Lancang River, its tributary, the Luosuo River, serves as an important habitat for the migration and spawning of red mahseer (*Tor sinensis*), one of the most famous economic fishes of Yunnan province in southwest China (Hong et al., 2022; Y. Peng, Hong, et al., 2022). These findings demonstrate that unregulated tributaries can provide habitats required by fish at different development stages.

Preservation of free flow is essential for tributaries to serve as alternative habitats of fish in dammed mainstreams. However, numerous tributaries of large rivers have been developed for individual or cascades of SHPs. In the United States, there are more than 75,000 reservoirs, and many of them are impounded by small dams (<10 m in height) that are now aged and in disrepair (Ahearn & Dahlgren, 2005). In China, more than 45,000 small dams have been built by the end of 2012 to meet rural electricity demand (Ding et al., 2019; Hennig & Harlan, 2018), and approximately 6,590 small dams are reported to be out of service due to their age and loss of function

(Gao et al., 2018). Removal instead of maintenance of these aged facilities has been growing around the world. Since the early 1900s, nearly 1,800 small dams have been removed from rivers in the USA (Fox et al., 2022). In Europe, at least 4,000 dams and weirs have been removed since the mid-1990s (Kim & Choi, 2019). Removal of small dams in tributaries can open up spawning and rearing habitats in previously inaccessible regions upstream, which has shown positive effects on fish diversity of the dammed mainstreams (Barbarossa et al., 2020; Lasne et al., 2015; Magilligan, Graber, et al., 2016; O'Connor et al., 2015; Y. Peng, Hong, et al., 2022). Foley, Bellmore, et al. (2017) reported that anadromous fishes, such as salmonids, passed the former dam site within days to weeks after the removal of the Marmot dam in the Sandy River, USA, a tributary of the Columbia River. Similarly, following the removal of small dams in the Jidu River, a tributary of the Lancang River, seven migratory species recolonized newly accessible habitats (Hong et al., 2022). In addition to the direct effect of reconnection and upstream access, dam removal has strong influences on fish physical habitat by changing sediment regime and channel morphology, which increase the heterogeneity of hydraulic features and create new habitats for fish species (Hatten et al., 2016; Im et al., 2011; Magilligan, Nislow, et al., 2016). The removal of a small dam in the Heishui River (Figures 17a–17c), a tributary of upper Yangtze River, has increased the percentage of suitable spawning habitat for *Jinshaia sinensis* by a factor of four (Figure 17e), due to the change in river morphology and hydrological regimes following the removal (L. Tang et al., 2021).

Although removing small dams to restore the natural conditions of rivers is shown effective to conserve fishes in dammed rivers, removals of large dams still face great challenges due to social-economic constraints and intensive as well as long lasting ecological consequences (O'Connor et al., 2015). To restore the access of salmonids to their spawning grounds in the mainstream of Elwha River, two large dams, the Elwha Dam and Glines Canyon Dam, have been removed, resulting in increased species richness and functional stability of the riverine ecosystem (Foley, Warrick, et al., 2017; Shaffer et al., 2018; Warrick et al., 2015). Similar achievements have been made in the removal of the San Clemente Dam on the Carmel River, USA (Smith et al., 2020), which has gradually improved the spawning grounds of steelhead salmon near the original dam site and in its downstream reach (Harrison et al., 2018). Despite the visible ecological benefits, removal of large dams often comes at a huge cost, and long-term consequence of fish community demands further investigation.

After dam removal, naturalized artificial habitat, following the NbS concept, can be created to expand living spaces of fish (Figure 17d). The addition of gravel to rivers, known as gravel augmentation, is an early attempt at artificial habitat creation, which has proven to increase the available spawning grounds for Atlantic salmon and brown trout in regulated rivers (Barlaup et al., 2008; Pulg et al., 2008). Three types of artificial habitats (straw bales, straw tubes and moss tubes) have been implemented to enhance egg production of *Galaxias maculatus*, an important fishery species in New Zealand (Hickford & Schiel, 2013). In the Youjiang River, a tributary of the Pearl River, China, artificial habitats made of bamboo and palm slices have been deployed to serve as spawning grounds for fish that produce sticky eggs and as refuges that improve the survival rates of juvenile fishes (D. Guo et al., 2020). The installation of large woody debris can also restore degraded river ecosystems due to dam construction through "rewilding," which has been proven to significantly improve the abundance of food resources and thereby increase the population of fishes in the restored reaches (Thompson et al., 2018). In the lower Mulde River, Germany, fish abundance increased nearly 10-fold eight months after the installation of large wood (Anlanger et al., 2022).

Tributaries cannot offer an identical replacement for the degraded habitats of previously undammed mainstreams, as the former have lower discharge, longitudinal distance, morphological variability, and habitat complexity than the latter. Discharge and its variability are essential to provide flow-related cues that initiate fish maturation and spawning, or create conditions for recruitment of larvae and juveniles. The longitudinal distance is critical for fish species that require long egg-drifting distances for survival. To date, quantitative methods for determining suitable tributaries for fish spawning, foraging and refuging have not been established. Future studies should attempt to coordinate the relations between conservation efforts in the mainstream channel and its tributaries to help achieve maximum effectiveness. In addition, despite the removal of a large number of dams worldwide over the past decades, our knowledge concerning these effects is still limited due to the lack of long-term monitoring data, which is critical to quantify the rate, magnitude and sequence of tributary habitat recovery to dam removal.

4.5. Efficiency Assessment on Conservation Measures

A variety of measures to conserve fish species impacted by river damming are available and each measure can be effective under specific conditions. However, a challenge is to select appropriate measures based on real

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Table 2
Summary of Advantages, Disadvantages and Applicable Conditions of Fish Conservation Measures

Conservation measures		Advantages	Disadvantages	Suitability of applications
Fish passage facilities	Fishway	1. Promote timely fish passage 2. Reduce damage to fish bodies	Only effective for fish species with strong swimming abilities	All types of dams with a water head between upstream and downstream within 60 m
	Fish lifts	1. Space-saving 2. Easy to arrange in the dams	1. Complex mechanical facilities 2. Higher possibility of failure 3. Limited number of passed fishes	Concrete gravity dams with a water head between upstream and downstream over 60 m
	Fish collection and transportation system	1. Flexible 2. Adjust the replenishment flow according to the fish preference	1. High power consumption 2. Complex operation and management 3. Fish mortality during transportation	All types of dams with a water head between upstream and downstream over 60 m
	Fish-friendly turbine passage	Ecological friendly turbines can allow for the safe passage of small objects	Physically damage or traumatize fishes	Low and medium water head hydropower plants
	Juvenile bypass system	1. Long length, with good ecological landscape function 2. Effectively reduce the mortality rate of fish passing through the dam 3. Easy to adjust and expand the trial run after completion	1. Need more space 2. High requirements of local terrain conditions	All types of dams with a water head between upstream and downstream within 30 m, and rely on tributary projects
Artificial breeding and release		1. More convenient operation and management 2. Relatively mature technology 3. Protect fish species and increase fish populations	1. Longer exploration time 2. Reducing survival chance of wild individuals 3. Dilution of genetic diversity in wild populations	All dammed rivers, especially for conservation of endangered or economic fish species
Reservoir ecological operation		1. Restore the structure and function of river ecosystems; 2. Promote the fish spawning	1. Loss of social and economic benefits; 2. Difficulties in coordinating departments; 3. Difficult to meet the needs of different fish species simultaneously	All types of dams with large or medium-sized reservoirs
Habitat compensation in tributaries		1. Provide compensatory habitat for fish affected by hydropower in the mainstream; 2. Restore the natural connectivity of the river; 3. Promote changes in the diversity of river characteristics; 4. Promote fish reproduction	1. Limited compensation ability of the tributaries without sufficient free-flowing length; 2. Demolition of small dams in tributaries causes fish casualties and adenosis	The presence of tributaries with high habitat similarity to the dammed mainstream

situations and cost-effectiveness. Table 2 summarizes the major conservation measures and their advantages, disadvantages as well as applicable conditions. We acknowledge that environmental decisions are complex and require a nuanced understanding of local context and will almost always involve trade-offs.

Fishways are of benefit to fish species with strong swimming ability, but are mainly suitable for dams where the water head is <60 m. Fish lifts are space saving and mainly suitable for concrete gravity dams where the

Table 3
Summary of Evaluation Indicators for Fish Conservation Measures

Conservation measures	Evaluation indicators	Description and calculation
Fish passage facilities	Fish passage effectiveness	The potential effect of fish passage facilities on fish proliferation by checking that the passage facility is capable of letting all target species pass through within the range of environmental conditions observed in nature during the migration period. Calculations are based on the monitoring data of fish species, numbers, sizes, life stages, and behavior under the specific conditions of the operating fish passage
	Fish passage efficiency	The ratio of the number of fish species and quantities of fish individuals that migrate upstream through the fish passage facility to the number of fish species and quantities of fish individuals that demand to pass the dam in a specific period
Artificial breeding and releasing	Survival rate after releasing	Mark the fry to be released using marking techniques, and calculate the percentage of fish containing the number of marks in the fish catch by recapture
	Catch rate	The percentage of the catch in a certain water body and a certain period of time to the total resource of the fishing object in the water body during the same period
Reservoir ecological operation	Ecological flow replenishment	Replenishing the flow through reservoir operations to meet the minimum flow demand of downstream ecosystems
	Spawning volume	The spawning volume that is monitored for the spawning grounds during the reservoir ecological operation
Habitat compensation in tributaries	Habitat diversity	The overall richness of various types of habitats that accommodate various organisms
	Fish diversity	Biodiversity of indigenous fish species, including species richness, species abundance, and phylo genetic diversity
	Fish populations	The total number of fishes that inhabits a certain area

water head is >60 m, but they are mechanically complex and have limited passage capacity. Fish collection and transportation systems are flexible in space and time, and suitable for dams with water head >60 m, but they are complicated to operate and usually cause a high mortality rate during transportation. Fish-friendly turbines are designed for low and medium water head hydropower plants, which can decrease the mortality and mechanical damage to fish (Hogan et al., 2014; Pracheil et al., 2016; Watson et al., 2022). Juvenile bypass systems are mostly used where the water head is <30 m and there is a tributary present. Artificial breeding and release are effective to protect endangered fish species and restore the resources of economic fish species, but it could affect the survival and genetic diversity of the wild population. Reservoir ecological operation is an effective non-engineering method for fish conservation in dammed rivers and is particularly applicable to large and medium-sized reservoirs, but it may cause certain loss of social-economic benefits. Habitat compensation in tributaries can be a potential approach to conserve fish species that permanently lose their original habitats in the impounded mainstream upstream of high dams, but their effectiveness depends on the ecological status of the tributaries and the future development of the mainstream.

Quantitative evaluation on the effects of conservation measures is essential to select proper approaches and improve their efficiencies. Table 3 summarizes the major indicators and methods to assess these different conservation measures.

Passage effectiveness and efficiency are the main indicators to evaluate the capability of fish passage facilities (Bravo-Córdoba et al., 2021). Passage effectiveness is used to describe qualitatively the potential effect of fish passage facilities on fish proliferation by checking that the passage facility is capable of letting all target species pass through within the range of environmental conditions observed in nature during the migration period. Passage efficiency is a quantitative evaluation indicator of fish passage effectiveness, which is defined as the ratio of the number of species and quantities of fish individuals that migrate upstream through the fish passage facility to the number of species and quantities of fish individuals that demand to pass the dam in a specific period (Larinier, 2008). The average efficiency of fish passage facilities is 50–60% (Hershey, 2021). Evaluation of the effectiveness of artificial breeding and release depends on the specific objectives of the measure, and generally focuses on the growth of fry and the contribution to target fish resources as well as the related economic, ecological and social benefits (Rytwinski et al., 2021). Ecological restoration aims at conserving endangered species, and the evaluation mainly focuses on the survival rate and natural reproduction of artificially hatched fry after

Table 4
Summary of the Costs and Benefits of Conservation Measures

Conservation measures	Costs	Benefits
Fish passage facilities	1. Denil fishway: approximately US $124,000 per vertical meter with low maintenance and operation costs	1. Denil fishway cost: average passage efficiency is only 16%
	2. Fish lifts: roughly US $2.4 million to install and annual maintenance charge of 5%	2. Fish lifts: relatively high operation efficiency
	3. Fish collection systems: high mortality loss and operational cost	3. Fish collection systems: high passage efficiency
	4. Juvenile bypass system: relatively low construction and operation cost	4. Juvenile bypass system: average passage efficiency is 70%
Artificial breeding and releasing	1. Range from millions to hundreds of millions of USD for different scales of releasing and different bred fish species (H. J. Chen, 2019)	1. "Ecological restoration": conserved the endangered native fish populations and prevent their extinction. "Resource restoration": improved fishery with high economic values
	2. A total of 31.55 million endemic fishes, including 24.16 million economic fishes which cost about US $0.48 billion	2. The number of fish species increased by 18 species in the Yangtze River basin, effectively restoring the fishery resources of the Yangtze River (Sun & Wang, 2020)
Reservoir ecological operation	1. The power generation of cascade reservoirs decreased by 1.76%	1. The ecological flow coordination degree increased by 17.45%, promoting the spawning of the four major carps (Dai et al., 2022)
	2. The Gezhouba Hydropower Station lost 0.15% of its power generation	2. The suitability of the spawning ground for Chinese sturgeon increased by 39% (Y. Y. Wang et al., 2013)
	3. The loss of power generation benefits is about 2.5%	3. Protect at least 50% of the target fish habitat in the river (D. Chen et al., 2014)
Habitat compensation in tributaries	1. The Waterworks Dam was removed at a cost of US $0.214 million	1. Two years after the removal of the dam, the number of fish species at the original site of Waterworks Dam increased from the previous 11 to 26 species (Catalano et al., 2007)
	2. The Marmot Dam was removed at a cost of US $4.86 million	2. The removal of the dam restored nearly seven miles of river to migratory habitat for steelhead, Chinook salmon and coho salmon (Xiao, 2021)

release (Lyu et al., 2021). Resource restoration aims at restoring fishery resources and improving the economic benefits of fisheries, and thus the evaluation has mainly focused on the catch rate. The evaluation indicators for reservoir ecological operation include replenishment of ecological flow and spawning volume of target fish in the downstream reach of the dam (J. Li et al., 2019), particularly, the amount of spawning volume during reservoir operation can well evaluate the effectiveness of ecological dispatch. The primary objective of habitat compensation in tributaries is to protect the biodiversity of indigenous fish species, and the indicators for effectiveness evaluation include habitat diversity, fish diversity and fish populations.

There are significant differences in the cost-benefits of different fish conservation measures for dammed rivers (Table 4). Fish passage has significant variations in cost-benefits, depending on the types of facilities. The Denil fishway and fish lift have relatively low cost-benefits, while the juvenile bypass system and fish collection system have relatively high cost-benefits. The Denil fishway costs approximately USD 124,000 per vertical meter and has low maintenance as well as operation costs, but their average passage efficiency is only 16% (Noonan et al., 2012). Fish lifts are expensive to build and operate, and costs roughly USD 2.4 million to install and an annual maintenance charge of 5% (Noonan et al., 2012), although it has relatively high passage efficiency. Fish collection systems need to temporarily preserve the transferred fish during long-distance transport, leading to high mortality loss and operational costs. Juvenile bypass systems have relatively low construction and operational costs, and the average passage efficiency can reach 70%. However, it demands more space, which limits its applicability.

The disposable investment of artificial breeding and release ranges from millions to hundreds of millions of USD, and the cost-benefits depends on the bred fish species and scales of release (H. J. Chen, 2019). For instance, Chinese sturgeon spawns in the autumn, so they need to be incubated and reared indoor using heating devices to promote their growth, which is expensive to maintain (Wei et al., 2004). Ecological restoration for the endangered

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native fish species can prevent their extinction in dammed rivers, and the value cannot be simply capitalized. Resource restoration for fishery improvement in dammed rivers can bring high economic values. From 2005 to 2018, a total of 31.55 million endemic fishes, including 24.16 million economic fishes that cost about US $0.48 billion, have been released into the upper Yangtze River. The release of economic fishes has effectively restored fishery resources, and the release of rare fishes has increased the number of fish species from 22 in 2006 to 40 in 2018 (Sun & Wang, 2020).

It is widely perceived that reservoir ecological operations may sacrifice social-economic interests due to the dedicated discharge of ecological flow or water head loss for withdrawing temperature stratified water. The temperature regulation device on the Shasta Dam resulted in an estimated US $63 million loss of hydropower revenue between 1987 and 1996 (Hallnan et al., 2020). However, many studies have shown that by optimizing the operation of reservoirs, the ecological benefits can be ensured with a marginal loss, or even an increase of socio-economic benefits. Under the optimal operation scheme, the Jinping cascade reservoirs in the Yalong River, China, only sacrifice annually 2.5% hydropower production to conserve more than 50% habitat for *Schizothorax chongi* in the dewatered reach (D. Chen et al., 2014). In the upper Yangtze River, under an optimal operation scheme, the hydropower production loss of the cascade dams is only 1.76%, while the fulfillment of ecological flow increases 17.45%, which greatly promoted the spawning of FMCCs (Dai et al., 2022). X. Wang et al. (2020) proposed an optimized operation for the Three Gorges and Gezhouba cascade reservoirs that the total hydropower production increased by 250,089.2 MW·h and the area of suitable spawning grounds of Chinese sturgeon increased by 2.16%. Cioffi & Gallerano (2012) optimized hydropower production and fish habitat protection for the Pieve di Cadore Reservoir in the Piave River, Italy, and the results showed that the area of fish habitat could be increased with little loss of power generation. W. Chen & Olden (2017) designed a reservoir release scheme, which could create proper conditions to favor native over non-native fish, while human water demands were barely sacrificed. In general, reservoir ecological operation is an effective non-engineering conservation measure with high cost-benefits.

Studies have shown that the cost of removing small weirs (≤3.0 m in height) is US $69,000 on average or US $23,000 per meter height, which is less than 20% of the cost of building a fish passage or less than 12% of the cost of building a fish ladder (Garcia de Leaniz, 2008), and dam removal can significantly increase fish species richness. The removal of the Waterworks Dam in the Baraboo River, USA, a tributary of the Wisconsin River, cost approximately US $0.214 million in 1998. Two years after the removal, the number of fish species increased from 11 to 26 at the original dam site (Catalano et al., 2007). The Marmot Dam in the Sandy River, a tributary of the Columbia River, was removed at a cost of approximately US $4.86 million. The removal has restored nearly seven miles of river habitat for migratory fishes of steelhead, Chinook and coho salmons (Xiao, 2021). In general, habitat compensation and removing small dams in tributaries is likely a cost-effective approach to conserve fish diversity in dammed mainstreams.

5. Future Perspectives

5.1. Strategic Plans for Development and Conservation

Mitigation actions should be taken to minimize the potential impacts on fish during the complete process of river damming, including planning and operation. Planning of dams should be conducted at a system level to ensure that decisions are made in a more holistic manner. Prior to dam construction, the intensity of hydropower development should be determined at a basin scale, in order to balance river ecosystem conservation and economic benefits. It is also imperative to develop strategic dam planning, especially at the basin or regional scale, by performing multi-criteria optimization schemes (Flecker et al., 2022). Adequate investigations should be conducted to identify the siting of dams so as to minimize impacts on fish spawning, feeding and wintering grounds within the local hydro-geophysical constraints. Research on the impacts of dam construction on river ecosystem services, such as water supply, sediment transport, and biodiversity maintenance, should be strengthened. The planning of dams on mainstream and tributary rivers must be collaborative, and consider the optimal combination of high dams, low dams and run-of-river dams, which is important to reduce impacts on the river ecosystem at a basin scale (Couto and Olden, 2018; Couto et al., 2021; Schmitt et al., 2019). For fish that have lost their habitats in a mainstream that has been dammed, it is valuable to investigate the possibility of restoring tributaries to provide fish with alternative habitats.

Although there are plenty of studies concerning native fish conservation in dammed rivers, most focus on a specific issue (e.g., such as fish passage or habitat restoration), and comprehensive conservation strategies that consider the habitat requirements of fish species throughout their life history are lacking. Existing conservation measures that aim at restoring the physical habitats for fish have had limited effectiveness, and there is demand for more studies to refine these measures and ensure they better achieve their intended goals. Specifically, the effectiveness and efficiency of the measures need to be assessed quantitatively by using long-term monitoring data of dammed rivers, so that emerging problems can be identified in a timely manner, and thereby aid improved designs for more efficient measures. It is of great value to develop a framework to assess systematically the effectiveness and efficiency of conservation measures for target fish species from the genetic to population, metapopulation, community, and ecosystem levels. NbS have shown a high potential to conserve fish species in dammed rivers and deserve more attention in future studies. Moreover, it is important to incorporate more target fish species when investigating and planning a conservation program. Finally, consideration of hydrokinetic energy and submerged turbines is valuable, as these can generate electricity without many of the drawbacks of dams, although the power yield is less.

5.2. Long-Term Systematic Observations

One important aspect of the knowledge gap concerning the impacts of river damming on fish and associated conservation measures is the lack of long-term monitoring data. Compared to the long-term records of natural rivers from gauge-stations, similar data for dammed rivers are relatively short-term. Dam construction also causes inconsistencies between data before and after impoundment. Changes in river morphology are usually slow, and thus the evolution of channel morphology after river damming, and its impacts on fish physical habitats, demand longer monitoring periods. Hysteresis exists in the response of river ecosystems to hydro-geophysical changes, which also requires sufficiently long observations. TDG supersaturation only occurs during the occasional flood discharge of dams, providing few monitoring opportunities for data collection. It is also difficult, if not impossible, to obtain the near-field data of TDG. Moreover, the changes to the physical habitat and adaptation of fish species in dammed rivers may interact with each other, and these changes increase the complexity of evaluating the impact of dam construction on fish communities and developing conservation measures. Therefore, there is an urgent need to establish dedicated monitoring networks in dammed rivers to strengthen the collection of long-term and systematic data to improve our understanding of the impacts of river damming on fish. Future hydro-geophysical monitoring of large rivers can be revolutionalized by observing from satellites, such as the SWOT mission. Emerging technology, such as eDNA, otolith microchemistry, and biotelemetry, can be used to characterize the dynamics of fish communities in dammed and undammed rivers, thereby providing useful comparisons. Such long-term monitoring data concerning hydro-geophysical conditions and fish communities will deepen knowledge on the impacts of river damming on fish, which will then provide a fuller scientific basis for developing conservation strategies.

Available information on the impact of dams on fish is based mainly on statistical analyses of data from field observations and laboratory experiments concerning the relationships between key hydro-geophysical factors and various fish-related endpoints. Some studies examine the behavioral responses of target fish species to variations of key hydro-geophysical factors in the laboratory to establish suitability curves, which are then used to develop fish habitat models for impact assessment or prediction. These studies have made significant contributions to evaluating the impacts of river damming and the design of fish conservation measures. In future, the adoption of genomic, transcriptomic, proteomic, metabolomic and bioinformatic methods can be a viable approach to investigate the physiological mechanisms of how altered hydro-geophysical conditions affect gonad development, sex differentiation, gene regulation, and gene expression of target fish species (Natri et al., 2019; Ortega-Recalde et al., 2020). In addition, neurotoxic effects of river damming on fish behavior, personality and cognition could, in turn, potentially generate feedback loops that may amplify the effects on fish. Therefore, integrative approaches that combine field observations with novel technologies (e.g., molecular omics techniques, biotelemetry) are recommended to bridge the knowledge gap in assessing river damming impacts on fish. This will enable the development of more reliable models to predict long-term consequences, and thus support the implementation of effective conservation measures.

5.3. Complex Effects of Climate Change and Land Cover Changes

Climate change has dramatic impacts on river hydrology and thermal regimes, and thus affects the migration, reproduction, growth and distribution of fish species in various ways. Regional patterns of warming-induced changes in surface hydroclimate are complex, with evidence of increases and decreases in the magnitude of precipitation and runoff, as well as frequency, depending on the local context (Milly et al., 2005). The mean and high water temperature of global rivers are projected to increase under climate change, with the impact varying between regions and across seasons. Climate change may thus exacerbate the effect of river damming on fish habitats. Reservoir operation has disturbed natural hydrological regimes and riverine hydrodynamic conditions, and climate change could bring additional alterations by affecting the patterns of global precipitation and snowmelt. Climate warming may increase river water temperatures, prolong stratification and decrease vertical mixing in reservoirs. Such prolonged stratification intensifies anoxia, which promotes the release of nutrients from sediment and stimulates eutrophication in reservoir waters, thus affecting fish community structure and food web dynamics. Meanwhile, increases in water temperature reduce the dissolved oxygen content of water bodies, and the stratification of reservoirs intensifies the deficiency of dissolved oxygen in the bottom layer, which affects the survival of benthic fish species. However, reservoir operation can also mitigate impacts of future climatic variability and climate change on fish habitats, for example, by releasing cold water to offset impacts of warming temperatures on cold-water fish species (Benjankar et al., 2018). Climate change and reservoir retentions jointly influence river sediment regime, which affects river morphology and substrate composition, thereby impacting on fish habitat (J. Li et al., 2021). Future studies concerning the effects of climate change on fish should take into account changes in watershed soil erosion, sediment flux and nutrient loss, which play an increasingly important role in river ecosystems, when assessing the impacts of dams on fish (Best et al., 2022; J. Li et al., 2021). Due to the lack of integrated data concerning climate change, dam regulation and the evolution of fish communities, the interactive multi-stressor impacts of climate change and river damming on fish demand further investigation.

Climate change and dam construction also affect land use, which can directly or indirectly impact river ecosystems. For example, climate change affects the amount and distribution of vegetation, agriculture and forestry, and dam construction can promote rapid urbanization along the river. This significantly increases impervious surface areas that lead to higher flood flows and earlier flood timing, and thus intensifies the impact on fish in dammed rivers. The development of industrial and residential areas results in increased discharge of industrial wastewater and domestic sewage, which could change local water temperatures and nutrient levels, and thereby affect fish migration, spawning and feeding. Therefore, the impacts of river damming on fish could become extraordinarily complex under the effects of climate and land use change. This highlights the need to consider the full range of stressors affecting rivers, identify the major factors, and assess both their interactions and timescales of their effects in future studies (Best & Darby, 2020). Advances in numerical modeling and data collection could be used to develop virtual watersheds, where different climate change forcings can be used to simulate processes in river-reservoir systems (Benjankar et al., 2018; Tranmer et al., 2020). Preliminary implementations of this methodology have shown its benefits in understanding the impact of dam operations on fish habitat.

Data Availability Statement

Most of data supporting the figures are available via the cited references. Data of Figures 1a and 1b are available through Lehner et al. (2011). Data of Figures 1c and 1d are available through Zarfl et al. (2015). Data of Figure 3a are calculated from Hydrological Data of Changjiang River Basin in Annual Hydrological Report P. R. China, including average monthly discharge data of Pingshan station (2007–2010) and Xiangjiaba hydrological station (2016–2020). Data of Figure 3b are available from Hydrological Data of Changjiang River Basin in Annual Hydrological Report P. R. China, including average monthly discharge data of Ningnan hydrological station in 2015 and 2019. Data of Figure 3c are from the authors (Q. Li, 2023). Data of Figure 3d are available from Q. Chen et al. (2021). Data of Figure 5a are calculated from Hydrological Data of Changjiang River Basin in Annual Hydrological Report P. R. China, including average monthly water temperature data of Pingshan station (2007–2010) and Xiangjiaba hydrological station (2016–2020). Data of Figure 5c are available through T. Li et al. (2021). Data of Figure 6b are available through Y. Wang et al. (2015). Data of Figure 16 are available through Q. Chen et al. (2021). Data of Figure 17e are available through S. He et al. (2021).

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