The Living Planet Index (LPI) for migratory freshwater fish

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TECHNICAL REPORT

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GLOSSARY

Migration/Migratory
The movements animals undertake between critical habitats to complete their life cycle. Often, this is a seasonal or cyclical movement between breeding and non-breeding areas.

Migratory freshwater fish
In this report, any fish species classified in GROMS as catadromous, anadromous, amphidromous, diadromous or potamodromous.

GROMS
The Global Register of Migratory Species (GROMS) supports the Bonn Convention by summarising the state of knowledge about animal migration.

Diadromous
Fish species that travels between saltwater and fresh water as part of its life cycle. This category usually includes catadromous, anadromous and amphidromous species but is used for some species in GROMS that have not been assigned to any of these three categories.

Catadromous
Fish species that migrates down rivers to the sea to spawn, e.g. European eel *Anguilla anguilla.*

Anadromous
Fish species that migrates up rivers from the sea to spawn, e.g. salmon and Atlantic sturgeon *Acipenser oxyrinchus.*

Amphidromous
Fish species that travels between freshwater and saltwater, but not to breed, e.g. some species of goby, mullet and gudgeon.

Potamodromous
Fish species that migrates within freshwater only to complete its life cycle, e.g. catfishes and White sturgeon *Acipenser transmontanus.*

Mega-fish
Refers to large-bodied fish that spend a critical part of their life in freshwater or brackish ecosystems and reach at least 30kg.

Species
A group of living organisms consisting of similar individuals capable of exchanging genes or interbreeding.

Population
In the Living Planet Database (LPD), a population is a group of individuals of a single species that occur and have been monitored in the same location.

Time series
A set of comparable values measured over time. Here, these values are abundance estimates of a set of individuals of the same species monitored in the same location over a period of at least two years using a comparable method.

Index
A measure of change over time compared to a baseline value calculated from time series information.

Data set
A collection of time series from which an index is calculated.

SUMMARY

Migratory freshwater fish (i.e. fish that use freshwater systems, either partly or exclusively) occur around the world and travel between critical habitats to complete their life cycle. They are disproportionately threatened compared to other fish groups but global trends in abundance, regional differences and drivers of patterns have not yet been comprehensively described. Using abundance information from the Living Planet Database, we found widespread declines between 1970 and 2016 in tropical and temperate areas and across all regions, all migration categories and all populations.

Globally, migratory freshwater fish have declined by an average of 76%. Average declines have been more pronounced in Europe (-93%) and Latin America & Caribbean (-84%), and least in North America (-28%). The percentage of species represented was highest in the two temperate regions of Europe and North America (almost 50%).

For the continents of Africa, Asia, Oceania, and South America, data was highly deficient, and we advise against making conclusions on the status of migratory freshwater fish in these areas. Potamodromous fish, have declined more than fish migrating between fresh and salt water on average (-83% vs -73%). Populations that are known to be affected by threats anywhere along their migration routes show an average decline of 94% while those not threatened at the population level have increased on average. Habitat degradation, alteration, and loss accounted for around a half of threats to migratory fish, while overexploitation accounted for around one-third.

Protected, regulated and exploited populations decreased less than unmanaged ones, with the most often recorded actions being related to fisheries regulations, including fishing restrictions, no-take zones, fisheries closures, bycatch reductions and stocking (these were most common in North America and Europe). Recorded reasons for observed increases tended to be mostly unknown or undescribed, especially in tropical regions. This information is needed to assemble a more complete picture to assess how declines in migratory freshwater fishes could be reduced or reversed. Our findings confirm that migratory freshwater fish may be more threatened throughout their range than previously documented.

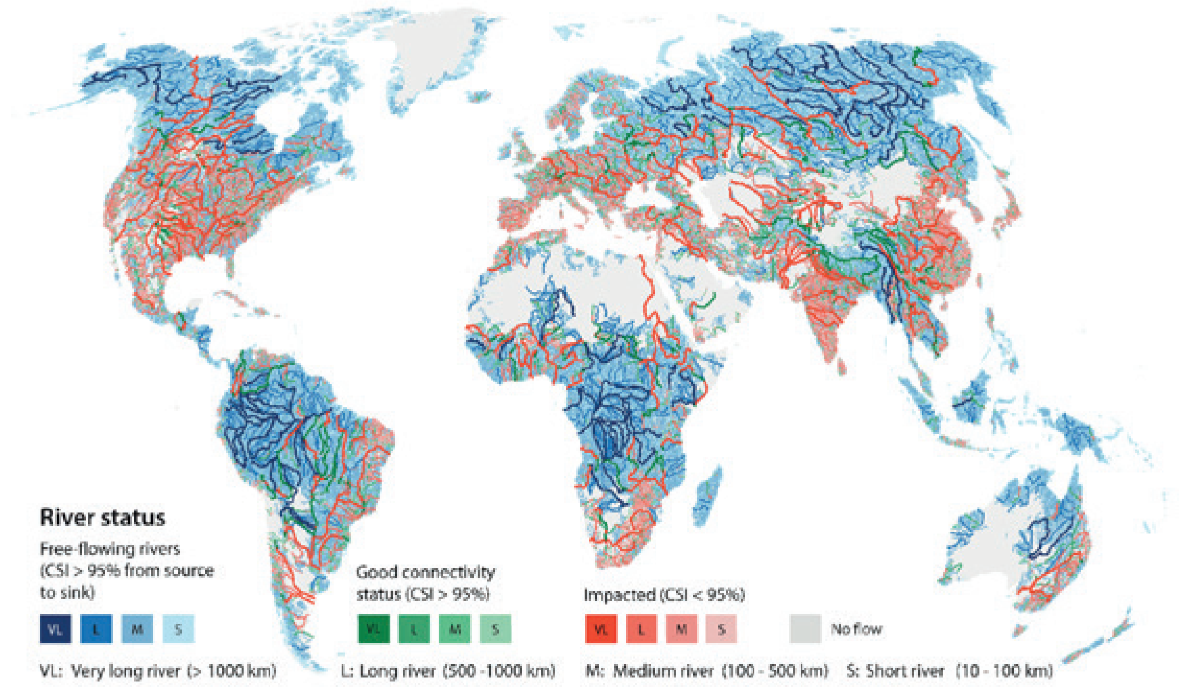
FISH HEADING UPSTREAM THE JURUENA RIVER, SALTO SÃO SIMÃO, MATO GROSSO-AMAZONIAN STATES, BRAZIL

BOX 1

FREE-FLOWING RIVERS

A free-flowing river occurs where natural aquatic ecosystem functions and services are largely unaffected by changes to connectivity and flows allowing an unobstructed exchange of material, species and energy within the river system and surrounding landscapes beyond. Free-flowing rivers provide a multitude of services including cultural, recreational, biodiversity, fisheries, and the delivery of water and organic materials to downstream habitats including floodplains and deltas. The connectivity provided by free-flowing rivers is critical for the life history of many migratory fish that depend on both longitudinal and lateral connectivity to access habitats necessary for the completion of their life cycle. A recent global assessment of the connectivity status of rivers globally found that only 37% of rivers longer than 1,000 km remain free-flowing over their entire length and 23% flow uninterrupted to the ocean (Grill *et al.* 2019). Very long FFRs are largely restricted to remote regions of the Arctic and of the Amazon and Congo basins (Figure 1). In densely populated areas only few very long rivers remain free flowing, such as the Irrawaddy and Salween. Dams and reservoirs and their up- and downstream propagation of fragmentation and flow regulation are the leading contributors to the loss of river connectivity.

FIGURE 1
Free-flowing river status of rivers globally (from Grill *et al.* 2019).



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INTRODUCTION

Migration consists of the regular, seasonal movements animals undertake between critical habitats to complete their life cycle (Dingle and Drake 2007). Often, this is the movement between breeding and non-breeding areas. In fish, it can be distinguished from other types of movement because it takes place between two or more well-separated habitats, occurs regularly (often seasonally), involves a large fraction of a population, and is directed rather than random (Northcote 1978). Migratory fish occur around the world, with some species moving large distances while others undertake migration on a more local scale. Thousands of known fish species have tendencies to migrate within or between rivers and oceans with over 1,100 of these species where migration is required for their survival (Lucas *et al.* 2001; Brink *et al.* 2018). For example, Pacific Salmon return from the ocean to the same river where they were born to breed, while Congolli (*Pseudaphritis urvillii*) where males and females live separately and need to migrate in order to breed (e.g. Zampatti et. al 2010). Here, we define migratory freshwater fish species to be those that use freshwater habitats for at least some part of their life cycle.

There is evidence that freshwater species are at greater risk than their terrestrial counterparts (Collen *et al.* 2009b; IUCN 2020). Almost one in three of all freshwater species are threatened with extinction (Collen *et al.* 2014), and migratory fish are disproportionately threatened compared to other fish groups (Darwall & Freyhof 2016). Moreover, mega-fishes (species that spend a critical part of their life in freshwater or brackish ecosystems and reach 30kg) such as Beluga sturgeon (Huso huso) or the Mekong giant catfish, are particularly vulnerable to threats (58%; Carrizo *et al.* 2017). Catches in the Mekong River basin between 2000 and 2015, for example, have decreased for 78% of freshwater fish species, and declines

SOCKEYE SALMON MIGRATING FREELY TO THEIR SPAWNIG GROUNDS. ILIAMNA LAKE, ALASKA
© Jason Ching

are stronger among medium-to large-bodied species (Ngor *et al.* 2018). However, it is likely that our knowledge is biased towards these charismatic, mega-fishes, and that smaller, less iconic species may be overlooked (e.g. Yarra pygmy perch; Saddlier *et al.* 2013).

One of the largest issues is the blockages of migration routes and lack of free-flowing rivers globally (Grill *et al.* 2019; see Box 1). Many artificial barriers, such as dams, culverts, road crossings and weirs impede the movement of migratory fish and reduce their ability to complete their lifecycle (Winemiller *et al.* 2016). Dams and other river infrastructures can also significantly change the flow regime, affecting the extent and connectivity of, for example, downstream floodplain habitats, as well as the timing and magnitude of critical cues crucial for migration and live stage transition (see Box 2). Climate change will continue to exacerbate the impacts of altered habitats on freshwater ecosystems and add additional stressors such as pollution, thermal stress, water diversion, water storage, or invasive species proliferation (Ficke *et al.* 2007). In addition, because migration is typically cyclical and predictable, migratory fish can be easily exploited (Allan *et al.* 2005). On top of these obvious and well known threats, there are also many emerging threats (e.g. microplastic pollution, freshwater salinisation) to freshwater ecosystems and the fish they support (Reid *et al.* 2019). With knowledge of the current and predicted threats, a global overview of the status and trends of migratory freshwater fish is needed to assess impacts and drivers of change on this group, and to examine if trends are consistent among regions.

Biodiversity indicators are an important tool to present a broad overview of trends in migratory fish health at the global scale. Various metrics, such as species extinction risk and abundance, can provide insight into the driving forces behind observed trends (Böhm *et al.* 2016; Spooner *et al.* 2018) and can be used to model projections under future scenarios (Visconti *et al.* 2016). To date, the first global analyses of this kind using abundance trends in migratory freshwater fish populations revealed an overall decline amongst species since 1970 (WWF 2016; Brink *et al.* 2018). However, data coverage tends to be skewed towards temperate regions of North America and Europe (Limburg and Waldman 2009; Heino *et al.* 2016; McRae *et al.* 2017) so the extent to which this trend is consistent among all regions of the world has not yet been well explored.

GATHEGA DAM

Dams like the Gathega Dam in New South Wales, Australia not only block the migration route of migratory fish, but also block sediment transport and destroy river habitat. © WWF

This report presents an update of the same global analysis using a more recent data set with improved representation of species monitored in areas generally classified as tropical. We used the Living Planet Index (LPI) method (Loh *et al.* 2005; Collen *et al.* 2009a; McRae *et al.* 2017), a global measure of biological diversity that is being used to track progress towards the Aichi Biodiversity Targets (SCBD 2010). The LPI tracks trends in abundance of a large number of populations of vertebrate species in much the same way that a stock market index tracks the value of a set of shares or a retail price index tracks the cost of a basket of consumer goods. We examine more closely how trends in migratory freshwater fish differ between different regions of the world and between species undertaking different kinds of migration, and explore possible drivers for the patterns we observe.

BOX 2

DAMS

The number of dams has increased substantially in the past six decades for many purposes such as irrigation, water storage, hydroelectric power, navigation and flood control (Lehner *et al.* 2011). It is reported that there are 57,985 large dams worldwide, with countless small dams (McCully 1996; ICOLD 2020). Now worldwide only 37% of large rivers over 1,000 km are free flowing (Grill *et al.* 2019) and these are mostly in remote locations. Dams often have major impacts on migratory fish as they decrease connectivity and alter flow regimes. In the upper Paraná River in Brazil damming changed the river water regime leading to a smaller flooded area downstream. The migratory Streaked prochilod (Prochilodus lineatus) is dependent on flooding as a mechanism for dispersing into lagoons where juveniles live for 1-2 years. Without flooding they are unable to complete this stage in their life cycle and numbers have been reduced to critical levels (Gubiani *et al.* 2006). But water flow alterations do not necessarily cause decreases in all migratory freshwater fish. For example, a number of detritivorous species benefitted from the explosive development of attached algae below a newly constructed dam in French Guiana (Merona *et al.* 2005).

In addition to changing the hydrology of a river, dams can also create a physical barrier for migratory fish to spawn.. In the Yangtze river, dams have reduced the river distribution of the Chinese sturgeon by 50% and they can no longer reach their original spawning grounds. The Chinese sturgeon has so far been able to adapt and spawn in an extremely different environment, however, they are on the brink of extinction and with further dams proposed the species will not survive without conservation efforts (Zhuang *et al.* 2016). These impacts, in addition to water quality issues (e.g. thermal pollution, dissolved oxygen alteration, heavy metal accumulation) signal a difficult future for migratory fish in obstructed river systems.

However, there has also been efforts to balance biodiversity with dam benefits. Following the construction of hydroelectric dams in the Penobscot River (USA), migratory fish populations started to decline, some of them dramatically. This led to the Penobscot River Restoration Project being set up by local stakeholder groups. By removing the two most seaward dams and incorporating fish passages, six migratory fish species regained access to nearly their full historical range (Opperman *et al.* 2011). Opportunities were also used to increase electricity generation strategically at certain remaining dams to ensure that overall generation did not decrease (Opperman *et al.* 2011). With the impact of large dams predicted to greatly increase habitat fragmentation in tropical and subtropical river basins (Barbarossa *et al.* 2020), strategic river management at multiple scales, and setting conservation priorities for species and basins at risk will be vital.

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RESULTS AND DISCUSSION

DATA SET

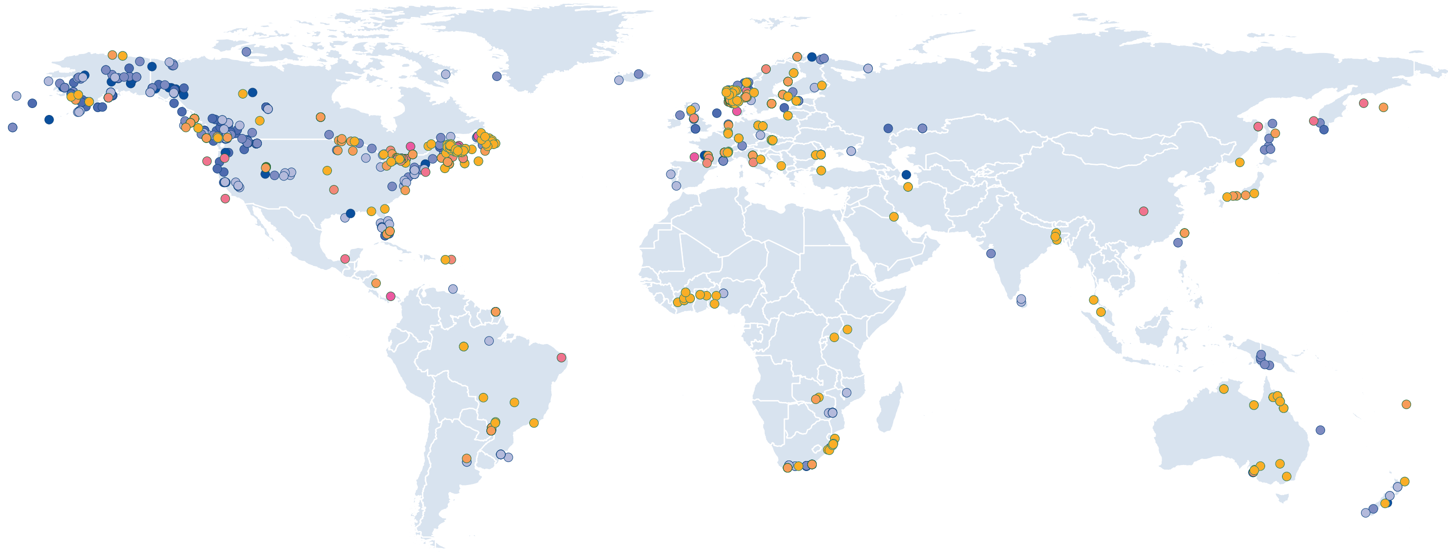
We extracted, from the Living Planet Database (LPD; LPI 2020), abundance information for 1,406 populations of 247 fish species listed on the Global Register of Migratory Species (GROMS; Riede 2001) as anadromous, catadromous, amphidromous, diadromous or potamodromous, i.e. completing part or all of their migratory journey in freshwater. These species will be referred to as 'migratory freshwater fish' in this report. Information on the method used, the interpretation of the LPI ('The LPI, its calculation and interpretation') and a list of species (Table A1) can be found in the Appendix. Non-native populations were not included in the final data set.

This represents an increase of 757 populations and 85 species since the last published trend information in 2016 (WWF 2016), i.e. a 52% increase in the number of species included (Table 1). Data for these new populations were collected from scientific journals, government or unpublished reports, or received from in-country contacts in the case of unpublished data. The majority of new data were added since an unpublished 2018 analysis, which was based on 981 populations of 180 species. Some were a result of including diadromous fishes, which were previously excluded, or a result of the recoding of the GROMS category of existing LPD populations. Most of these new populations are time series of between 2 and 20 years in length from around the world, many starting to fill gaps in areas such as Africa, Australia and South America (Table 1, Figure 1). Despite this, many large data gaps remain, especially in the tropics and large parts of Asia (Figure 1, Table 2).

TABLE 1
Increase in the LPD data set of fishes listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous since the last published index in 2016 (WWF 2016).

DATA SET	SUBSET	NUMBER OF SPECIES (2016)	NUMBER OF SPECIES (2020)	% CHANGE SINCE 2016
Global		162	247	52%
Zone	Temperate	94	108	15%
	Tropical	74	150	103%
Region	Africa	24	43	79%
	Asia & Oceania	34	77	126%
	Europe	37	49	32%
	Latin America and Caribbean	28	46	64%
	North America	61	63	3%

FIGURE 1
Map of 1,406 monitored populations of 247 species of fishes listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous included in this analysis. Blue points denote populations used for the last published index for migratory freshwater fish in the Living Planet Report 2016 (WWF 2016). Orange-pink points denote those populations that have been added since 2016. Different shades denote the length of the time series in years between 1970 and 2016.



New populations	Existing populations
2-9 years	2-9 years
10-19 years	10-19 years
20-29 years	20-29 years
30-39 years	30-39 years
40-48 years	40-48 years

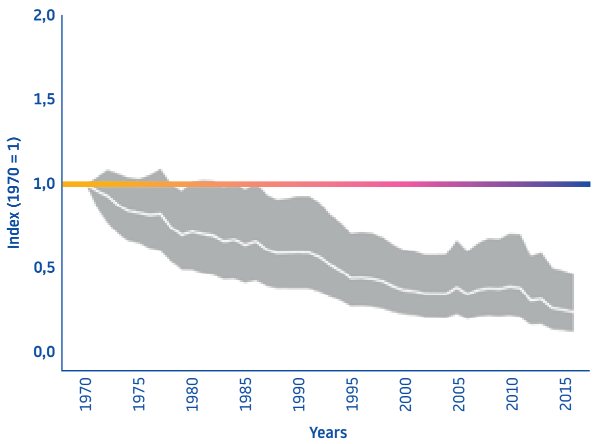
GLOBAL TREND

The 247 monitored species showed an overall average decrease of 76% between 1970 and 2016 (bootstrapped 95% confidence interval: -88% to -53%; Figure 2). This is equivalent to an average 3% decline per year. Because the LPI describes average change, this means that although populations of these monitored species are, on average, 76% less abundant in 2016 compared to 1970, it should be recognised that species could have decreased more or even increased over the same period.

As seen in Figure 3a, the majority of species are declining (56%), while 43% have increased on average. When examining the total change for each species in more detail, we see that the majority of species trends are at the extremes, being either very positive or very negative (dark green and dark red bars in Figure 3b). While there are plenty of species decreasing less than the most extreme cases, smaller increases - ranging from around 5% to 80% - are observed much less (Figure 3b). Stable species, i.e. those changing by less than 5% over the monitoring period, are rare (Figures 3a and 3b). Overall, this suggests that there are not just more declining species but that declining species are showing greater change than increasing species.

FIGURE 2

Average change in abundance of -76% between 1970 and 2016 of 1,406 monitored populations of 247 species of fishes listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous. The white line shows the index values and the shaded areas represent the bootstrapped 95% confidence interval (-88% to -53%).



The index displays a fairly consistent decline until the mid-2000s, after which the rate of decline slows a little, resulting in a more stable yet overall downward trend. A more negative trend can be seen again after 2011. When examining average change by decade, it becomes clear that the largest negative change occurred in the 1970s (-3.9%), 1990s (-4.5%) and between 2010 and 2016 (-7.7%), with very little change on average in the 2000s (Figure 4). Both the lack of change in the 2000s and the large decline in the 2010s may be explained by changes in data availability. A larger number of declining populations leave the index after 2000, leading to a more stable trend, while the number of available populations reduces in the 2010s due to publication lag. In both cases, a smaller data set is more heavily influenced by the trends of its remaining populations (see 'Limitations' section).

The global index is based on monitoring data from locations around the world, although most populations were sampled in the temperate regions of North America and Europe (Figure 1, Table 2). It represents 21% of 1,158 GROMS-listed migratory freshwater fish species, with representation for different GROMS categories ranging from 14% in the amphidromous to 40% in the catadromous migration categories (Table 2). Analysis of the proportional representation across regions revealed a significant imbalance of represented areas, with under-representation from Africa and Asia & Oceania, while species in Europe and North America were well exemplified (Table A2). In terms of GROMS categories, amphidromous species are significantly under-represented, while anadromous, catadromous and diadromous species are over-represented (Table A2). Species counts in the potamodromous and freshwater-saltwater combined categories are not significantly different to expected proportions (Table A2).

Overall, the global index suggests that monitored populations of migratory freshwater fish have a similar trend to freshwater vertebrate species overall, which have shown an average decline of 83% over roughly the same period (WWF 2018). This may be surprising, considering the larger number of threats migratory fish are exposed to due to travelling long distances and traversing different habitats. However, it should be noted that the freshwater LPI also includes information on other taxonomic groups, of which tropical amphibians show a most precipitous decline, which is driving the freshwater trend. Similarly, the overall index for migratory freshwater fish may mask differences in different subsets of the underlying data, for example temperate and tropical areas, regions, and GROMS categories, so these are explored in more detail below.

FIGURE 3A

The proportion of 247 migratory freshwater fish species (listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous) with a declining (pink-orange), stable (blue) or increasing (green) species-level trend. A stable trend is defined as an overall average change of ±5%.

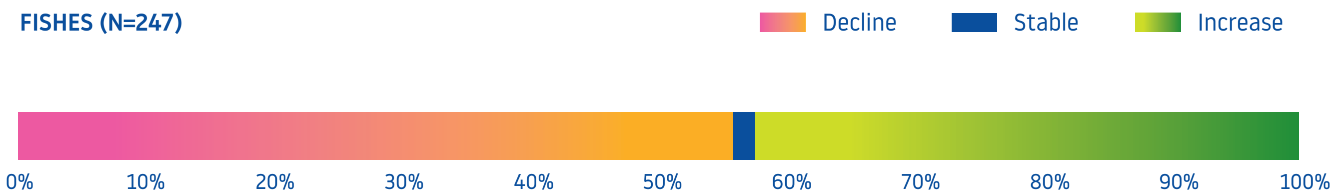


FIGURE 3B

Histogram of the total average change of 247 migratory freshwater fish species (listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous). Please note that '±5%' represents a stable trend.

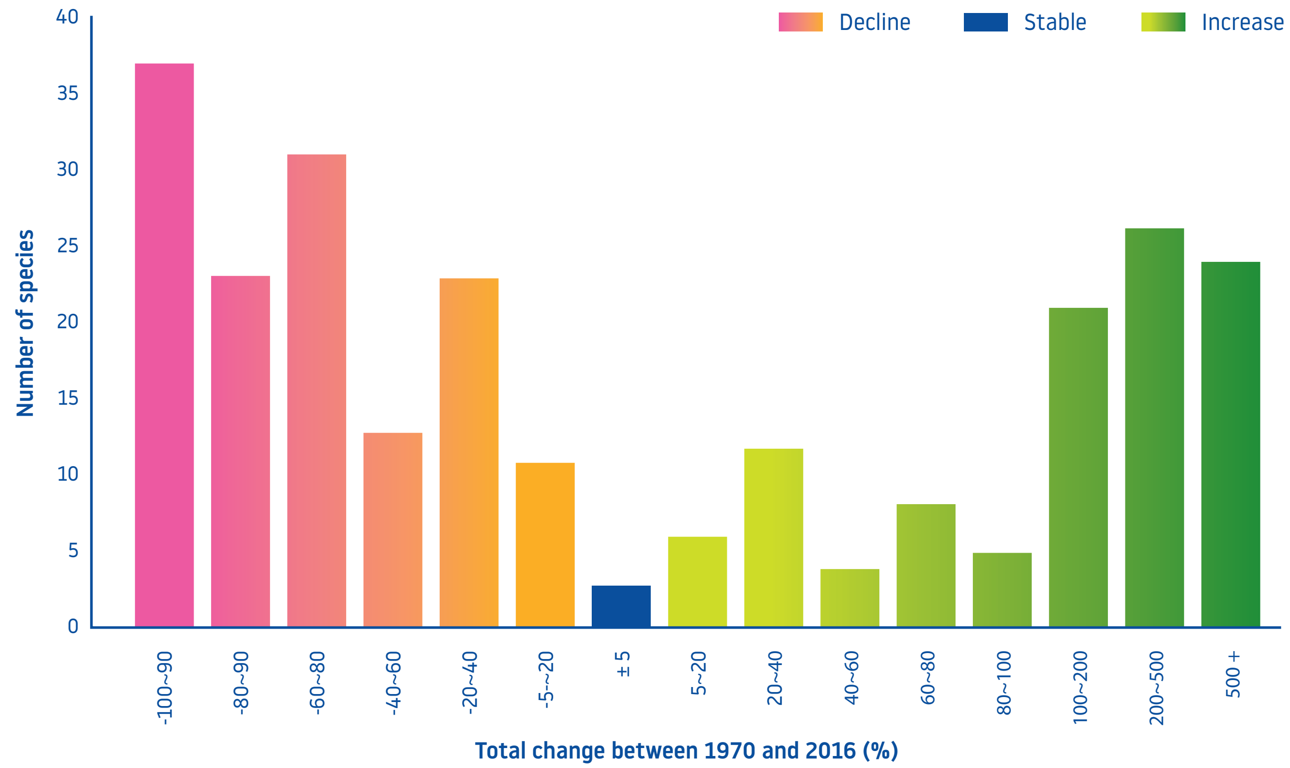


FIGURE 4

Average annual change in population abundance for 1,406 monitored populations of 247 species of fishes listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous by decade: 1970s, 1980s, 1990s, 2000s and 2010-2016. Please note that the more negative recent annual trend may be due to reduced data availability, leading to rapidly declining species dominating a smaller data set. The small change in the 2000s may be due to a larger number of declining populations leaving the index during this period than populations joining the index.

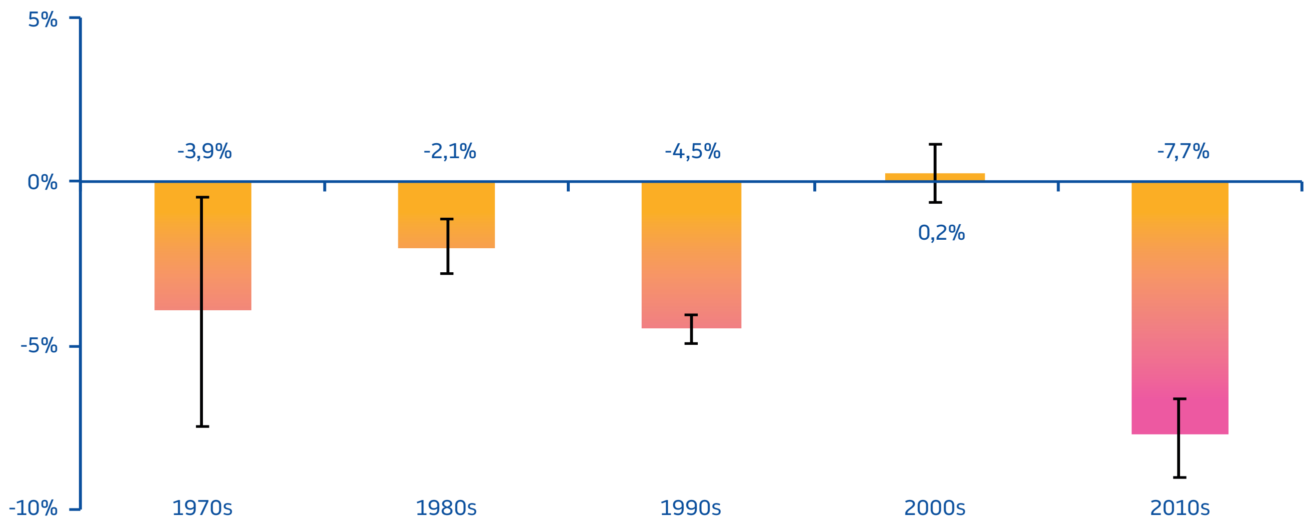


TABLE 2

Number of populations and species of migratory freshwater fish (GROMS-listed as anadromous, catadromous, amphidromous, diadromous or potamodromous), the number of expected species (according to GROMS), and the percentage representation for each subset for which an index was calculated. Please refer to the appropriate sections for explanations of the different data sets.

DATA SET	SUBSET	POPULATIONS	SPECIES	EXPECTED SPECIES	% REPRESENTED
Global		1.406	247	1.158	21%
Zone	Temperate	1.073	108	-	-
	Tropical	358	150	-	-
Region	Africa	104	43	325	13%
	Asia & Oceania	165	77	804	10%
	Europe	408	49	108	45%
	Latin America and Caribbean	80	46	183	25%
	North America	649	63	141	45%
GROMS	Potamodromous	390	109	572	19%
	Fresh- & Saltwater combined	1.016	138	586	24%
	Amphidromous	*144*	*44*	*324*	*14%*
	Anadromous	*738*	*59*	*174*	*34%*
	Catadromous	*116*	*28*	*70*	*40%*
	Diadromous	*18*	*7*	*18*	*39%*
Threat status	Threatened	290	116	-	-
	No threats	175	83	-	-
	Unknown threat status	941	161	-	-
Management	Managed	359	63	-	-
	Unmanaged	428	163	-	-

TROPICAL AND TEMPERATE ZONES

The LPD divides the world into temperate and tropical zones based on biogeographic realms as defined by Olsen *et al.* (2001). The temperate zone includes the Nearctic and Palearctic (this roughly equates to North America, Europe and Central Asia), and the tropical zone the remaining areas of the world. Migratory freshwater fish have declined on average in both zones, although they have fared slightly better in temperate areas (-79% vs -82%; Figure 5). The overall declines correspond to an average change of 3.4% per year for temperate populations and 3.6% per year for tropical populations. The temperate trend declined continuously with few short-term fluctuations (Figure 5a; see also Figures 6a and 6b). The tropical index contained more time series than the temperate, but still showed a high degree of short-term fluctuations, as indicated by the wider confidence interval (Figure 5b; see also Figures 6c and 6d).

The high variation of the tropical index is because many of the tropical species are represented by very short time series (on average 7.6 years compared to 13.8 years in temperate populations). Short-time series result in a greater turnover of data, i.e. many time series enter and leave the data set at different times between 1970 and 2016. Thus, at any given time, fewer species were contributing to the tropical index, making it more vulnerable to trends of a few populations or set of species.

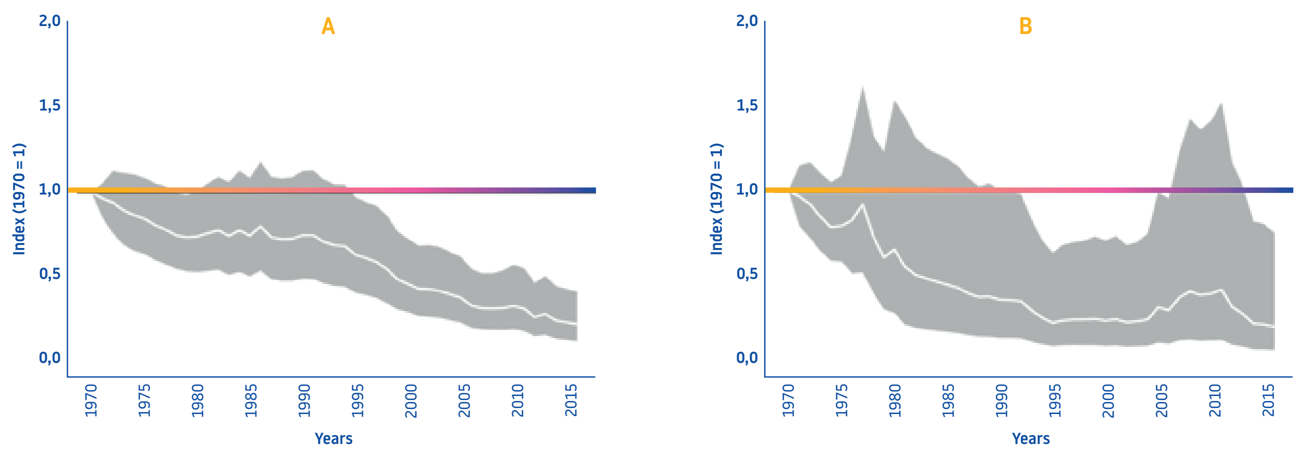
RELEASING A TAGGED MEKONG GIANT CATFISH

Mekong River, Cambodia. © Zeb Hogan

FIGURE 5

Average change in abundance of monitored migratory freshwater fishes (GROMS-listed as anadromous, catadromous, amphidromous, diadromous or potamodromous) between 1970 and 2016 in
a) temperate regions (79%; 1,073 populations of 108 species) and
b) tropical regions (82%; 358 populations of 150 species).

The white lines show the index values and the shaded areas represent the bootstrapped 95% confidence intervals.



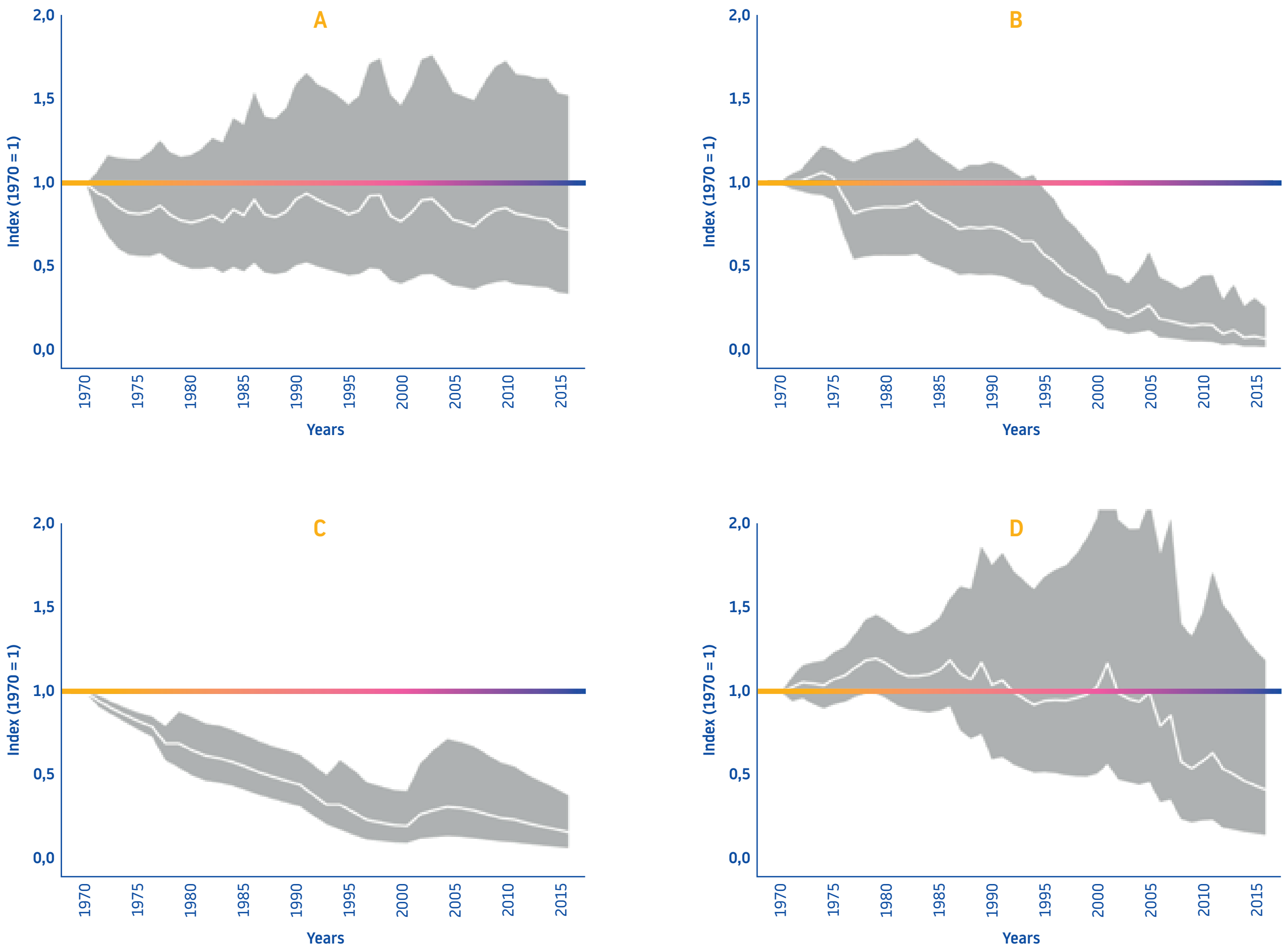
REGIONS

The data set can be divided into different political regions, following the internationally accepted UN Geographic Region classification (United Nations Statistics Division, n.d.). When examining trends for migratory freshwater fish in these regions a picture of widespread average declines emerges, ranging from -28% in North America to -93% in Europe (Figure 6). With almost half of species represented in these two temperate regions (Table 2), the trends are likely to be the most reliable. Only Asia-Oceania and Africa show a significantly lower proportion of species represented in the data set than would be expected based on actual species numbers (Table A2), so the trends may not reflect as accurately what is occurring in these regions.

FIGURE 6

Average change in abundance of monitored migratory freshwater fishes (GROMS-listed as anadromous, catadromous, amphidromous, diadromous or potamodromous) between 1970 and 2016 in
a) North America (-28%; 649 populations of 63 species)
b) Europe (-93%; 408 populations of 49 species) and
c) Latin America and Caribbean -84% since 1980; 80 populations of 46 species)
d) Asia-Oceania (-59%; 165 populations of 77 species).

The white lines show the index values and the shaded areas represent the bootstrapped 95% confidence intervals. Please note that the index for Africa is not shown here because the resulting trend is noisy, likely due to a small and biased data set. The Latin America & Caribbean index is for 1980-2016. The sharp decline in Oceania from 2000 onwards coincides with more populations entering and leaving the index than previously.



BOX 3

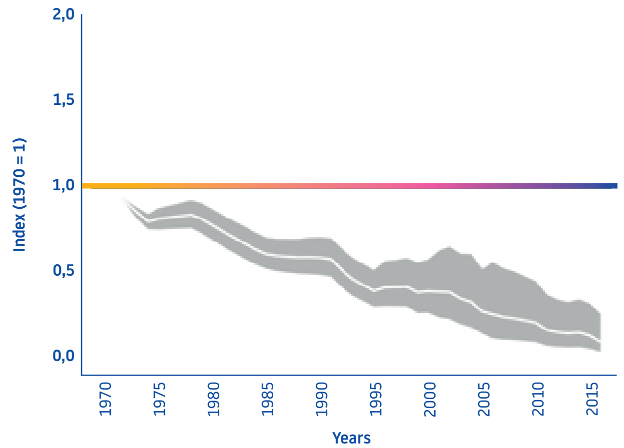
LPI FOR STURGEONS

Sturgeons (*Acipenseridae*) are one of the oldest families of bony fishes that inhabit the freshwater bodies of Eurasia and North America. Sturgeons are considered to be 'megafauna' species, as they have a slow growth rate and therefore tend to reproduce at a later stage in life. For this reason, they cannot adapt quickly to changes in the environment, which makes them particularly susceptible to threats (Ripple *et al.* 2019). According to the International Union for the Conservation of Nature (IUCN), 21 of the 25 species of sturgeon are threatened, with 16 classified as Critically Endangered, 2 as Endangered and 3 as Vulnerable (IUCN 2020). The main threats to sturgeon species are trade and overfishing (they are harvested for their roe), habitat loss and degradation, as well as pollution. As sturgeons are anadromous, i.e. they spawn upstream and feed in river deltas, they are vulnerable to any alteration of the river flow such as dam construction that might block their migratory routes to spawning and feeding grounds (Carrizo *et al.* 2017; He *et al.* 2017).

The LPI for migratory freshwater fish contains abundance information on 14 of the 25 species of *Acipenseridae*, and it is possible to calculate an index for the group. Overall, monitored sturgeon populations have declined by 91% on average between 1970 and 2016 (Figure 1). The vast majority either do not have any information recorded as to whether there are known threats to the population (47%) or have known threats (53%), with the most commonly recorded threat being exploitation (55%), followed by habitat degradation and change (31%). Only the three North American species of sturgeon in the data set are showing a positive trend overall. This may be because most declines in North American sturgeon species occurred earlier in the 20th century prior to 1970 (the earliest year considered in the LPI) when it is thought overfishing collapsed populations. North American sturgeon species now appear to have stabilised at a low level relative to historic values.

FIGURE 1

Average change in abundance of -91% between 1970 and 2016 of 36 monitored populations of 14 *Acipenseridae* species. The white line shows the index values and the shaded areas represent the bootstrapped 95% confidence interval (range: 75% to -97%). Please note that 4 populations of 3 species of sturgeon had to be excluded because they had a pronounced impact on the index.



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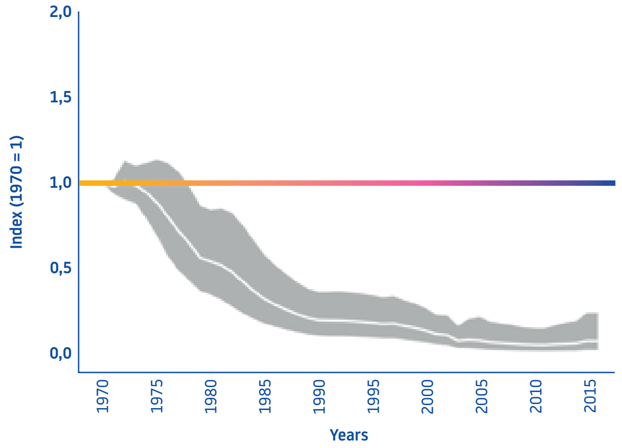
BOX 4

LPI FOR EELS

The migration of the European eel (*Anguilla anguilla*) during its life cycle is one of the longest and most complex in the anguillid group (Tsukamoto *et al.* 2002). Whilst the continental phase of the eel's life-history is relatively well-studied, we know little about the marine phase. The eel's migration begins in the open waters of the North Atlantic, from where the species uses the Gulf Stream to reach European waters. There, eels metamorphose into so-called 'glass eels' (an intermediary stage in the eel's complex life history before the juvenile, or elver, stage) and migrate upstream into rivers, where they spend 5-20 years feeding and maturing. Mortality in this phase is high, as the eels are threatened by recreational and commercial fisheries, the presence of hydropower and pumping stations, and pollution. The individuals that survive will become sexually mature and begin their 5000 km migration back to their spawning ground in the Sargasso Sea as so-called 'silver eels'.

FIGURE 1

Average change in abundance of -92% between 1970 and 2016 of 29 monitored populations of 7 anguillid species. The white line shows the index values and the shaded areas represent the bootstrapped 95% confidence interval (range: 76% to -97%).



The complexity of their life cycle makes eels particularly vulnerable to anthropogenic threats. European eel is listed as Critically Endangered by the IUCN Red List of Threatened Species due to a decline of 90-95% in the recruitment of the species in the last 45 years across a large portion of its distribution range (Jacoby & Gollock 2014). According to the International Council for the Exploration of the Sea (ICES), the recruitment of glass eels to European waters in 2018 is 2.1% of the 1960-1979 level in the North Sea and 10.1% in the rest of Europe. The steepest declines were observed between 1980 and 2010, but recruitment levels have remained low ever since (ICES 2018).

But the situation is no better for other Anguilla species according to the IUCN Red List, with 6 of the 16 species Threatened, 4 Near Threatened, 4 Data Deficient and only 2 Least Concern (IUCN 2020). The LPI for migratory freshwater fish comprises 29 populations of 7 of these anguillid species: *A. anguilla, australis, dieffenbachii, japonica, obscura, reinhardtii* and *rostrata*, mostly from Europe and North America. While this data set is nowhere near complete, it paints a similar picture, with an average decline of 92% between 1970 and 2016 (Figure 1). Over 60% of these populations are considered to be threatened, specifically by habitat loss, exploitation and also climate change.

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Tsukamoto, K., Aoyama, J., and Miller, M. J. (2002) Migration, speciation, and the evolution of diadromy in anguillid eels. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1989-19989.

Interestingly, the trend for the Latin America and Caribbean region is based on one of the smallest datasets comprising only 46 species, yet these represent a quarter (25%) of expected species (Table 2). This may be due to the fact that the GROMS classification system has not been updated recently, and older taxonomy might miss species that have been split from other species since then or those that have been more recently described. The trend appears to follow a similar trajectory until the mid-2000s, after which it increases and then decreases again (this is also seen in the tropical index; Figure 5b). This is due to a number of potamodromous species from Brazil, which increased following a drought in 2005 (Freitas *et al.* 2012). It is believed that the drought and its extended low water periods caused an abundance of fish carcasses and terrestrial plants detritus that elevated the nutrient levels in returning flood waters. As algivores or detritivores dominate the migratory species here, they would have benefitted from this nutritional pulse.

All of the other regions show trends that are less smooth with many spikes and dips, which could be attributed to a number of different factors: shorter time series entering and leaving the indices at different times and causing abrupt changes in the index; monitoring biases leading to under- and overestimation of abundance at different times during the monitoring; and potentially real cyclical patterns in the abundance of some species.

MIGRATION CATEGORIES

Fishes that are potamodromous (i.e. complete their migration entirely within the freshwater system) and species that migrate between freshwater and saltwater systems (i.e. those categorised in GROMS as anadromous, catadromous, amphidromous or diadromous) are likely to be exposed to different threats in the different systems, and may therefore show different trends. Splitting the data set into these two categories reveals that the equivalent of an average annual decline of 3.8% results in potamodromous fishes being 83% less abundant on average, with most of the decline occurring in the 1970s and 1980s. By contrast, the fish species migrating between fresh- and saltwater decrease more steadily, but the overall average change is less at 73% (Figure 7). Nearly a quarter of fish species migrating between fresh- and saltwater are represented (Table 2), making this a perhaps more reliable trend. Please refer to Boxes 3, 4 and 5 for more detailed information on some of the more iconic anadromous, catadromous and potamodromous species.

FIGURE 7

Average change in abundance between 1970 and 2016 of monitored freshwater fishes migrating
a) between fresh- and saltwater (-73%; 1,016 populations of 138 species of fishes listed on GROMS as anadromous, catadromous, amphidromous or diadromous) or
b) within freshwater only (-83%; 390 populations of 109 species listed on GROMS as potamodromous).

The white lines show the index values and the shaded areas represent the bootstrapped 95% confidence intervals.

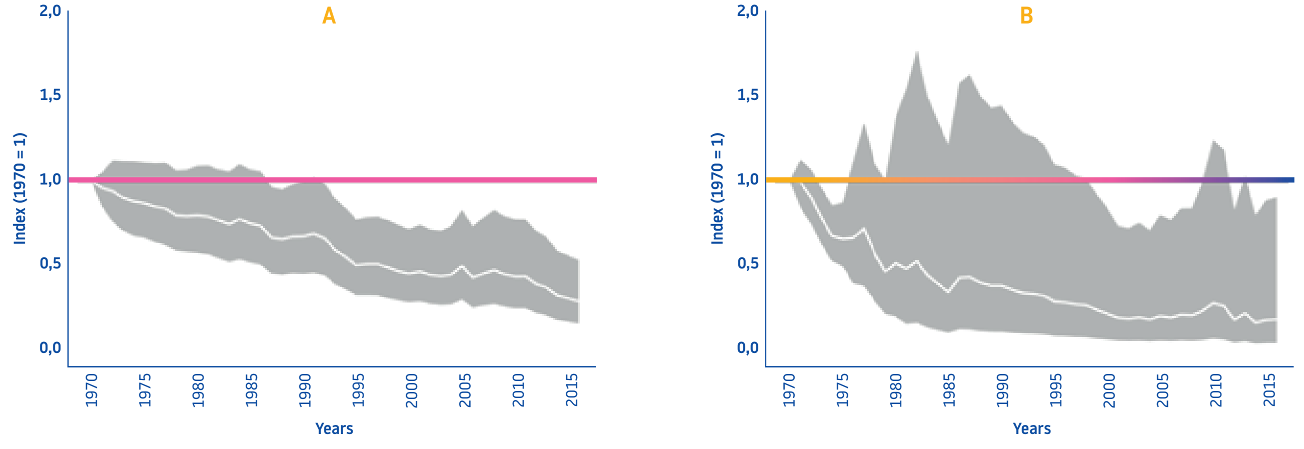
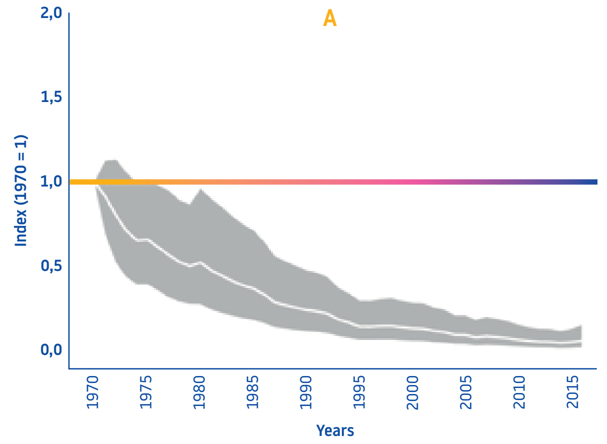
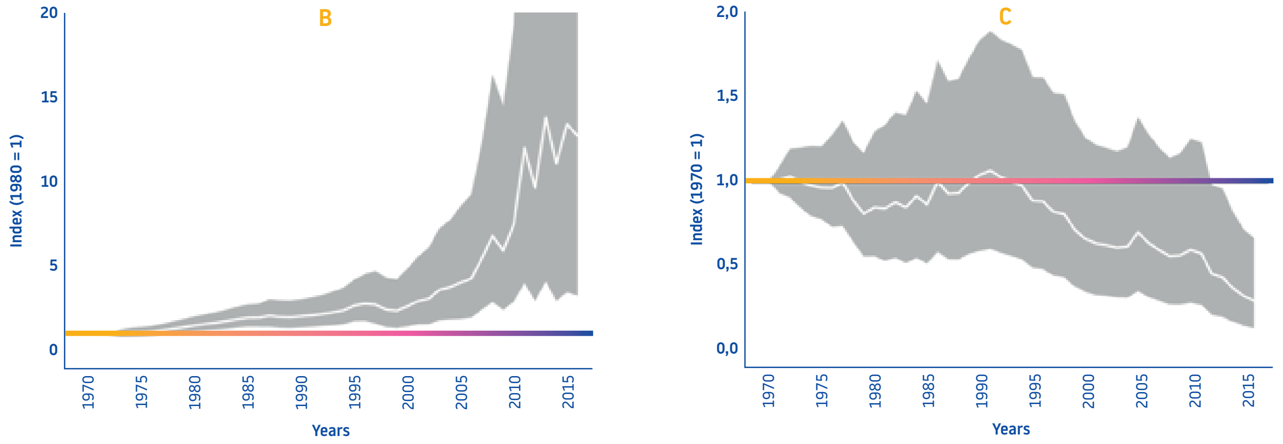


FIGURE 8

Average change in abundance of monitored migratory freshwater fishes (GROMS-listed as anadromous, catadromous, amphidromous, diadromous or potamodromous) between 1970 and 2016 that are
a) threatened (-94%; 290 populations of 116 species)
b) not threatened (+1171%; 175 populations of 83 species) and
c) with unknown threat status (-71%; 941 populations of 161 species).

The white lines show the index values and the shaded areas represent the bootstrapped 95% confidence intervals. Please note that the y-axis scale is different for populations that are not threatened.





THREATS

In the LPD, we record for each population whether it is affected by threats, not threatened or whether its threat status is unknown, based on information given in the data source. This particular 'threat status' is specific to the population, and does not correspond to the threat status for a species or "population" as recorded in the IUCN Red List (IUCN 2020). When dividing the data set in this way, we see that populations that are not threatened have increased on average, while those affected by threats show a serious average decline of 94% (Figure 8). Interestingly, species populations with unknown threat status - where no specific threat is mentioned in the data source, which is often the case with large-scale or multi-species papers - show an average decline of -71% between 1970 and 2016. In combination with the apparently increasing non-threatened species populations, this indicates that populations with unknown threat status are also under pressure even though no threat information was not documented.

In addition to identifying whether a population is affected by threats, the LPD allows for up to three threats to be recorded for each population. They are grouped into broad categories, following the Red List classification (IUCN 2020): habitat degradation and change, habitat loss, exploitation, invasive species, disease, pollution and climate change (Figure A3). This more detailed information on population-level threats was available for 290 populations of 116 species, totalling 414 recorded threats. While most populations were only reported to be affected by one threat, just over one-third mentioned multiple threats. The most reported threat was habitat degradation and change (40%), which together with habitat loss accounted for nearly 50% of all reported cases (Figure 9a). The second most reported threat was overexploitation, which accounted for around one-third of all threats (Figure 9a). At the regional level, habitat-related threats were most often mentioned for Europe, North America, and Oceania, while overexploitation was most commonly reported in Africa and Asia (Figure 9b).

BOX 5

GOLDEN MAHSEER

The Golden mahseer (*Tor putitora*) is a potamodromous migratory fish that makes its home in the rivers of the Himalayan region, within the basins of the Indus, Ganges and Brahmaputra rivers. These powerful swimmers travel far and fast during their migrations upstream to reach their spawning grounds. Many questions remain about this mighty fish including their migration patterns, reproductive behaviors, recruitment dynamics, and critical habitats, as well as information how human activities impact these various components. Like other large migratory fish, Golden mahseer are listed as endangered on the IUCN Red List of Threatened Species.

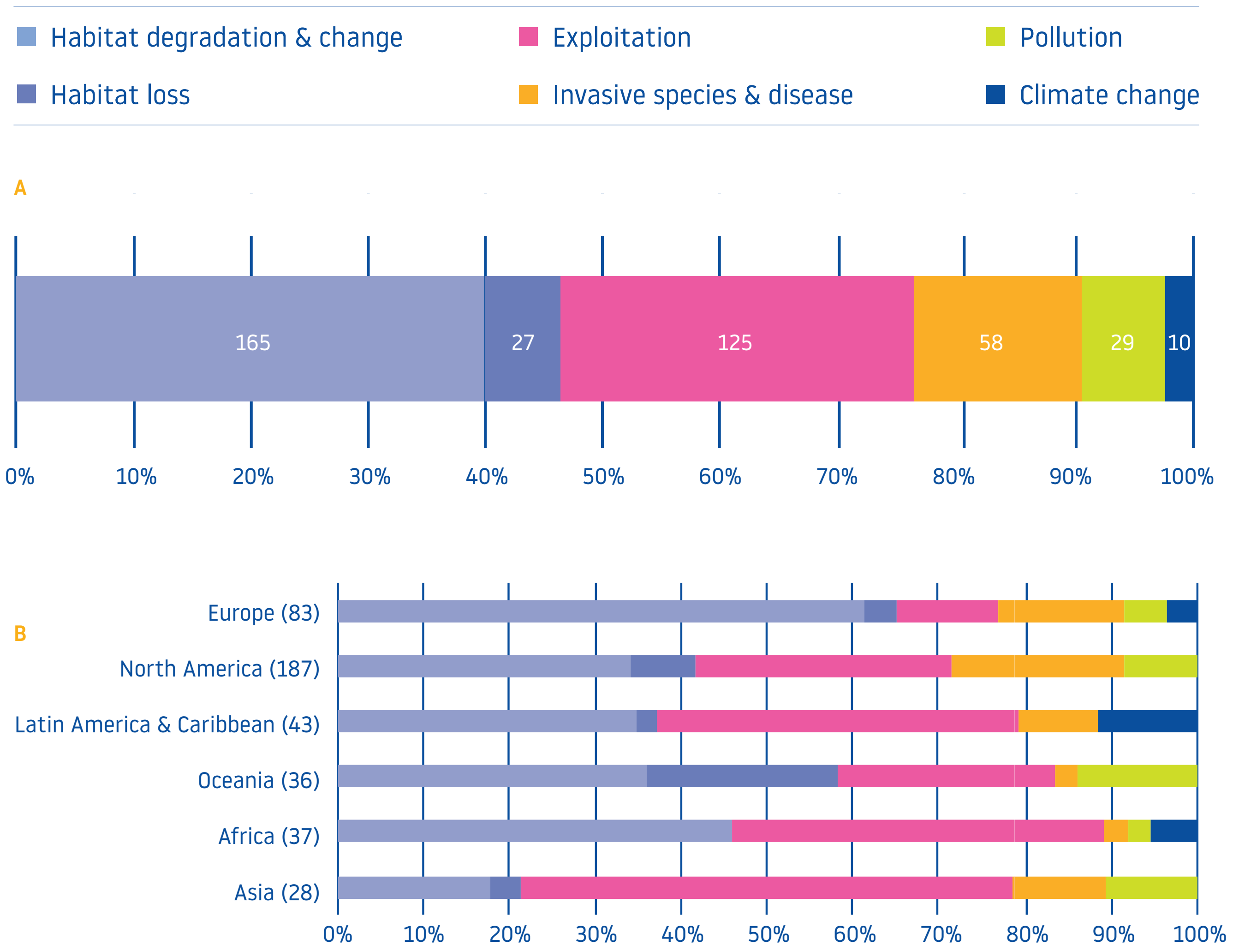
The increase of human development within the range of mahseer has taken its toll, especially when so little data exists on the biology and migration patterns of Golden mahseer. Hydropower projects continue to be built at a rapid pace, and the associated construction impacts of sand-mining, road building, siltation, etc., are detrimental to the health of all fish. Add in the stress of unregulated fishing and over-exploitation, the future for sustainable mahseer populations looks dim. There is an urgent need to not only protect mahseer, but the freshwater ecosystems that provide their food and necessary habitats to thrive and reproduce. Yet hope lies with the number of possible solutions that have been tested or explored: education programs that focus on the ecosystem services of rivers, conservation initiatives that benefit local communities, cooperative agreements among stakeholders that focus on the benefits of clean water and healthy fish, ecotourism and recreational management plans that can provide local economic resources, protected area or national park offset agreements with hydropower developers, and the application of less destructive sources for renewable energy. All these solutions will require pressure for cooperation and action among scientists, conservation organizations, anglers, industry stakeholders, and most significantly the local citizens who realize the true cost of losing this magnificent migratory fish.

GOLDEN MAHSEER

FIGURE 9

The distribution of threats for monitored migratory freshwater fishes listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous
a) globally and
b) for different regions.

Threat information was available for 290 populations of 116 species, totalling 414 recorded threats. The numbers in the bars (brackets) correspond to the number of times a threat was listed (globally or in each region).



While these figures give some indication of what is affecting populations in this data set, they are not representative of the distribution of threats to all migratory freshwater fish species globally and in different regions of the world. Habitat degradation, alteration and loss, and over-exploitation are undoubtedly serious issues for migratory freshwater fish, however other important threats have not been reported as often or are even absent from some of the regions (Figure 9a). For example, there is a large amount of evidence of the current and future impact of climate change on migratory fish (Ficke *et al.* 2007), including in the Oceania region, where millions of fish have been lost in Australia over the past decade to drought and flooding (Vertessy *et al.* 2019). Similarly, there is evidence of pollution and habitat loss causing particularly serious issues in many parts of Africa (O'Brien *et al.* 2019).

But even the more prominent categories in the data set relating to habitat are not overly informative due in their broadness. Habitats can be affected by a multitude of drivers of change, including dam-building, other infrastructure development, wetland drainage, floodplain disconnection, over-abstraction of water, or sand-mining. A finer-scale reclassification of these broad threat categories akin to the sub-categories of threats on the IUCN Red List (IUCN 2020) but with a specific freshwater focus may help to disentangle these effects and identify the main drivers and any regional differences. Clearly, much information is missing and needs to be added for more detailed analysis in future updates to this indicator.

THE 64 M HIGH GLINES CANYON DAM (AKA UPPER ELWHA DAM) DURING REMOVAL

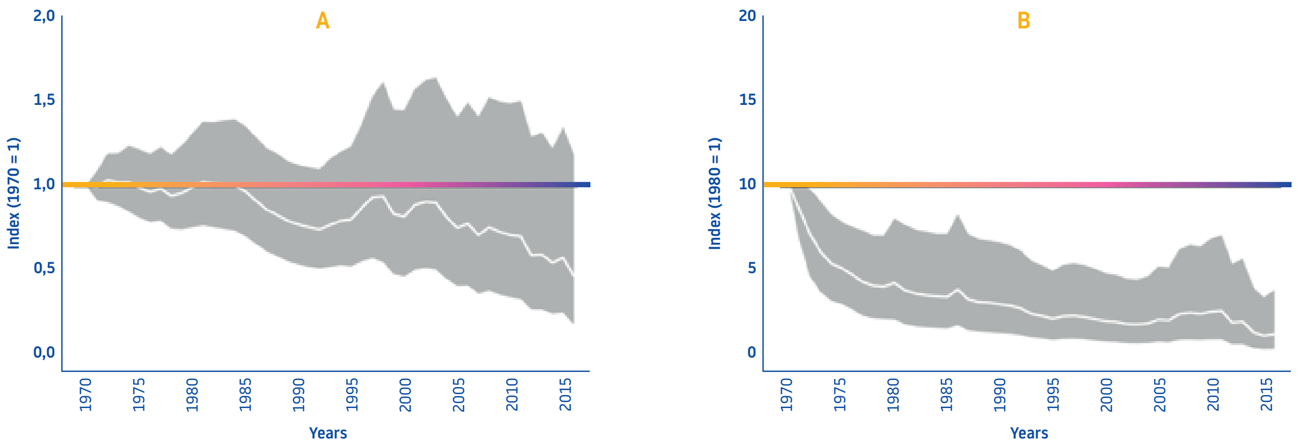
FIGURE 10

Average change in abundance of monitored migratory freshwater fishes (GROMS-listed as anadromous, catadromous, amphidromous, diadromous or potamodromous) between 1970 and 2016 that are

a) managed (-54%; 359 populations of 63 species) and

b) not managed (-87%; 428 populations of 163 species).

The white lines show the index values and the shaded areas represent the bootstrapped 95% confidence intervals.



MANAGEMENT

Once threats have been identified, it may be possible to mitigate their effect on population trends through management. For migratory freshwater fish species, these management actions can comprise a variety of different approaches, including management of fisheries, habitat restoration, dam removal, setting up conservation sanctuaries, species-focused management and legal protection. Information on whether a population is managed in this way is included in the LPD for each population. We find that populations of migratory freshwater fish species that are recorded to receive some form of management have declined less (-54%) than unmanaged populations (-87%, Figure 10). This suggests that management could potentially have a positive effect on some populations.

In addition to recording whether or not a population is managed, the LPD also allows for these management actions to be described in more detail. Of the 359 populations of 63 species that were recorded as managed, the majority (327 or 91%) listed one management action (7% listing two, 2% listing three). When combining these management activities into broader categories, we find that most are related to fisheries management (46%, Figure 11), which includes strategies such as fishing restrictions, stocking, bycatch reductions and the establishment of no-take zones. Habitat management - comprising restoration of habitat and connectivity, land use regulations and water quality management - accounted for only 11% of recorded management activities, despite the prominence of habitat-related threats (Figure 9). For around a third of managed populations (35%), management activities were 'unknown', i.e. no information was given about the nature of the management. Filling these knowledge gaps by going back to the relevant data sources would help with building up a more complete picture of possible ways in which declines in migratory freshwater fishes may be reduced or reverted, or to establish which strategies may not be associated with a positive trend.

One issue to consider for the results for management presented above is that other factors may have contributed to the observed difference, including life history characteristics, timing and efficacy of management, or differences relating to the location of monitoring. The trends in managed and unmanaged populations may, for example, be confounded by region. The majority of managed populations (80%) and species (51%) were monitored in North America, where there is an abundance of fisheries management agencies, better records of management activities, and which also shows the smallest overall average decline of any region (Figure 6a). By contrast, unmanaged species populations tend to be more evenly spread across regions. This issue is discussed in more detail in the 'Results in context' section below.

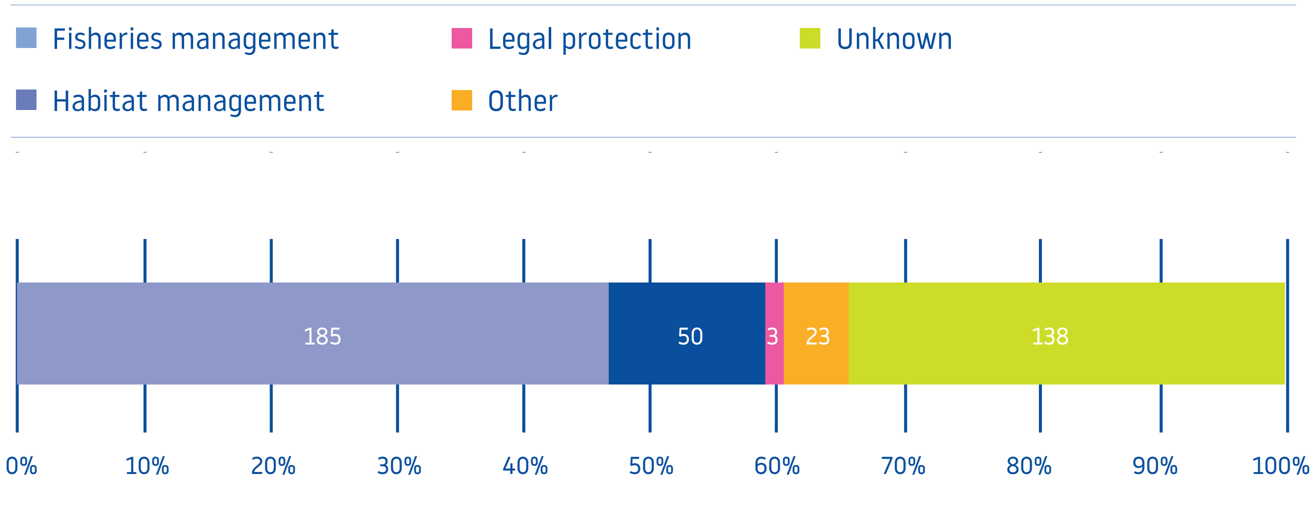
Lastly, it is worth noting that despite receiving some form of management attention, managed populations are still declining. There could be a number of possible reasons for this, for example that management activities may be newly implemented, insufficient, ineffective or even inappropriate. Some strategies may even be detrimental, for example stocking can lead to genetic bottlenecking and is often carried out with hatchery-reared strains that are less suited to the natural habitat and may negatively impact wild strains of e.g. salmon. Overall, there is a great need to add management success data to model the connection between population declines or increases and management strategies.

REASONS FOR POPULATION INCREASE

As seen in the previous section, managed populations appear to show a smaller average decline in abundance than unmanaged populations. However, managed populations in the LPD are still not increasing. Assuming that management interventions are indeed responsible for the difference in the trends, this suggests that they may only be sufficient in slowing as opposed to reversing declines in this particular selection of species. To identify successful interventions, we therefore examined consistently increasing populations in the LPD for which reasons for this increase are coded into broad categories (such as management, legal protection or removal of threat). This information is available for only a small number of populations and we show the results for each region below (Figure 12). Increases recorded in the temperate regions of Europe and North America have been primarily attributed to management (55% and 20% respectively) and unknown reasons (67% and 35% respectively), with removal of threats and legal protection playing a smaller role. In tropical regions, the most common reasons were 'unknown' or 'other'. In the majority of cases, these 'other' reasons were species with tolerance of higher salinity benefitting from climate-related changes in estuaries. Interestingly, 50% of 8 populations that are increasing in the Latin America & Caribbean region are benefitting

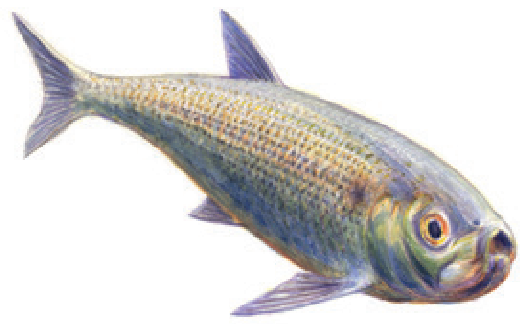
FIGURE 11

Management actions undertaken in managed populations of monitored migratory freshwater fishes (GROMS-listed as anadromous, catadromous, amphidromous, diadromous or potamodromous). Management information was available for 359 populations of 63 species, totalling 399 recorded management actions. The numbers in the chart correspond to the number of times each management type was listed. Fisheries management includes fishing restrictions, stocking, bycatch reductions, supplementary feeding, no-take zones. Habitat management includes habitat restoration, habitat management, connectivity restoration, land use regulations, water quality management. Legal protection includes protected areas, species protection. Other includes management plan, removal of invasive species, threat management, tagging.



from range shifts. These are detritivore species who benefitted from the explosive development of attached algae below a newly constructed dam in French Guiana (Merona *et al.* 2005).

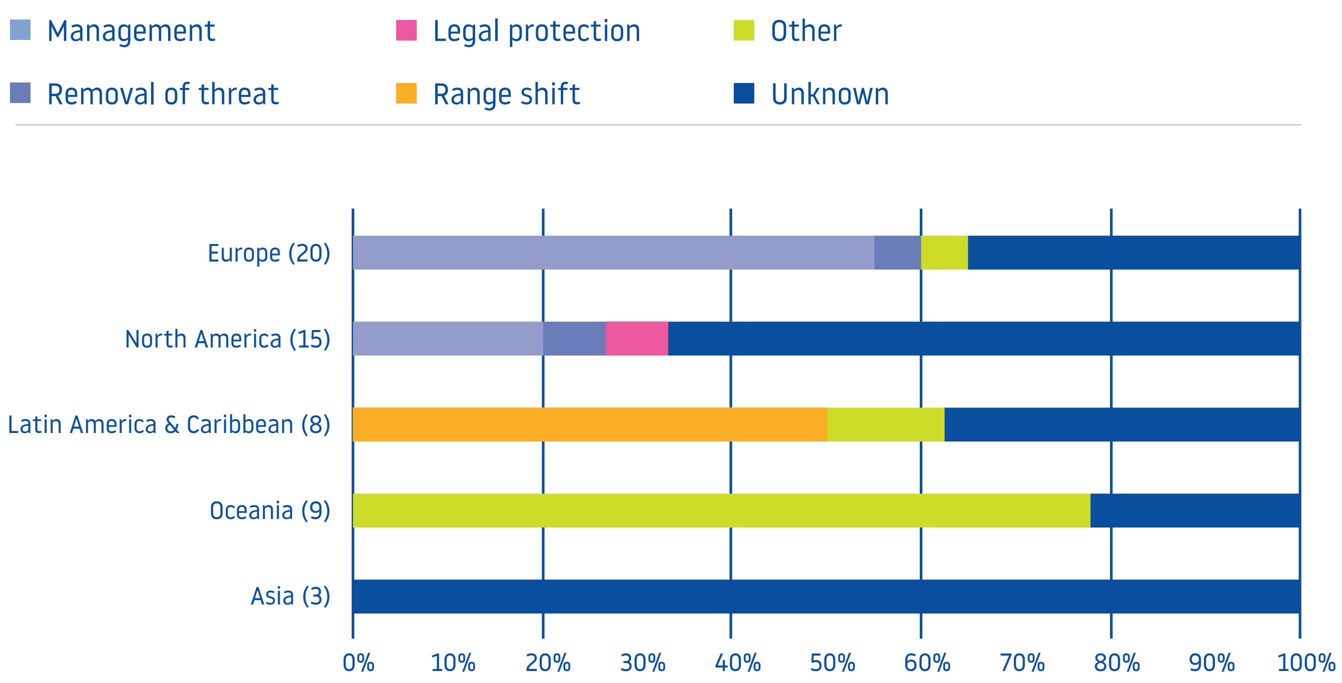
ALEWIFE



With only limited information available, these findings provide only a snapshot of what led to abundance increases in specific populations and cannot be considered representative of the different regions. A preliminary check for populations with unknown reasons suggested that these tended to come from multi-species papers unlikely to provide this information for each species individually. It is important to highlight that increases are not necessarily due to specific actions or documented habitat or management changes but could simply describe natural population dynamics. The time frame of monitoring may also be of importance, inasmuch as some actions or changes may not be beneficial in the long-run. For example, the French Guiana study above describes increases immediately following dam construction, which would have likely led to stabilisation of the system with declining abundance of native species over a longer period.

FIGURE 12

The distribution of reasons for increase for monitored migratory freshwater fishes listed on GROMS as anadromous, catadromous, amphidromous, diadromous or potamodromous. Information on reasons for an observed increase was available for 53 populations of 38 species, totalling 55 mentions of reasons. Multiple reasons may be listed for each population. The numbers in brackets correspond to the number of reasons listed (in each region)



BOX 6

RESTORING DUTCH SWIMWAYS

The Wadden Sea borders the North Sea coast of Denmark, Germany and the Netherlands, and is the largest intertidal area in the world. It formed 7500 to 6000 years ago when sea level rise decelerated and sediment dynamics started to shape a large transition zone between the fresh water habitats of northern Europe and the marine habitats of the North Sea (Reise 2005). The Wadden Sea is an important hub for migrating fish along their migratory routes - Swimways - by providing access to the large catchments of northern Europe; including the large rivers Eider, Ems, Elbe, Rhein (partly) and Weser. Through the millennia migrating fish have used the shallow area and complex coastline as a reliable access point for moving towards or from their breeding grounds; but also as a nursery area and/or an important stop-over site for feeding and resting. Today, the coastal plain comprise 24 000 km² but 15 000 km² of this is embarked marshes (Reise 2005), and human activities have for most of the coastline created a sharp and impermeable barrier that separates fresh from marine water habitats.

The large scale embankments started already in the early 20th century, and as a consequence of barriers in combination with fishing, natural populations of iconic diadromous species such as allis shad (*Alosa alosa*), Atlantic salmon (*Salmo salar*), Atlantic sturgeon (*Acipenser sturio*), sea trout (*Salmo trutta*), and North Sea houting (C*oregonus oxyrinchus*) all became Critically Endangered or were lost from the system (Lotze 2005). The Dutch Wadden Sea coastline is currently a 250 km long sea wall where the only entry points for fish are through about 60 one-direction tidal gates, sluices and pumping stations (Huisman 2019). These entry points provide insufficient passage for fish into the intertidal area. Today eight species of diadromous species are observed in the area, of which most are still Critically Endangered (Tulp *et al.* 2017).

However, there is an increasing realisation that we need to restore the Dutch Swimway for fish and therefore the government have in 2018 started a large program to mitigate the negative ecological effects of the sea wall. In addition to a number of fish passes and fish friendly pumping stations that have been built (Huisman 2019); future measures include installing large transitional zones and softening the edges of the coastline (https://www.helpdeskwater.nl/onderwerpen/water-ruimte/ecologie/programmatische-aanpak-grote-wateren).

A key project as part of this program, addresses one of the major bottleneck for fish migration in the Netherlands by building a 6 km long artificial river with a meandering river bed, that will provide a near-natural brackish water gradient that connect lake Ijssel with the Wadden Sea (Fish Migration River). Lake Ijssel is a 1200 km² large former estuary that was closed off by a 32 km long barrier (the "afsluitdijk") and transformed to a fresh water reservoir in 1932. The coming decade will tell if the estimated 100's of millions of migrating fish that every year have been waiting outside the discharge sluice (Griffioen *et al.* 2014), will find their way into the ecosystem and if threatened species will be able to recover in the catchment area.

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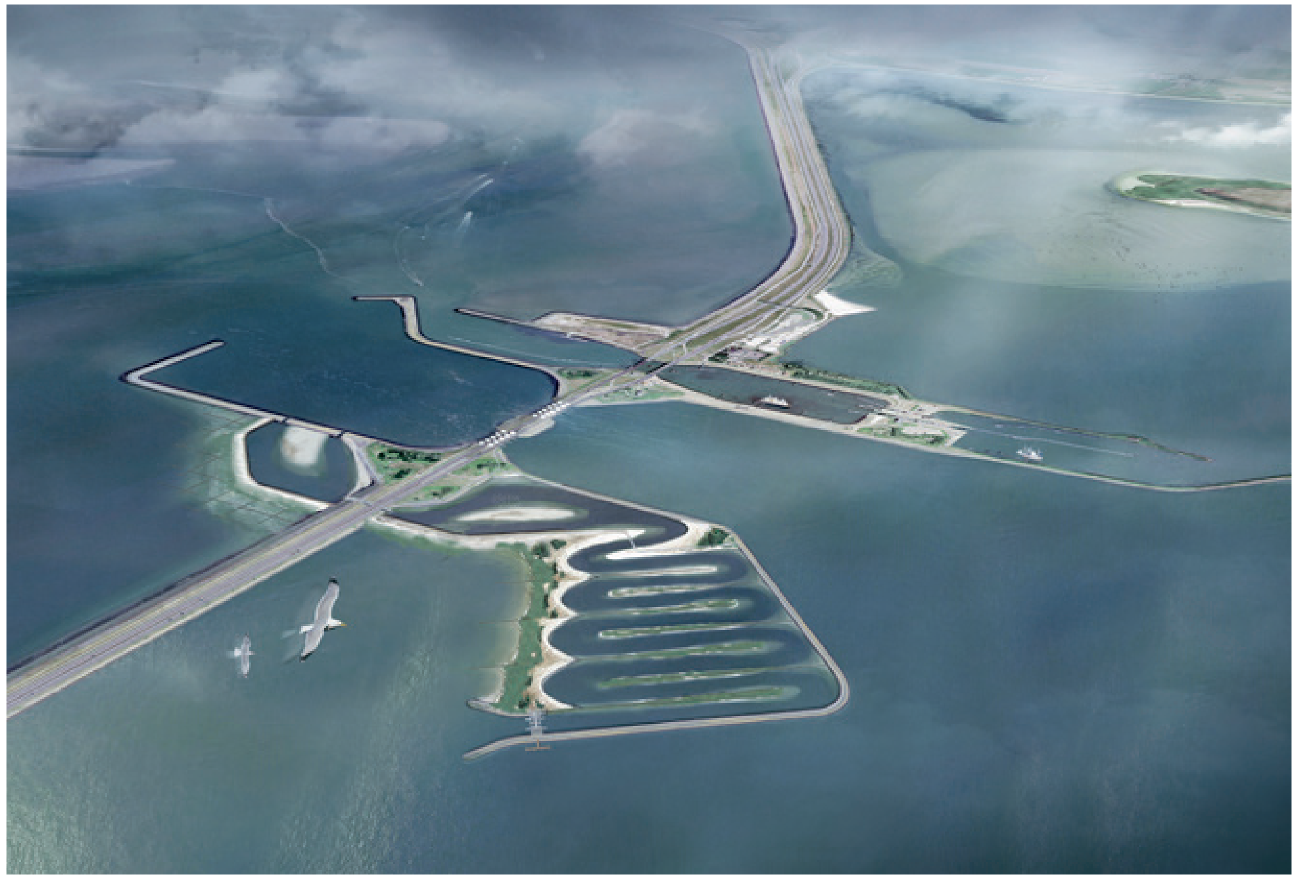
RESULTS IN CONTEXT

The findings presented in this report indicate that migratory freshwater fish have been declining since 1970 throughout their global distribution. Average declines are apparent in tropical and temperate zones, all regions and migration categories, and even in those populations that are not explicitly described as exposed to threats such as habitat change, climate change and pollution. The overall decline in migratory freshwater fish populations is staggering at -76%, which is in line with the overall decline observed for other freshwater vertebrate populations (83%; WWF 2018). Following publication of the 2020-2 version of the IUCN Red List all freshwater fish in the database are now coded according to their "movement patterns". Of the 907 freshwater fish species coded as being migratory just over 21% of these are threatened, 51 species being Critically Endangered (IUCN, 2020b). This highlights the bleak future faced by migratory freshwater fish, and the need for urgent action (Tickner et al. 2020). Specific findings are put into context below, as far as possible with the current data set and taking into account the limitations of the study (see next section).

AFSLUITDIJK

One of the major initiatives to restore Dutch Swimways is the construction of the fish migration river in the Afsluitdijk, started in 2020. © Feddes-Olthof/Provincie Fryslan



DECREASES ARE PARTICULARLY PRONOUNCED IN EUROPE (-93%) AND LATIN AMERICA & CARIBBEAN (-84%)

The findings from Europe are broadly in line with the fact that 37% of freshwater fish are threatened with extinction on the European Red List (Freyhof & Brooks 2011). One particularly prominent threat is fragmentation - there is a lack of free-flowing rivers in Europe (Grill *et al.* 2019), with a high level of fragmentation through dams (Barbarossa *et al.* 2020) and over 1.2 million barriers across the continent (Belletti *et al.* 2020). Few rivers are still unaffected by dams or other barriers (Garcia de Leaniz *et al.* 2019) and these contain very few remaining viable migratory fish populations in Europe (van Puijenbroek *et al.* 2019). Mechanisms are being developed to restore stream connectivity in Europe's rivers by removing barriers (see Box 6), in particular starting with a small proportion of the 15% of dams that have been found to be obsolete (Garcia de Leaniz *et al.*, in prep). This would be in line with the European Biodiversity strategy for 2030 which has a target of "at least 25,000 km of rivers will be restored into free-flowing rivers by 2030" (European Commission 2020).

In South America, many large rivers are still free-flowing (Grill *et al.* 2019), which support some of the most biodiverse fish assemblages on Earth. For many Neotropical fish (not just migratory species), national policies have historically encouraged unsustainable practices (e.g. hydropower, mining, water diversion), and recent decades have witnessed a sharp increase in harmful activities (Pelicice *et al.* 2017). Although showing one of the largest average declines in this analysis, it is likely that the situation is actually much worse; this is not fully captured in the current LPD data set because of limited data availability for the region. Most of the data used are from estuarine regions or very large rivers (Amazon, Parana and La Plata, for example) where there is a relatively good monitoring network based on freshwater fisheries catch data. In addition, declines are predicted to get much worse with the increasing construction of dams in areas such as the Amazon (Barbarossa *et al.* 2020).

NORTH AMERICA SHOWS THE SMALLEST AVERAGE DECLINE OF ANY REGION (-28%)

The North American region is characterised by a lack of long and free-flowing rivers (Grill *et al.* 2019) and high level of fragmentation through dams (Barbarossa *et al.* 2020). Dam removal has had a positive effect on fish abundance in some rivers (e.g. Penobscot, Elwha; Bellmore *et al.* 2019), in contrast to many other regions of the world that are expanding hydropower production (Zarfl *et al.* 2015). The smaller average decline in the LPI for this region could have several explanations. Major declines in North America may have occurred prior to 1970, and have simply stabilised at a lower level over the past few decades. Many dams were built prior to 1970 in North America, and fish have been intensively exploited here since European settlement (Humphries and Winemiller 2009). Populations of sturgeon, paddlefish, and salmon likely experienced their greatest declines prior to 1970 (Humphries and Winemiller 2009). This concept of 'shifting baselines' is problematic for the monitoring of population declines in fishes worldwide (Humphries and Winemiller 2009). It should also be noted that data in the LPD is biased towards rivers in northern parts of the region where unobstructed rivers are more prevalent. It is also possible that the smaller average decline in North America is due to management effort, as 45% of North American fish populations in the LPI receive some form of management, whereas for all other regions it is less than 10%. However, most of the management actions recorded in our data set were classified as 'fisheries management' actions (e.g. fishing restrictions, stocking, bycatch reductions, supplementary feeding, no-take zones), which often produces stable trends because they are linked to quotas.

ASIA-OCEANIA HAS SHOWN CONSIDERABLE DECLINES (-59%) BUT INFORMATION IS LACKING FOR THIS REGION AND AFRICA

Both the Asia-Oceania and African regions are under-represented within the LPI dataset relative to the proportion of species expected based on the GROMS database. For Africa, this has restricted our ability to calculate average declines, and for Asia-Oceania, it seems likely the average decline calculated may underestimate the actual value. For instance, many migratory fish species with documented declines in Asia and Oceania (e.g. Mekong giant catfish *Pangasianodon gigas*; Golden mahseer *Tor putitora*, Silver perch *Bidyanus bidyanus*, Purple spotted *gudgeon Mogurnda adspersa*, Australian grayling *Prototroctes maraena*) are not included in the LPD. Our analysis indicated that exploitation and habitat loss and degradation are the most prevalent threats in this region. Given plans to vastly expand hydropower in Asia (particularly in the Mekong Basin), it is anticipated that habitat will be further degraded and lost, and that declines in migratory fish will accelerate in the region in the coming decades (Ziv *et al.* 2012). As the Mekong River is one of the most

SEATROUT

After ecosystem recovery measures being taken, seatrout is being released again into their natural habitat, The Netherlands. © Herman Wanningen

biodiverse river systems on Earth, developments in this region should be of major conservation concern (Dudgeon 2000). In Australia, the impact of drought is a considerable threat to the flow regimes of rivers and the migratory fish that depend on them (Morrongiello *et al.* 2011; Normile 2019; Vertessy *et al.* 2019).

Despite being unable to quantify declines in Africa due to a lack of data in the LPD, there is undoubtedly reason for concern given documented declines in the literature. For example, dams and weirs are having a severe negative effect on migratory species of *Labeobarbus spp.* some of which are already listed as endangered, vulnerable, or threatened (Shewit *et al.* 2017). Similar to the Asia-Oceania region, our analysis indicated habitat impacts and exploitation as the most prevalent threats to African migratory freshwater fishes. Indeed, many of these species are facing multiple stressors associated with rapid development in the region, with hydrological alteration, invasive exotics, and climate change noted as prominent threats (Fouchy *et al.* 2019). There are few programs actively monitoring fisheries across the continent, so time series are absent. Indeed, improving monitoring in the continent will be a critical first step to mitigating declines moving forward.

POTAMODROMOUS FISH DECLINE MORE THAN THOSE MIGRATING BETWEEN FRESH- AND SALTWATER (-83% VS -73%)

Our finding that potamodromous fish have faced greater declines than anadromous, catadromous diadromous and amphidromous fish combined was unexpected, as overall these species are considered to undertake shorter migrations but substantial variation exists. The migration of some potamodromous species can be as short as the lateral migrations many species undertake to adjacent floodplains (e.g. bream; Borcherding *et al.* 2005), while others undertake migrations spanning many 1000's of kilometres (e.g. Mekong giant catfish, Golden perch; Ngamsiri *et al.* 2007; Stuart *et al.* 2020). Potamodromous species that migrate large distances will be at greater risk to reduced connectivity (Lucas & Batley 1996) and will be particularly impacted by future climate change (Beatty *et al.* 2014). As freshwater ecosystems are considered to face greater threats than marine ecosystems (Reid *et al.* 2020), it may be that a life restricted to freshwater puts potamodromous species at greater relative risk. This aligns with our finding that migratory fish had lower overall declines than freshwater vertebrates. Nonetheless, it is generally accepted that compared to non-migratory species, migratory fish are exposed to a greater number of threats as they commonly travel long distances and traverse different habitats to complete their lifecycle (Robinson *et al.* 2009; Gienapp 2010).

We observed declines in all regions for potamodromous species except in Asia-Oceania. The most severely declining potamodromous species often comprised populations where threats were unreported. These tended to come from Europe, especially western and central countries such as Germany, France and Czechia. While this may hint at where the situation may be worst for this group of fish, many potamodromous species were missing from regions such as Asia-Oceania and Africa, so only limited conclusions can be drawn.

POPULATIONS WITH DOCUMENTED THREATS DECLINED BY AN AVERAGE 94%

As would be expected, populations with known threats are declining more than those without known threats. In the LPD, just under half of all reported threats to migratory freshwater fish were related to habitat degradation, change and loss, and around 30% were related to exploitation. This aligns with previous research that has suggested dam construction and fisheries harvest are among the greatest threats to freshwater species (Dudgeon *et al.* 2006). Interestingly, these threats were consistently the most prevalent for migratory freshwater fish for each individual region despite vastly different species and environments.

POPULATIONS WITH UNREPORTED THREATS DECLINED

Populations where it was unreported whether threats existed also showed a negative trend, suggesting that these populations may face threats that are simply unknown or go unreported. Fish tend to suffer from missing information on abundance trends and extinction risk (Cooke *et al.* 2016). For example, around 20% of freshwater fish (which includes non-migrants) are Data Deficient on the Red List (IUCN 2020), 76% of freshwater fish in Europe have an unknown population trend (Freyhof & Brooks 2011), and many more are not assessed at all. In fact, although work is underway to assess all described freshwater fishes by 2021/2, at the time of writing there were around 9,700 species of freshwater or freshwater/marine fish on the Red List (IUCN 2020), versus an estimated 17,800 freshwater fish species overall (Van der Laan 2020). It will be prudent for managers to gather more information about these populations to assess why declines are being observed - and if there are overlooked threats leading to declines. For example, it has been suggested that recreational fisheries are leading to an 'invisible' collapse for fish

VILHOLT DAM

Vilholt Dam, Jultland, Denmark - before removal. © Jan Nielsen

populations in North America (Post *et al.* 2002). Similarly, it may be difficult for monitoring programs to identify whether threats such as pollution or climate change are impacting a population - particularly for species where life-history data is lacking (Wootton *et al.* 2000).

POPULATIONS THAT RECEIVE A FORM OF MANAGEMENT DECREASED LESS THAN UNMANAGED ONES

We know that remarkable recoveries of migratory fish populations are possible with management intervention including the watershed-scale conservation of Westslope cutthroat trout (*Oncorhynchus clarkia*), pollution control benefiting anadromous fish in the Delaware River, the restoration of longitudinal connectivity in Segura River, and dam removal in the Penobscot River (Brink *et al.* 2018). Here, managed populations tended to decline less than unmanaged ones, with most management actions being related to the regulation of fisheries. A potential problem with this finding is that any data from commercial fisheries is based on quota-adjusted catch, which necessarily produces a stable trend, and this could in turn explain the smaller decline observed. It would be useful to examine the trends in species managed within a fishery versus species receiving other forms of management in the future.

Unfortunately, much of the information on management is missing - many listing unknown or other management - which reduces the conclusions we can draw from this analysis. It is also possible that management is simply more common for populations that had their main threats and declines initiated in the past before 1970. Management actions were most common in North America, where most threats to migratory fish were established in the early 20th century (e.g. dam construction, overfishing). It may not be that management has had an immense positive effect, but rather that populations receiving management may be those that have already stabilised at a low population level after historic declines not captured in this report. Interestingly, legal protection was not cited very often. In the US, listing under the Endangered Species Act may prompt management or conservation measures (Henson *et al.* 2018) but this may be missed as more immediate management strategies prompted by listing under the *ESA* (e.g. habitat restoration), may be cited by the data source instead.

RECORDED REASONS FOR INCREASES WERE MOSTLY UNKNOWN OR UNDESCRIBED

A small number of populations in the LPD comprise information on why they have increased. While these increases were regularly attributed to management intervention in temperate areas, most were unknown or undescribed, especially in tropical regions. This is probably because this information is taken directly from the data source, so if the authors do not discuss reasons for increase, 'unknown' will be chosen as a category. Indeed, in many cases it may be difficult to establish causation between a population increase and some other unrelated factor, unless before/after monitoring has been completed (Smokorowski and Randall 2017). Nonetheless, sharing 'bright spots' where populations are increasing will be immensely important for allowing others to learn and implement findings where we have been successful in reversing negative trends (Bennett *et al.* 2016).

RIVER GUDENAA

The reestablished River Gudenaa after Vilhot Dam removal. © Jan Nielson and Finn Sivebæk, DTU Aqua

LIMITATIONS

Although they are based on one of the bigger data sets on these species, there are a number of limitations to consider when interpreting trends. For instance, the length of a data series for a given population may vary greatly from a few years to multiple decades. For some regions, it was common for just a small number of populations with short time series to be influencing declines at any given point in time. When based on a smaller number of species, an index is easily influenced by very negative (or positive) trends, so a change to a steeper slope (whether this is negative or positive) may not be representative of the actual trend. Additionally, species are under-represented in a number of subsets, especially in Asia-Oceania and Africa and in the potamodromous migration category. Within these regions there are very few species in our analysis from some of the world's most biodiverse river basins where it is predicted there will be hundreds of fish extinctions in the coming decades (e.g. Mekong, Congo, Amazon, and Yangtze).

Further, our analysis does not include many of the most highly migratory, transboundary, high profile 'flagship' species including migratory catfish from the Mekong and the Amazon, migratory characins, sawfish, Silver perch, whiprays, Brycon spp. from South America, Taiman, Mahseer, Goonch, Chinese sturgeon, to name a few. For some of these species the data are not yet available, but for most the information has simply not been adopted into the LPD. It is therefore important to close some of the data gaps for future analyses, which will help with being able to draw more robust conclusions from the data. In addition, the GROMS coding used to classify species is very outdated, potentially leading to missing out on data for species that have changed taxonomy or were more recently described.

For this reason, future reports may want to investigate alternative approaches to classifying migration patterns in fish. As noted above, it is anticipated that all fish in the IUCN Red List will be classified as either migratory or non-migratory in the near future and that data on population trends will be noted where available. Both of these data sources will improve future investigations on migratory freshwater fish using the LPI.

BOX 7

RECOMMENDATIONS

Recommendations for improving our understanding of the fate of migratory freshwater fish and developing practical solutions that restore and protect migratory freshwater fish and the ecosystems upon which they depend. Broadly, recommendations were related to improving monitoring, augmenting data in the Living Planet Database, protecting free-flowing rivers and guiding basin-wide planning, addressing existing threats, adhering to ongoing conservation initiatives, and fostering public and political will. The list of recommendations is not presented in terms of priority nor is it entirely comprehensive. Where possible we acknowledge that there are ongoing conservation initiatives and efforts (e.g., development of policy statements) that are highly relevant to conservation of migratory freshwater fish such that what we share here is not entirely new but rather exploits and integrates ongoing activities.

IMPROVING MONITORING

- Encourage and establish long-term monitoring in many regions of the world where programs are currently lacking for freshwater migratory species (particularly Africa, South America, and Asia especially fish in the Congo, Mekong, Yangtze, Irrawaddy and Salween).
- Develop, share and adopt standardised stock assessment methods that enable more direct comparison among systems (Bonar *et al.* 2017).
- Identify and prioritise (including provision of necessary funding and capacity building) representative migratory fish species for long-term monitoring across different ecoregions.

AUGMENTING DATA IN THE LIVING PLANET DATABASE

- Incorporate additional existing migratory freshwater fish abundance data in the Living Planet Database (e.g. time-series abundance data exist but are not yet included for certain species in Africa, Oceania, Asia, and South America).
- Compile an updated comprehensive reference list of migratory freshwater fishes globally, based on a newer classification system than GROMS, to ensure that the Living Planet Database is more representative of this group. (Note that currently there are efforts to assess, map and classify all freshwater fish for migratory behaviour in the IUCN Red List by around 2022.)

PROTECTING FREE-FLOWING RIVERS AND GUIDING BASIN-WIDE PLANNING

- Explicitly recognise the importance of freshwater connectivity and inclusion of associated indicators such as the Connectivity Status Index (Grill *et al.* 2019) as well as accelerated implementation of environmental flows via improved measurement and tracking.
- Implement basin-wide planning to explore alternative development scenarios and assess relative risks and trade-offs for new water infrastructure, including natural infrastructure options, alternative energy options (in the case of hydropower), and options for increasing energy or water use efficiency.
- Create basin/river-specific policy protections for remaining free-flowing rivers or swimways that support an abundance of migratory fish species (Moir *et al.* 2016)
- Identify global swimways that are of high importance for migratory freshwater fish species to support transboundary management and help guide new developments like infrastructure in river basins (see Box 8).

ADDRESSING EXISTING THREATS

- Address general threats to migratory freshwater fish recognising the many interacting stressors (see Birk *et al.* 2020) and threats that yield cumulative effects (e.g. control all pathways for the introduction of invasive species; reduce pollution from excess nutrients, biocides, plastic waste, and other sources; mitigate climate change through nature-based solutions and emissions reductions to contribute to the goals set forth in the Paris Agreement).
- Investigate the relationship between life-history traits and external threats associated with the greatest declines in migratory freshwater fish species.

FOSTERING PUBLIC AND POLITICAL WILL

- Increase public engagement with migratory freshwater fish through outreach, awareness, and education campaigns (e.g. World Fish Migration Day; see Twardek *et al.* 2020).
- Develop collaborations with the Convention on Migratory Species to promote a greater focus on migratory freshwater fishes.
- Highlighting the positive economic outcomes that go hand in hand with the environmental benefits achieved of river restoration (see Box 9).

ADHERING TO ONGOING CONSERVATION INITIATIVES

- Adopt and implement the recommendations from the Emergency Recovery Plan for Freshwater Biodiversity (Tickner *et al.* 2020; see Box 10) and the UN-water input on freshwater-biodiversity linkages.
- Adopt the UN FAO Ten Steps to Sustainable Inland Fisheries (http://www.fao.org/3/a-i5735e.pdf) which emphasizes the need for science-based assessment and management of freshwater fish populations.
- Incorporate freshwater species considerations into post-2020 goals, targets and indicators, including those of migratory freshwater fish.

BOX 8

THE GLOBAL SWIMWAYS INITIATIVE

In September 2019 IUCN, UNEP-WCMC, the University of Cambridge and the World Fish Migration Foundation launched an initiative looking to connect fish, rivers and people globally. It uses the "Global Swimways" concept, where a swimway is defined as a path used in fish migration (similar to the concept of the 'flyway' for birds; Boere *et al.* 2006). Swimways may span distances of more than 1,000 km traversing oceans, lakes and rivers. The concept of Global Swimways are based on several criteria, like the number of migrating freshwater species and the number of threatened species. It is essentially an operational concept linked to freshwater fishes whose populations need to be managed over their entire migration range. The long-term ambition is to develop an updated global overview of migratory fish and swimways (with input from international experts). It is intended to provide decision makers with relevant and up-to-date information and to stimulate international information exchange, collaboration and awareness. Other organisation are more than welcome to join the efforts of the initiative.

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BOX 9

ECONOMICS OF RIVER RESTORATION

The restoration of rivers provides myriad economic benefits, most going hand in hand with the environmental benefits achieved. Large increases in populations of freshwater-sea migratory fishes, particularly through dam removals may result in resurgent recreational and commercial fisheries, both in rivers during their spawning runs and for the remainder of the year in coastal waters. Not only do such restorations provide economic value in landings of edible fish, but popular angling locations for these species attract visitors who may spend considerable sums on food, lodging and tackle. Re-opened rivers may increase other forms of recreation, such as canoeing, kayaking, and powerboating. In particular, when formerly polluted urban rivers are cleansed they can become major focal points for residents to interact with nature, generating economic activity through associated amenities. Finally, restored rivers may provide valuable ecological services, such as provision of potable water, habitat for resident fish and wildlife species, erosion control, and natural dispersal of nutrients and sediments.

BOX 10

EMERGENCY RECOVERY PLAN

Rivers, lakes and inland wetlands are home to an extraordinary array of life. Covering less than 1% of Earth's surface, these habitats host approximately one third of vertebrate species and more described fish species than the oceans (Strayer & Dudgeon 2010). But freshwater biodiversity is rapidly declining: globally, wetlands are vanishing three times faster than forests (Gardner and Finlayson, 2018), and the Living Planet Index shows that freshwater vertebrate populations have fallen more than twice as steeply as terrestrial or marine populations (WWF & ZSL, 2018).

Recommendations to address wider biodiversity loss have too often assumed, simplistically, that measures designed to improve land management will inevitably benefit freshwater ecosystems, or have neglected to consider freshwater biodiversity at all. This has obscured distinct threats to freshwater flora and fauna and precluded effective action. Such threats are well-documented.

In 2019, an international group of freshwater ecosystem experts gathered to define priorities for bending the curve of freshwater biodiversity loss. Borrowing from post-disaster recovery planning processes, they set out an ambitious but pragmatic Emergency Recovery Plan for global freshwater biodiversity (Tickner *et al.* 2020). The group used the Plan to generate thirteen specific recommendations for improving selected CBD and SDG targets and indicators.

The Plan is structured around six priorities for action: 1) Allowing rivers to flow more naturally; 2) Reducing pollution; 3) Protecting critical wetland habitats; 4) Ending overfishing and unsustainable sand mining in rivers and lakes; 5) Controlling invasive species; and 6) Safeguarding and restoring river connectivity through better planning of dams and other infrastructure. Each priority action has already been implemented successfully in one or more situations across the globe, providing proof of concept and lessons that can inform scaling-up of actions.

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CONCLUSIONS AND RECOMMENDATIONS

Arising from this analysis and synthesis is a recognition that more work is needed to understand the fate of migratory freshwater fish and develop practical solutions that restore and protect these animals and their habitats (see Box 7 for a list of recommendations). For example, there is much opportunity to improve information collected (especially in low and middle income countries in the global south) such that the LPD is as complete and comprehensive as possible. Some of the trends identified here may reflect regional trends driven by the availability of stock assessment data.

Overall, however, the evidence is clear that many migratory freshwater fish are imperilled and there is a dire need to identify and embrace solutions before it is too late. There are already a number of policy documents and other solutions-oriented activities that can be used to guide such activities (e.g. 'curve-bending' actions in Tickner *et al.* 2020).

BRINGING THE UNDERWATER WORLD UP TO THE SURFACE IS IMPORTANT TO CREATE AWARENESS AND SUPPORT
Source: Berg River, Western Cape, South Africa ©Jeremy Shelton

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BOX 11

CLIMATE CHANGE IN OCEANIA

Data deficiencies meant that climate change did not feature as a major issue in the Oceania. Nevertheless, it has been a significant concern for migratory freshwater fish; particularly in Australia. Two significant drought events (the millennium drought 1996-2009; 2017-current), a major flood (2010/2011) and a series of bushfires (2019-20) placed significant pressure on freshwater resources. The most recent drought event saw the most significant string of fish kill events in recent history. The drought left over 1,000km of the Darling River with no flow, and reduced to a series of pools. It led to a significant fish kill, which gained substantial international attention, where over 3 million fish were estimated to have perished in the midst of a blue-green algal event. Between the two major droughts was a significant flood event. The floods inundated areas of floodplain habitat which had not experienced river flow for over 20 years. Leaf litter and detritus on the floodplain was rapidly broken down by a bacterial bloom which created sub-lethal dissolved oxygen levels. These led to the suffocation of hundreds of thousands of native fish in over 500km of the Murray and Edward River systems. Finally, a series of intense bushfires swept through over 30 catchment regions during the summer of 2019/20.

FIGURE 1

Drought-related fish kills from the Darling River (Australia) in 2018/2019. Low river flows, blue green algae and low oxygen led to the deaths of over 3 million migratory fish species.

These events left large areas of the catchment covered with ash and silt. With no ground cover vegetation, successive rainfall events washed the ash and silt into main river channels. Rivers turned to black mud and millions of native fish were reported to have perished. An investigation into some of these fish kills identified a sustained increase in extreme weather events which have occurred since the 1960's. Extreme weather events are expected to intensify with ongoing global warming. So, managing these weather extremes, to minimise impacts on migratory freshwater species, will be a priority action moving forward. Studies into the fish kills are ongoing, but this new data will be able to be incorporated into future LPI calculations.

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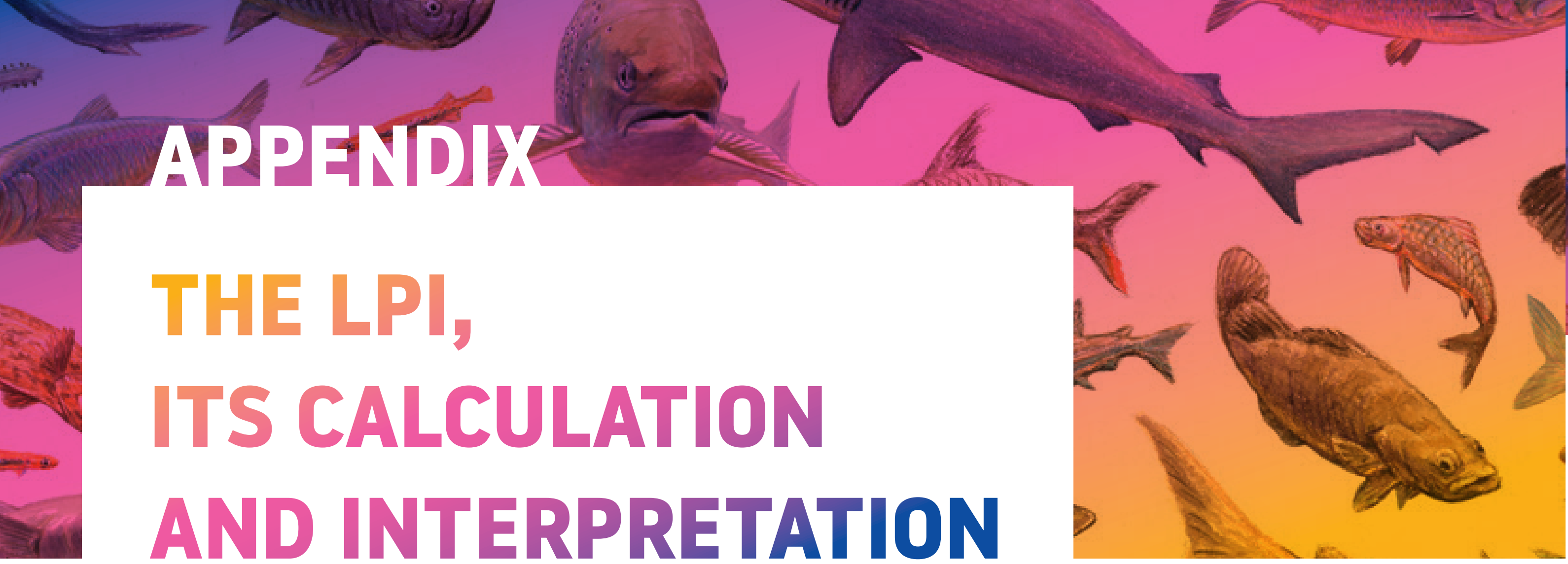


APPENDIX

THE LPI, ITS CALCULATION AND INTERPRETATION

The LPI is one of a suite of global indicators used to monitor progress towards the Aichi biodiversity targets agreed by the Convention on Biological Diversity's (CBD) in 2010 (SCBD 2010). It tracks trends in abundance of a large number of populations of vertebrate species in much the same way that a stock market index tracks the value of a set of shares or a retail price index tracks the cost of a basket of consumer goods. The data used in constructing the index are time series of either population size, density (population size per unit area), abundance (number of individuals per sample) or a proxy of abundance (e.g. the number of nests or breeding pairs recorded may be used instead of a direct population count). The underlying database (Living Planet Database, LPD; LPI 2020) currently contains data on nearly 26,700 populations of 4,582 vertebrate species from around the world, collected from a variety of sources.

Using a method developed by ZSL and WWF, species population trends are aggregated and weighted to produce the different Living Planet Indices. For each population, the rate of change from one year to the next is calculated. If the data available are from only a few, non-consecutive years, a constant annual rate of change in the population is assumed between each data year. Where data are available from many years (consecutive or not) a curve is plotted through the data points using a statistical method called generalized additive modelling. Average annual rates of change in populations of the same species are aggregated to the species level and then higher levels (Collen *et al.* 2009a).

A deeper dive for calculation of the global index can be found in The Living Planet Report 2018 (WWF 2018). Please note that although the global index is normally weighted by species richness in different taxonomic groups and geographic regions (McRae *et al.* 2017), this report is based on unweighted indices. This is because the indices presented are based on only one taxonomic class, and the coverage is not good enough to split geographically or by GROMS category.

Like the global index presented biennially in the Living Planet Report, the index for migratory freshwater fish starts at a value of 1 in 1970. If the LPI and confidence limits move away from this baseline, we can say there has been an increase (above 1) or decline (below 1) compared to 1970. These values represent the average change in population abundance - based on the relative change and not the absolute change - in population sizes. The shaded areas in each graph show 95% confidence limits. These illustrate how certain we are about the trend in any given year relative to 1970. The confidence limits always widen throughout the time series as the uncertainty from each of the previous years is added to the current year. For this report, we chose an end year of 2016 as this is latest year for which we have a good amount of data. Data availability decreases in more recent years because it takes time to collect, process and publish monitoring data, so there can be a time lag before these are added to the LPD.

APPENDIX

SPECIES LIST

TABLE A1
Species included in this analysis and the number of available populations for each.

REGION	CLASS	BINOMIAL	COMMON NAME	GROMS CATEGORY	NO. OF POPULATIONS
Africa	Actinopteri	Alestes baremoze	Silversides	Potamodromous	4
		Ambassis gymnocephalus	Bald glassy	Amphidromous	1
		Brycinus imberi	Spot-tail	Potamodromous	2
		Brycinus leuciscus	Yellow-fin tetras	Potamodromous	2
		Brycinus macrolepidotus	True big-scale tetra	Potamodromous	1
		Brycinus nurse	Nurse tetra	Potamodromous	2
		Caranx sexfasciatus	Bigeye trevally	Diadromous	1
		Chanos chanos	Milkfish	Catadromous	1
		Chelon dumerili	Grooved mullet	Catadromous	7
		Chrysichthys maurus	Bagrid catfish	Potamodromous	2
		Clarias gariepinus	North African catfish	Potamodromous	5
		Crenimugil buchanani	Bluetail mullet	Amphidromous	2
		Crenimugil seheli	Bluespot mullet	Amphidromous	1
		Enteromius trimaculatus	Threespot barb	Potamodromous	2
		Epiplatys bifasciatus	No common name	Potamodromous	1
		Epiplatys spilargyreius	No common name	Potamodromous	1
		Gerres longirostris	Strongspine silver-biddy	Amphidromous	1
		Gilchristella aestuaria	Gilchrist's round herring	Diadromous	3
		Glossogobius giuris	Tank goby	Amphidromous	1
		Hilsa kelee	Kelee shad	Anadromous	3
		Hydrocynus forskahlii	Elongate tigerfish	Potamodromous	4
		Labeo congoro	Purple labeo	Potamodromous	1
		Labeo senegalensis	No common name	Potamodromous	1
		Labeo umbratus	Moggel	Potamodromous	1
		Lates niloticus	Nile perch	Potamodromous	1
		Leiognathus equula	Common ponyfish	Diadromous	1
		Lithognathus lithognathus	White steenbras	Amphidromous	7
		Marcusenius ussheri	Djii	Potamodromous	1
		Megalops cyprinoides	Indo-pacific tarpon	Anadromous	2
		Moolgarda cunnesius	Longarm mullet	Amphidromous	2
		Mugil cephalus	Flathead grey mullet	Catadromous	6
		Oligolepis acutipennis	Sharptail goby	Amphidromous	1
		Oreochromis mossambicus	Mozambique tilapia	Amphidromous	7
		Oreochromis niloticus	Nile tilapia	Potamodromous	1
		Osteomugil robustus	Robust mullet	Catadromous	1
		Petrocephalus bovei	No common name	Potamodromous	4
		Pseudomyxus capensis	Freshwater mullet	Catadromous	6

		Schilbe intermedius	Silver catfish	Potamodromous	3
		Schilbe mandibularis	No common name	Potamodromous	4
		Schilbe mystus	African butter catfish	Potamodromous	1
		Sillago sihama	Silver sillago	Amphidromous	1
		Terapon jarbua	Jarbua terapon	Catadromous	2
	Elasmobranchii	Carcharhinus leucas	Bull shark	Amphidromous	3
Asia	Actinopteri	Acipenser gueldenstaedtii	Danube sturgeon	Anadromous	2
		Acipenser nudiventris	Fringebarbel sturgeon	Anadromous	1
		Acipenser persicus	Persian sturgeon	Potamodromous	1
		Acipenser schrenckii	Amur sturgeon	Anadromous	1
		Acipenser sinensis	Chinese sturgeon	Anadromous	1
		Acipenser stellatus	Starry sturgeon	Anadromous	3
		Alburnus chalcoides	Danube bleak	Potamodromous	1
		Anguilla japonica	Japanese eel	Catadromous	5
		Anodontostoma chacunda	Chacunda gizzard shad	Anadromous	1
		Atherina boyeri	Big-scale sand smelt	Amphidromous	1
		Channa punctata	Spotted snakehead	Potamodromous	3
		Channa striata	Striped snakehead	Potamodromous	3
		Clarias macrocephalus	Bighead catfish	Potamodromous	1
		Coilia dussumieri	Gold-spotted grenadier anchovy	Amphidromous	1
		Eleginus gracilis	Saffron cod	Amphidromous	5
		Huso dauricus	Kaluga	Anadromous	1
		Huso huso	Beluga	Anadromous	3
		Mugil cephalus	Flathead grey mullet	Catadromous	2
		Nuchequula gerreoides	Decorated ponyfish	Amphidromous	2
		Oncorhynchus gorbuscha	Pink salmon	Anadromous	6
		Oncorhynchus nerka	Sockeye salmon	Anadromous	1
		Puntius sophore	Pool barb	Amphidromous	3
		Salmo salar	Atlantic salmon	Anadromous	2
		Selaroides leptolepis	Yellowstripe scad	Amphidromous	2
		Squalius cephalus	Chub	Potamodromous	1
		Thryssa hamiltonii	Hamilton's thryssa	Amphidromous	2
		Trichopodus pectoralis	Snakeskin gourami	Potamodromous	1
		Vimba vimba	Vimba bream	Anadromous	1
Europe	Actinopteri	Abramis ballerus	Zope	Potamodromous	1
		Abramis brama	Freshwater bream	Potamodromous	5
		Acipenser gueldenstaedtii	Danube sturgeon	Anadromous	1
		Acipenser ruthenus	Sterlet sturgeon	Potamodromous	1
		Acipenser stellatus	Starry sturgeon	Anadromous	1
		Alburnoides bipunctatus	Schneider	Potamodromous	5
		Alburnus alburnus	Bleak	Potamodromous	20
		Alosa alosa	Allis shad	Anadromous	2
		Alosa fallax	Twaite shad	Anadromous	3
		Ameiurus melas	Black bullhead	Amphidromous	1
		Anguilla anguilla	European eel	Catadromous	2
		Atherina boyeri	Big-scale sand smelt	Amphidromous	2
		Barbatula barbatula	Stone loach	Potamodromous	5
		Barbus barbus	Barbel	Potamodromous	10

	Blicca bjoerkna	White bream	Potamodromous	13
	Carassius carassius	Crucian carp	Potamodromous	5
	Carassius gibelio	Prussian carp	Potamodromous	6
	Chelon ramada	Thinlip grey mullet	Catadromous	1
	Chondrostoma nasus	Common nase	Potamodromous	6
	Cobitis taenia	Spined loach	Potamodromous	2
	Coregonus albula	Vendace	Anadromous	1
	Coregonus lavaretus	European whitefish	Anadromous	6
	Cyprinus carpio	Common carp	Potamodromous	2
	Esox lucius	Northern pike	Amphidromous	11
	Gasterosteus aculeatus	Three-spined stickleback	Anadromous	2
	Gobio gobio	Gudgeon	Amphidromous	9
	Gymnocephalus cernua	Ruffe	Potamodromous	11
	Huso huso	Beluga	Anadromous	1
	Lepomis gibbosus	Pumpkinseed	Potamodromous	1
	Leuciscus aspius	Asp	Potamodromous	2
	Leuciscus idus	Ide	Potamodromous	3
	Leuciscus leuciscus	Common dace	Potamodromous	8
	Lota lota	Burbot	Potamodromous	9
	Misgurnus fossilis	Weatherfish	Potamodromous	1
	Perca fluviatilis	European perch	Anadromous	36
	Phoxinus phoxinus	Eurasian minnow	Potamodromous	4
	Platichthys flesus	European flounder	Catadromous	8
	Pomatoschistus microps	Common goby	Amphidromous	2
	Rutilus rutilus	Roach	Potamodromous	31
	Salmo salar	Atlantic salmon	Anadromous	53
	Salmo trutta	Brown trout	Anadromous	65
	Salvelinus alpinus	Arctic char	Anadromous	5
	Sander lucioperca	Pikeperch	Potamodromous	5
	Scardinius erythrophthalmus	Rudd	Potamodromous	7
	Squalius cephalus	Chub	Potamodromous	18
	Tinca tinca	Tench	Potamodromous	9
	Vimba vimba	Vimba bream	Anadromous	1
Petromyzonti	Lampetra fluviatilis	River lamprey	Anadromous	1
	Petromyzon marinus	Sea lamprey	Anadromous	4
Latin America and Caribbean				
Actinopteri	Acarichthys heckelii	Threadfin acara	Potamodromous	1
	Anchoa mitchilli	Bay anchovy	Amphidromous	1
	Anchoviella lepidentostole	Broadband anchovy	Anadromous	1
	Astyanax bimaculatus	Twospot astyanax	Potamodromous	1
	Astyanax eigenmanniorum	Tetra	Potamodromous	1
	Brycon melanopterus	No common name	Potamodromous	1
	Centropomus parallelus	Fat snook	Amphidromous	1
	Centropomus undecimalis	Common snook	Amphidromous	1
	Colossoma macropomum	Cachama	Potamodromous	2
	Crenicichla lepidota	Pike cichlid	Potamodromous	2
	Curimata cyprinoides	No common name	Potamodromous	1
	Dajaus monticola	Mountain mullet	Catadromous	1

	Geophagus brasiliensis	Pearl cichlid	Potamodromous	1
	Gerres cinereus	Yellow fin mojarra	Amphidromous	1
	Gobiomorus dormitor	Bigmouth sleeper	Catadromous	2
	Hoplias aimara	No common name	Potamodromous	1
	Hoplias malabaricus	Trahira	Potamodromous	9
	Hypophthalmus edentatus	Highwaterman catfish	Potamodromous	3
	Leporinus friderici	Threespot leporinus	Potamodromous	3
	Lycengraulis grossidens	Atlantic sabretooth anchovy	Anadromous	1
	Megaleporinus obtusidens	No common name	Potamodromous	1
	Megalops atlanticus	Tarpon	Amphidromous	1
	Mugil curema	Silver mullet	Catadromous	2
	Mugil liza	Lebranche mullet	Catadromous	2
	Myleus ternetzi	No common name	Potamodromous	1
	Mylossoma aureum	No common name	Potamodromous	1
	Mylossoma duriventre	No common name	Potamodromous	1
	Oligosarcus robustus	Tambicu	Potamodromous	1
	Parapimelodus nigribarbis	No common name	Potamodromous	1
	Pimelodus maculatus	No common name	Potamodromous	3
	Pinirampus pirinampu	Flatwhiskered catfish	Potamodromous	3
	Plagioscion squamosissimus	South American silver croaker	Potamodromous	5
	Potamorhina latior	No common name	Potamodromous	1
	Prochilodus lineatus	Streaked prochilod	Potamodromous	4
	Prochilodus nigricans	Black prochilodus	Potamodromous	1
	Pterodoras granulosus	Granulated catfish	Potamodromous	4
	Rhinelepis aspera	No common name	Potamodromous	1
	Schizodon fasciatus	No common name	Potamodromous	1
	Semaprochilodus insignis	Kissing prochilodus	Potamodromous	1
	Serrasalmus altispinis	No common name	Potamodromous	1
	Steindachnerina insculpta	No common name	Potamodromous	2
	Trichiurus lepturus	Largehead hairtail	Amphidromous	2
	Triportheus albus	No common name	Potamodromous	1
	Triportheus angulatus	No common name	Potamodromous	1
	Zungaro zungaro	Gilded catfish	Potamodromous	2
Elasmobranchii	Potamotrygon motoro	South American freshwater stingray	Potamodromous	1
North America				
Actinopteri	Acipenser brevirostrum	Shortnose sturgeon	Anadromous	3
	Acipenser fulvescens	Lake sturgeon	Potamodromous	5
	Acipenser medirostris	Green sturgeon	Anadromous	3
	Acipenser oxyrinchus	Atlantic sturgeon	Anadromous	3
	Acipenser transmontanus	White sturgeon	Anadromous	8
	Alosa aestivalis	Blueback herring	Anadromous	2
	Alosa alabamae	Alabama shad	Anadromous	1
	Alosa pseudoharengus	Alewife	Anadromous	16
	Alosa sapidissima	American shad	Anadromous	11
	Ameiurus melas	Black bullhead	Amphidromous	1
	Anchoa mitchilli	Bay anchovy	Amphidromous	4
	Anguilla rostrata	American eel	Catadromous	10
	Catostomus commersonii	White sucker	Catadromous	13
	Centropomus undecimalis	Common snook	Amphidromous	10
	Coregonus artedi	Lake herring / Cisco	Anadromous	7
	Coregonus autumnalis	Arctic cisco	Anadromous	1
	Coregonus clupeaformis	Lake whitefish	Anadromous	9
	Cottus asper	Prickly sculpin	Catadromous	1
	Dorosoma cepedianum	American gizzard shad	Anadromous	4
	Dorosoma petenense	Threadfin shad	Anadromous	2
	Eleginus gracilis	Saffron cod	Amphidromous	2
	Esox lucius	Northern pike	Amphidromous	10
	Gambusia holbrooki	Eastern mosquitofish	Potamodromous	2
	Gerres cinereus	Yellow fin mojarra	Amphidromous	2
	Hiodon alosoides	Goldeye	Potamodromous	2
	Hypomesus transpacificus	Delta smelt	Anadromous	1
	Lepomis gibbosus	Pumpkinseed	Potamodromous	7
	Leptocottus armatus	Pacific staghorn sculpin	Amphidromous	4
	Lota lota	Burbot	Potamodromous	3
	Lucania parva	Rainwater killifish	Amphidromous	1
	Megalops atlanticus	Tarpon	Amphidromous	1
	Microgadus tomcod	Atlantic tomcod	Anadromous	29
	Morone americana	White perch	Anadromous	9
	Morone chrysops	White bass	Potamodromous	4
	Morone saxatilis	Striped bass	Anadromous	27
	Mugil curema	Silver mullet	Catadromous	1
	Myoxocephalus polyacanthocephalus	Great sculpin	Amphidromous	4
	Oncorhynchus clarkii	Cutthroat trout	Anadromous	6
	Oncorhynchus gorbuscha	Pink salmon	Anadromous	18
	Oncorhynchus keta	Chum salmon	Anadromous	37
	Oncorhynchus kisutch	Coho salmon	Anadromous	36
	Oncorhynchus mykiss	Rainbow trout	Anadromous	4
	Oncorhynchus nerka	Sockeye salmon	Anadromous	58
	Oncorhynchus tshawytscha	Chinook salmon	Anadromous	43
	Osmerus mordax	Rainbow smelt	Anadromous	9
	Platichthys stellatus	Starry flounder	Catadromous	8
	Prosopium cylindraceum	Round whitefish	Potamodromous	3
	Pungitius pungitius	Ninespine stickleback	Anadromous	67
	Salmo salar	Atlantic salmon	Anadromous	22
	Salvelinus alpinus	Arctic char	Anadromous	2
	Salvelinus confluentus	Bull trout	Anadromous	29
	Salvelinus fontinalis	Brook trout	Anadromous	38
	Salvelinus malma	Dolly varden	Anadromous	7
	Sander vitreus	Walleye	Potamodromous	24
	Scaphirhynchus albus	Pallid sturgeon	Potamodromous	1
	Spirinchus thaleichthys	Longfin smelt	Anadromous	1
	Stenodus leucichthys	Inconnu	Anadromous	1
	Thaleichthys pacificus	Eulachon	Anadromous	5
	Troglichthys rosae	Ozark cavefish	Potamodromous	1
	Xyrauchen texanus	Razorback sucker	Potamodromous	1
Elasmobranchii	Carcharhinus leucas	Bull shark	Amphidromous	2
	Pristis pectinata	Smalltooth sawfish	Amphidromous	2
Petromyzonti	Petromyzon marinus	Sea lamprey	Anadromous	1
Oceania Actinopteri	Acanthopagrus australis	Yellowfin bream	Diadromous	3

	Ambassis agassizii	Agassiz's glassfish	Potamodromous	1
	Ambassis interrupta	Long-spined glass perchlet	Potamodromous	1
	Ambassis miops	Flag-tailed glass perchlet	Amphidromous	2
	Amniataba percoides	Barred grunter	Potamodromous	3
	Anguilla australis	Short-finned eel	Catadromous	3
	Anguilla dieffenbachii	New Zealand longfin eel	Catadromous	5
	Anguilla obscura	Pacific shortfinned eel	Catadromous	2
	Anguilla reinhardtii	Speckled longfin eel	Catadromous	2
	Arrhamphus sclerolepis	Northern snubnose garfish	Diadromous	2
	Arripis trutta	Australian salmon	Anadromous	1
	Atherinosoma microstoma	Small-mouth hardyhead	Anadromous	3
	Butis butis	Duckbill sleeper	Amphidromous	2
	Caranx sexfasciatus	Bigeye trevally	Diadromous	2
	Chanos chanos	Milkfish	Catadromous	2
	Chelonodontops patoca	Milkspotted puffer	Anadromous	1
	Craterocephalus stercusmuscarum	Fly-specked hardyhead	Potamodromous	4
	Eleotris melanosoma	Broadhead sleeper	Amphidromous	1
	Eubleekeria splendens	Splendid ponyfish	Amphidromous	1
	Galaxias fasciatus	Banded kokopu	Amphidromous	1
	Gerres filamentosus	Whipfin silverbiddy	Amphidromous	3
	Giuris margaritaceus	Snakehead gudgeon	Amphidromous	1
	Glossogobius aureus	Golden tank goby	Amphidromous	1
	Glossogobius giuris	Tank goby	Amphidromous	2
	Hypseleotris compressa	Empire gudgeon	Potamodromous	3
	Kuhlia marginata	Dark-margined flagtail	Catadromous	1
	Kuhlia rupestris	Rock flagtail	Catadromous	2
	Lates calcarifer	Barramundi	Catadromous	9
	Leiognathus equula	Common ponyfish	Diadromous	3
	Leiopotherapon unicolor	Spangled perch	Potamodromous	3
	Maccullochella peelii	Murray cod	Potamodromous	2
	Macquaria ambigua	Golden perch	Potamodromous	2
	Macquaria australasica	Macquarie perch	Potamodromous	1
	Megalops cyprinoides	Indo-pacific tarpon	Anadromous	1
	Mesopristes argenteus	Silver grunter	Diadromous	2
	Mugil cephalus	Flathead grey mullet	Catadromous	3
	Nematalosa erebi	Australian river gizzard shad	Potamodromous	5
	Neoarius graeffei	Blue salmon catfish	Diadromous	1
	Neosilurus hyrtlii	Hyrtl's catfish	Potamodromous	1
	Notesthes robusta	Bullrout	Catadromous	2
	Nuchequula gerreoides	Decorated ponyfish	Amphidromous	1
	Psammogobius biocellatus	Sleepy goby	Amphidromous	2
	Redigobius bikolanus	Speckled goby	Catadromous	2
	Scatophagus argus	Spotted scat	Amphidromous	2
	Scortum ogilbyi	Leathery grunter	Potamodromous	1
	Sillago sihama	Silver sillago	Amphidromous	1
	Tandanus tandanus	Freshwater catfish	Potamodromous	1
	Thryssa scratchleyi	New Guinea thryssa	Catadromous	2
	Toxotes chatareus	Spotted archerfish	Amphidromous	4
	Toxotes jaculatrix	Banded archerfish	Amphidromous	1
Elasmobranchii	Carcharhinus leucas	Bull shark	Amphidromous	1

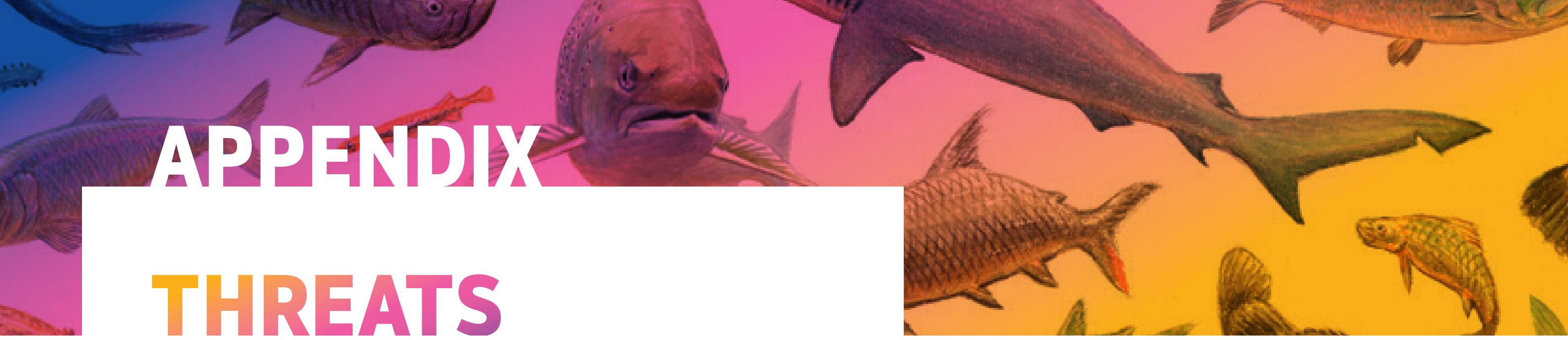
APPENDIX

REPRESENTATION

TABLE A2

Proportional representation of the data set used in this analysis. Proportion (LPI) is the proportion of species in the data set for each region or GROMS migration category compared to the total number of species across all regions or GROMS categories. The expected proportion is the proportion of species we would expect to find in each region or GROMS category out of all species listed on GROMS across the following categories: anadromous, catadromous, diadromous, amphidromous and potamodromous.

DATA SET	SUBSET	PROPORTION (LPI)	PROPORTION (EXPECTED)	X^2		REPRESENTATION
Region	Africa	0,17	0,28	11,41	***	under
	Asia & Oceania	0,31	0,69	125,77	***	under
	Europe	0,20	0,09	21,62	***	over
	Latin America and Caribbean	0,19	0,16	0,99	NS	over
	North America	0,26	0,12	28,08	***	over
GROMS	Potamodromous	0,44	0,49	2,05	NS	under
	Fresh- & Saltwater combined	0,56	0,51	2,05	NS	over
	Amphidromous	0,18	0,28	10,36	***	under
	Anadromous	0,24	0,15	10,92	***	over
	Catadromous	0,11	0,06	7,99	***	over
	Diadromous	0,03	0,02	1,25	NS	over



APPENDIX

THREATS

FIGURE A3

Descriptions of the different major threat categories used in the Living Planet Database (from WWF 2018). This classification is also followed by the IUCN Red List and based on Salafsky *et al.* 2008.

THREAT		DESCRIPTION
HABITAT CHANGE AND DEGRADATION		This refers to the modification of the environment where a species lives, by complete fragmentation or reduction in the quality of key habitat. For freshwater habitats, fragmentation of rivers and streams and abstraction of water are common threats.
HABITAT LOSS		This refers to the modification of the environment where a species lives, by complete removal of key habitat.
OVEREXPLOITATION		There are both direct and indirect forms of overexploitation. Direct overexploitation refers to unsustainable fishing, whether for subsistence or for trade. Indirect overexploitation occurs when non-target species are killed unintentionally, for example as bycatch in fisheries.
POLLUTION		Pollution can directly affect a species by making the environment unsuitable for its survival (this is what happens, for example, in the case of an oil spill). It can also affect a species indirectly, by affecting food availability or reproductive performance, thus reducing population numbers over time.
INVASIVE SPECIES AND DISEASE		Invasive species can compete with native species for space, food and other resources, can turn out to be a predator for native species, or spread diseases that were not previously present in the environment. Humans also transport new diseases from one area of the globe to another.
CLIMATE CHANGE		As temperatures change, some species will need to adapt by shifting their range to track suitable climate. The effects of climate change on species are often indirect. Changes in temperature can confound the signals that trigger seasonal events such as migration and reproduction, causing these events to happen at the wrong time (for example misaligning reproduction and the period of greater food availability in a specific habitat).

TECHNICAL REPORT