

Disappearing giants: a review of threats to freshwater megafauna

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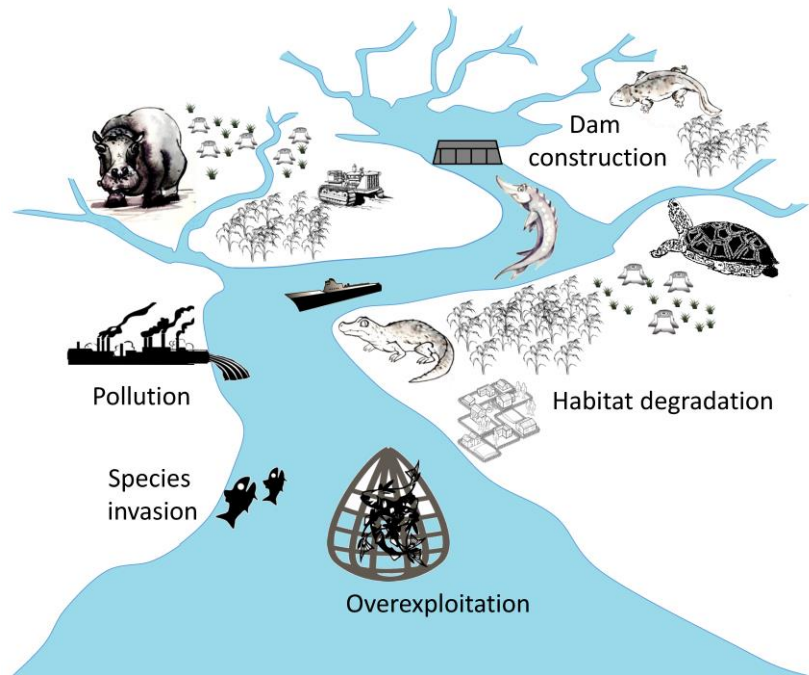
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Abstract

Charismatic megafauna species may act as both flagship and umbrella species. They influence local environments and biotas, determine related ecosystem processes and functions, and are associated with high levels of biodiversity. However, the intrinsic characteristics of megafauna species including long lifespan, large body size, sparseness and/or rarity, late maturity and low fecundity, as well as high market value, make them very prone to extinction. Up to now, scientific interest and conservation efforts have mainly focused on terrestrial and marine megafauna, while freshwater species have received comparatively little attention, despite evidence suggesting that freshwaters are losing species faster than marine or terrestrial realms. The high susceptibility of freshwater megafauna to multiple threats, coupled with immense human pressure on freshwater ecosystems, places freshwater megafauna amongst the most threatened species globally. The main threats include overexploitation, dam construction, habitat degradation, pollution and species invasion. These threats increase mortality, decrease productivity and reduce fitness, causing the decline of populations and the extinction of freshwater megafauna species. Given the essential ecological and biological roles of freshwater megafauna, further research should focus on their distribution patterns, extinction risks and population dynamics, thereby improving the knowledge base for conservation planning. Finally, freshwater megafauna-based conservation strategies may raise public awareness for freshwater conservation and therefore benefit a broader range of freshwater species and functions.

Graphical/Visual Abstract and Caption



Freshwater megafauna are facing a wide range of threats that could lead to the decline of populations, reduction of genetic variability, and species extinction.

INTRODUCTION

Animals are classified according to various characteristics and traits, including size. The term megafauna refers to disproportionately large-bodied animals and is often associated with prehistoric large terrestrial vertebrates weighting more than 44 kg (ca. 100 pounds)^{1, 2}. More recently, however, the concept of megafauna has been extended beyond a uniform weight threshold³⁻⁵, to cover both extinct and extant species in terrestrial, marine and freshwater ecosystems⁶⁻⁸.

Megafauna species receive significant attention due to their charismatic nature and their susceptibility to extinction⁹⁻¹¹. They are, therefore, often used as flagship and umbrella species, promoting public awareness¹² and stimulating funding for environmental conservation^{13, 14}. For instance, the “big five” (i.e. buffalo, elephant, lion, leopard, and rhinoceros) are important flagship species for sub-Saharan Africa, having secured strong public attention and subsequent support¹⁵. Recently, research on megafauna has increased (Figure 1), but with the scientific interest and conservation efforts mainly focusing on terrestrial and marine ecosystems. In contrast, freshwater megafauna remain underrepresented both in science and in public awareness¹⁶. At the same time, freshwaters are among the most threatened ecosystems globally; with species populations declining much faster than in terrestrial and marine realms¹⁷⁻¹⁹. Furthermore, the concept of megafauna is rarely considered in freshwater research and conservation. Indeed, we still lack an official definition of freshwater megafauna. In the present review, we define freshwater megafauna as all animals

with a body mass of at least 30 kg that spend an essential part of their life in freshwater or brackish ecosystems. Based on a 30 kg threshold, freshwater megafauna species include representatives of fishes, reptiles, mammals and amphibians.

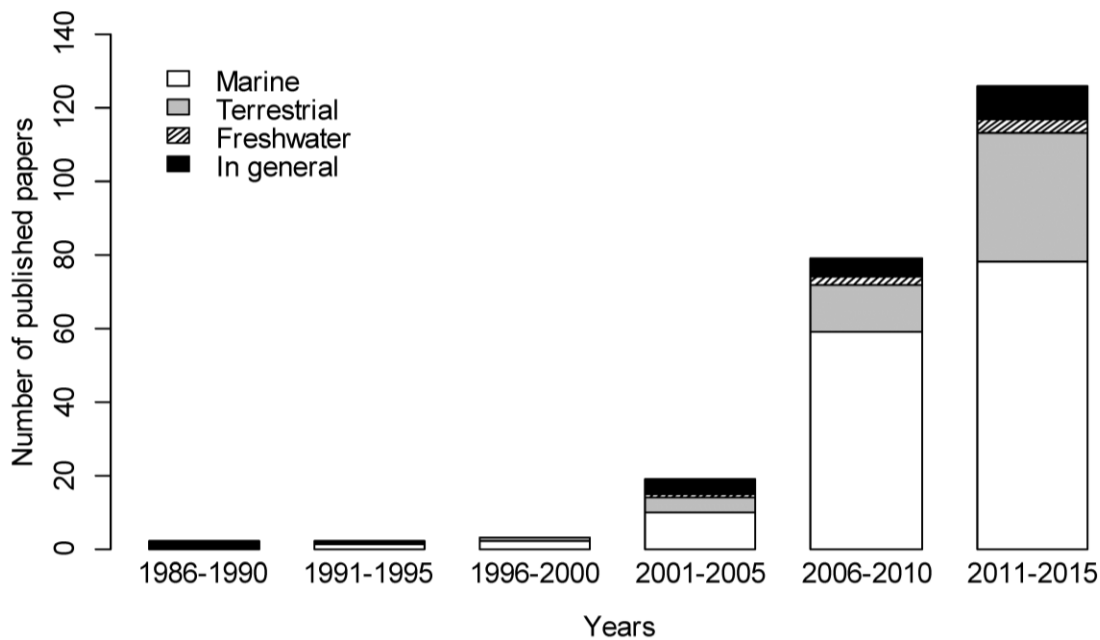


FIGURE 1. Numbers of publications focused on megafauna in different ecosystems (for details on the underlying methodology see Supporting Information).

Megafauna species shape ecosystems and their related processes, often representing key ecosystem engineers²⁰⁻²². For example, beavers (the American Beaver, *Castor canadensis* and the Eurasian Beaver, *Castor fiber*) alter stream morphology through dam building, thereby changing hydrological and biogeochemical processes, as well as affecting in-stream and riparian biotas²³⁻²⁵. The American Alligator (*Alligator mississippiensis*) modifies the Everglades landscape by creating and maintaining small ponds which, in turn, provide habitat and refugia for many additional plants and small animals²⁶. Freshwater megafauna may also increase the nutrient flow between freshwater, terrestrial and marine ecosystems. For instance, anadromous freshwater megafauna (e.g. the Atlantic salmon, *Salmo salar* and the Chinook Salmon, *Oncorhynchus tshawytscha*) transfer large amounts of nutrients from the ocean to freshwaters and finally to terrestrial systems^{27, 28}, shaping productivity and food web dynamics in river and riparian systems.

Many freshwater megafauna species are top predators. Their extirpation would often lead to marked effects on local community structure through trophic cascades. For examples, the loss of large predatory fish might release small planktivorous species from predation, thus altering consumption pressures on zooplankton and phytoplankton²⁹. Moreover, freshwater megafauna may create habitat for other species, such as through the creation of ponds and holes by hippopotamus or crocodilians so providing dry-season refugia for many fish species^{22, 26}. The decline of Brown Trout (*Salmo trutta*), mainly due to habitat fragmentation, threatens the Freshwater Pearl Mussel (*Margaritifera margaritifera*), because it is an important host for the parasitic mussel larvae³⁰. These

few selected examples emphasize the potentially far-reaching ecological and biological consequences of freshwater megafauna loss.

A high proportion of the world’s freshwater megafauna species are under threat³¹⁻³³. Indeed, 54% (i.e. 84 out of 155 assessed species) of freshwater megafauna are already listed as threatened (Critically Endangered, Endangered or Vulnerable; for details see Supporting Information), based on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species™ (hereafter IUCN Red List)³⁴. Four species are Critically Endangered (Possibly Extinct), including the Chinese Paddlefish (*Psephurus gladius*), the world’s longest freshwater fish, which has not been seen since 2003³⁵; the Baiji (*Lipotes vexillifer*), which could represent the first human-caused extinction of a cetacean species³⁶; the Yangtze Sturgeon (*Acipenser dabryanus*); and the Adriatic Sturgeon (*Acipenser naccarii*). Today, both sturgeon species are strongly dependent on artificial stocking to maintain their populations in the wild^{37, 38}. The Atlantic (or Common) Sturgeon (*Acipenser sturio*), once the most common sturgeon species across Europe, is now restricted to the Garonne River (France) and is experiencing an ongoing decline³⁹.

Many freshwater megafauna species inhabit remote areas and their decline or loss will often go unnoticed due to poor monitoring. For instance, despite its large size, the Freshwater Whipray (*Himantura dalyensis*) still lacks information on many of the threats it faces and was only recently recognized as a separate species⁴⁰. Discussion on the taxonomy of *Arapaima* spp. is still ongoing^{41, 42}, and the assessment of *Arapaima* (*Arapaima gigas*) needs updating as it is still listed as Data Deficient on the IUCN Red List, in spite of increasing evidence that it is seriously threatened by overexploitation^{43, 44}. Although research on the conservation status has been conducted for individual species and taxonomic groups, such as sturgeons and paddlefishes, we lack a collective overview of the threat status for all freshwater megafauna at the global scale. Intending to fill this important information gap, this paper provides a comprehensive overview of the threats facing freshwater megafauna, and of the subsequent impacts. In addition, we highlight the urgent need for great focus on the conservation of freshwater biodiversity.

THREATS TO FRESHWATER MEGAFUNA

The loss of freshwater megafauna is mainly driven by overexploitation, dam construction, habitat degradation, pollution and species invasion, along with the compounding impacts of climate change (Table 1). The interacting and combined impacts of these threats have led to a decline in population size and range reduction for many freshwater megafauna species^{45, 46}. Although there remains a lack of understanding of the influence of climate change on freshwater megafauna, global warming and drought are likely to increase habitat degradation, further increasing direct impacts of human activities. The Freshwater Whipray, for example, is considered highly susceptible to climate change effects due to its rarity and high degree of habitat specialization⁴⁷. For the Caspian Seal (*Pusa caspica*), warmer winters in the future might reduce the stability of ice breeding habitats and cause increased mortality among pups⁴⁸. In addition, global warming is likely to have severe impacts on crocodylians and turtles with temperature-dependent sex determination, altering sex ratios and affecting population demographics⁴⁹.

TABLE 1. Major threats to freshwater megafauna

Threats	Impact	Examples
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Overexploitation	Increased mortality due to intentional harvest or by-catch; depletion or extirpation of local populations	<i>Arapaima gigas</i> ^{43, 44} , <i>Andrias davidianus</i> ^{50, 51} , <i>Crocodylus rhombifer</i> ⁵²
Dam construction	Blocked migration pathways for migratory species; reduced access to spawning grounds; fragmented population; altered natural flow and thermal regime, thus influencing fitness and reproduction; drought and habitat loss at downstream locations	<i>Acipenser gueldenstaedtii</i> ⁴⁶ , <i>Acipenser sinensis</i> ⁵³ , <i>Gavialis gangeticus</i> ⁴⁵ , <i>Kobus leche</i> ⁵⁴
Habitat degradation	Loss and fragmentation of required habitats and spawning grounds; increased injury and death due to conflict with humans (e.g. settlement, agriculture, shipping)	<i>Crocodylus niloticus</i> ⁵⁵ , <i>Hucho perryi</i> ⁵⁶ , <i>Pteronura brasiliensis</i> ⁵⁷ , <i>Trichechus manatus</i> ⁵⁸
Pollution	Increased mortality due to acute toxicity and bioaccumulation; degraded water quality (e.g. eutrophication and sedimentation) resulting in chemical barriers to fish movement and reduced fitness; endocrine disruption leading to developmental and reproductive abnormalities	<i>Crocodylus moreletii</i> ⁵⁹ , <i>Huso dauricus</i> ⁶⁰ , <i>Pusa sibirica</i> ⁶¹
Species invasion	Competitive exclusion of native species; introduced diseases; increased mortality through predation and toxicity of venomous species; modified food web structure; hybridization and introgression with native species	<i>Acipenser nudiiventris</i> ⁶² , <i>Clarias macrocephalus</i> ⁶³ , <i>Crocodylus johnstoni</i> ⁶⁴ , <i>Hypselobarbus mussullah</i> ⁶⁵ , <i>Tomistoma schlegelii</i> ⁶⁶
Climate change	Loss of suitable habitat due to changes in temperature, precipitation patterns, and extreme events (e.g. drought or flood); potential impact on development and growth in reptiles	<i>Alligator sinensis</i> ⁶⁷ , <i>Pusa caspica</i> ⁴⁸

Compared to other aquatic organisms, freshwater megafauna are typically more susceptible to hunting pressure and ecosystem degradation due to their long lifespan, large body size, late maturity and low fecundity^{68, 69}. They are exposed to a diverse array of threats before reaching maturity. Many freshwater megafauna species (e.g. the South American River Turtle, *Podocnemis expansa*, and the False Gharial, *Tomistoma schlegelii*) require at least ten years to reach sexual maturity^{66, 70} while others (e.g. the Beluga, *Huso huso* and the Siamese Crocodile, *Crocodylus siamensis*) have generation times of 20 years or more^{32, 71}. Consequently, it may require many years to restore local populations to previous levels⁷². Unless actions are taken to change things, the current trajectory is for an increasing decline in the condition of freshwaters habitats, particularly in the species-rich Global South⁷³⁻⁷⁵.

Overexploitation

Overexploitation is a threat to many freshwater organisms, but it has often been accepted due to its long history throughout human civilization⁷⁶. Harvesting in an unsustainable way has led to major adverse impacts on freshwater species worldwide⁷⁷. Freshwater megafauna are particularly targeted as their meat, skin and eggs are often prized as high-value commodities, and they are often considered an “open access” free resource. For instance, sturgeons and paddlefishes have experienced a long history of intense overexploitation for caviar, pushing them to the brink of extinction³². The global population of Siamese Crocodile has declined by more than 80% during the

past 75 years due to hunting for its skin and the collection of eggs and living individuals⁷¹. The Critically Endangered Chinese Giant Salamander (*Andrias davidianus*), the world's largest amphibian, is experiencing an ongoing population decline because of the capture of wild individuals for their highly prized meat^{50, 51}.

Although many freshwater megafauna species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), poaching remains a common phenomenon in many regions globally. For example, meat consumption has caused a sharp decline in the Cuban Crocodile (*Crocodylus rhombifer*), a species listed in CITES Appendix⁷⁸. Relative to marine species, the capture of freshwater species is limited; however, it provides a critical source of animal protein for many local people, especially for poor communities in remote and rural areas^{79, 80}. In Southeast Asia, which contributes more than a quarter of the total global inland capture fishery production⁸¹, Giant Carp (*Catlocarpio siamensis*), Mekong Giant Salmon Carp (*Aaptosyax grypus*), Giant Pangasius (*Pangasius sanitwongsei*) and Mekong Giant Catfish (*Pangasian odongigas*) are on the brink of extinction, mainly due to overharvesting and the construction of dams (see section below).

Representing another form of exploitation, recreational fishing is a popular activity worldwide contributing approximately 12% of the global fish harvest⁸². Large freshwater fishes have been regarded as trophies since historical times, and popular use of terms such as “monster fish” and “river monsters” has increased the fascination for large freshwater fish⁷². Recreational exploitation does of course add increasing pressure on freshwater megafauna and may have led to the decline of species such as Siberian Taimen (*Hucho taimen*) and Largetooth Sawfish (*Pristis pristis*)^{83, 84}. On the other hand, popular media coverage on large fish and recreational fishing could help create an incentive and greater awareness to protect freshwater life⁸⁵.

Given the intrinsic sparseness of freshwater megafauna and their declining population size, the opportunities for encountering mates for reproduction are more limited⁸⁶. Moreover, the sparseness and/or rarity of these species can make them more attractive and valuable for exploitation and poaching⁸⁷. It is also worth noting that the incidental capture as by-catch is a potentially significant threat for many freshwater megafauna species. For example, Turvey et al.³⁶ suggested that unsustainable by-catch in local fisheries was the primary factor responsible for possible extinction of the Baiji. Similarly, the Yangtze Finless Porpoise (*Neophocaena asiaeorientalis* ssp. *asiaeorientalis*) is subject to incidental by-catch in gillnets⁸⁸. In the Caspian Sea region, by-catch in legal and illegal fisheries may cause the death of several thousand Caspian Seals each year, representing a significant level of mortality for this threatened species in addition to intentional harvesting⁴⁸.

Dam construction

For centuries, people have built dams along rivers for flood regulation, water supply, irrigation, navigation, recreation, and hydropower generation⁸⁹. Driven by rapid human population growth and increasing energy demand, the number of dams has increased strongly during the past six decades⁹⁰. Fragmentation and modified flow regime, both caused by dams, are among the most important anthropogenic impacts to the functioning of freshwater ecosystems^{91, 92}. For example, dams create physical obstructions to fish migration routes. Although various types of fish passages have been

designed to improve connectivity along rivers, their efficiency often remains low, especially for species other than salmonids for which they were originally designed⁹³.

Many freshwater megafauna species undertake long-distance migrations between breeding and feeding areas, therefore they are highly susceptible to blockage by dams. For example, during the past 60 years, the Russian Sturgeon (*Acipenser gueldenstaedtii*) has lost access to 70% of its spawning sites in the Caspian basin and to almost all spawning grounds in the Black Sea basin due to dam construction⁹⁴. In addition, dams affect the thermal regime⁹⁵ and may cause increased pollutants⁹⁶, which could affect the growth and reproduction of freshwater megafauna. Angilletta et al.⁹⁷ suggested that a modified thermal regime might have negative impacts on spawning activity and embryo development of Chinook Salmon. The spawning activity of the Chinese Sturgeon (*Acipenser sinensis*), for example, has been delayed and reduced by an increased water temperature downstream of the Three Gorges and the Gezhouba Dams (Yangtze River)^{53,98}.

In addition to adverse impacts on fishes, dams have led to increased mortality levels and genetic isolation of African Manatee (*Trichechus senegalensis*) populations⁹⁹. Most rivers inhabited by Gharial (*Gavialis gangeticus*) have been dammed for irrigation and other purposes. Subsequent seasonal droughts in previously perennial rivers may affect Gharial individuals that are not able to cross land in search of alternative water sources or dig tunnels to avoid periods of drought⁴⁵. Dam construction and other river engineering projects (e.g. channel straightening, levee construction and dredging) may fundamentally affect floodplain inundation and lateral connectivity, leading to habitat loss of many freshwater megafauna species. For instance, droughts and altered flooding regimes due to damming have led to an estimated 50% decline in the population of Kafue Lechwe (*Kobus leche* ssp. *kafuensis*) on the Kafue Flats (Zambia)⁵⁴.

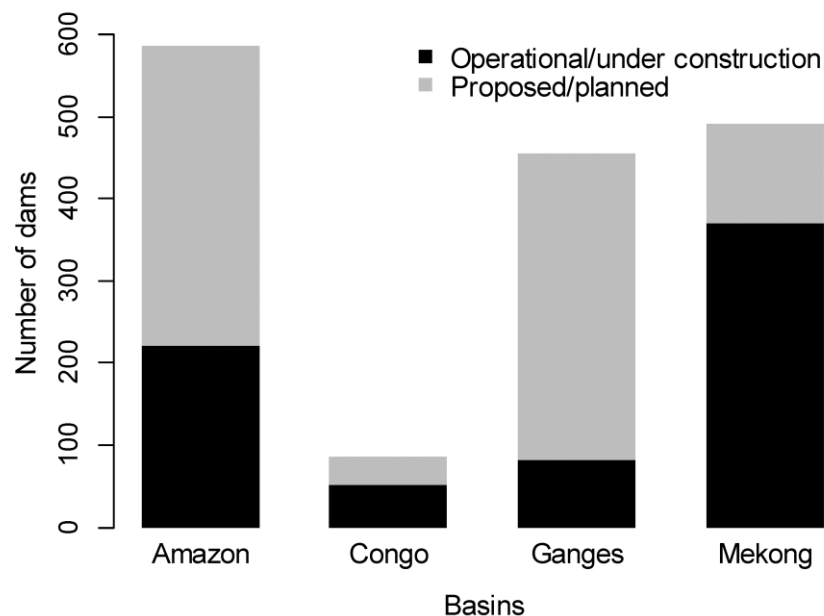


FIGURE 2. Numbers of hydropower dams in four selected megafauna-rich basins^{73, 90, 100}.

Many hydropower dams are planned or are under constructions in the Amazon, Mekong, Congo and Ganges River basins (Figure 2)^{73, 90, 100}, which drain among the most species-rich river basins in the world. The boom in dam construction may threaten many freshwater megafauna species, including the Irrawaddy Dolphin (*Orcaella brevirostris*), Boto (*Inia geoffrensis*), Amazonian Manatee (*Trichechus inunguis*), Ganges River Dolphin (*Platanista gangetica ssp. gangetica*) and Giant Otter (*Pteronura brasiliensis*). It is also reported that already threatened tapirs (e.g. Baird's Tapir, *Tapirus bairdii*) were illegally hunted to feed construction workers during the construction of Chalillo Dam in Belize¹⁰¹, representing one of many additional impacts of dam construction including creation of infrastructure such as roads, and settlements and land-use change.

A global boom in hydropower and its subsequent impacts

Hydropower is a well-established technology for electricity production, accounting for about 80% of renewable energy production globally. Hydropower dam construction is currently accelerating worldwide, meeting increasing energy demands, in some case mitigating climate change consequences and closing the so-called electricity access gap. There are spatially explicit data available for 3700 hydropower dams (> 1 MW) worldwide that are either under construction or planned, which will more than double hydropower capacity within the next decades⁷³. In addition to electricity production, hydropower dams may serve as flood control infrastructure, and their respective reservoirs provide recreational services, food through aquaculture, as well as water for irrigation and industrial/domestic supply. However, hydropower development can also have severe social, economic and ecological consequences. Depending on the location and size of a reservoir, human populations may have to be relocated. Transboundary conflicts may arise from alterations in water availability downstream of dams. Land use change, river fragmentation, and alteration of flow, sediment and thermal regimes cause habitat loss, restrict the movement of aquatic organisms, and alter biodiversity and ecosystem processes¹⁰⁰. However, knowledge on the expected social, economic, and ecological ramifications is limited and remains under-valued by practitioners. There is an urgent need to integrate the economic, environmental and social dimensions of future hydropower dams, thereby supporting decision making for dam construction and subsequent operation aims to reduce potential impacts and maximize benefits for both, humans and nature alike. Finally, we must be aware that the majority of dams are constructed for irrigation, drinking water and flood control – not for hydropower production; however, comprehensive data on those dams are missing.

Habitat degradation

Habitat degradation in freshwater ecosystems is caused by diverse human activities, creating direct (e.g. disturbance due to sand extraction and river straightening) and indirect impacts posed by environmental changes within the catchment (e.g. subsequent influence of deforestation and agricultural activities)⁷⁷. For example, sand and pebble extraction along the Manipur River (Myanmar/India) has led to a rapid decline in populations of *Hemibagrus microphthalmus*¹⁰². Similarly, gold mining as well as sand and gravel extraction from river beds in Mongolia, have caused serious degradation of Siberian Taimen habitats, leading to the decline of mature individuals¹⁰³.

The dependence of freshwater megafauna on freshwater habitats imparts on them a high chance of encountering human settlements and activities, aggravated by their large range requirements of intact and hydrologically connected habitats¹⁰⁴, increasing their susceptibility to anthropogenic disturbance. The global increase of shipping activities represents a serious threat to sturgeons, freshwater cetaceans and manatees due to their frequent encounters with vessels. Indeed, collisions with shipping vessels have increased substantially, causing the death of many Yangtze Finless Porpoise¹⁰⁵ and approximately 30% of documented Florida Manatee (*Trichechus manatus ssp. latirostris*) mortalities each year⁵⁸.

In South America, Giant Otter populations have declined sharply following expansion of human settlements, habitat degradation due to gold mining and deforestation, and hunting⁵⁷. Many crocodylians, including Muggers (*Crocodylus palustris*), Slender-snouted Crocodile (*Mecistops cataphractus*) and Nile Crocodile (*Crocodylus niloticus*), are threatened by habitat destruction caused by anthropogenic activities. In addition, they are regularly killed by local people as they are regarded as a threat to humans and domestic livestock^{106, 107}. With rapid human population growth, urbanization, agricultural and industrial expansion, there is an increasing likelihood of conflict due to encroachment by humans into the natural habitats of freshwater megafauna¹⁰⁸. In Africa, for example, the historical habitats of African Clawless Otter (*Aonyx capensis*) have been significantly degraded by deforestation, bush clearing, overgrazing, water abstraction and the draining of wetlands¹⁰⁹. The Pygmy Hippopotamus (*Choeropsis liberiensis ssp. liberiensis*), which is endemic to the Upper Guinea forest of west Africa, is seriously threatened by habitat destruction as its historical forest habitat has been cut for the creation of human settlements, farms and plantations^{110, 111}. Increasing mining activities and associated infrastructure development will put further stress on this threatened species¹¹². Similarly, the Sakhalin Taimen (*Hucho perryi*) has suffered from major habitat changes in Russia due to logging, road construction and rapidly expanding oil and gas developments, while its habitats in Japan are under threat from river channelization, agricultural and urban expansion⁵⁶.

Pollution

A wide range of chemical compounds are applied globally for purposes such as pest control and fertilizers in agriculture, industrial manufacturing, and as everyday products ranging from detergents to antibiotics. A substantial proportion of these pollutants ends up in freshwater ecosystems through diverse pathways including direct discharge, surface runoff and atmospheric deposition¹¹³. The toxic effects of some chemical pollutants can cause mortality in freshwater megafauna species such as the death of an estimated 4000 Caspian Seals along the coast of Kazakhstan due to pollution from agricultural and industrial sewage¹¹⁴. Other notable examples include the mortality of five Yangtze Finless Porpoises in the Dongting Lake (China) within a single week due to the toxic effect of a pesticide (i.e. Hostathion) and, possibly, long-term exposure to heavy metals (e.g. mercury and chromium)¹¹⁵. This represents a significant loss as the current population in the Dongting Lake is only around 90 individuals with an estimated 500 more individuals living in the main channel of the Yangtze River¹¹⁶.

Compared to most aquatic organisms, freshwater megafauna species are at higher risk of chronic effects and bioaccumulation of chemicals due to their long life span and high trophic level.

Both, the Amur Sturgeon (*Acipenser schrenckii*) and the Kaluga Sturgeon (*Huso dauricus*) are exposed to the cumulative effects of environmental pollution from oil exploitation, agricultural activities and mining operations in the Amur River basin^{60, 117}. Though pollutants might not be directly lethal to freshwater megafauna, they may reduce fitness and fecundity and make them more susceptible to disease. As a top predator in Lake Baikal, the Baikal Seal (*Pusa sibirica*) is exposed to bioaccumulation of contaminants (e.g. polychlorinated biphenyls), which induce a suppression of its immune system and may have contributed to an outbreak of morbillivirus, which indirectly led to a mass mortality event in the late 1980s⁶¹.

On the global scale, toxicants released by human activities have been identified as a major threat to freshwater ecosystems by The Millennium Ecosystem Assessment¹¹⁸. Organic pollutants and heavy metals have been considered as the greatest threat to freshwater organisms. These pollutants enter freshwaters through waste water treatment plants, industrial discharge, mining drainage and runoff from agricultural soils and urban surfaces¹¹⁹. They have been found in fine sediments¹²⁰, causing extirpation of the benthic fauna¹²¹, which is an important food resource for some freshwater megafauna species (e.g. sturgeons). Pollutants carried by sediments can also lead to an increased mortality of sturgeons due to their direct toxic effects¹²². In North America, elevated concentrations of organic pollutants and heavy metals have been detected in the tissue and egg samples of Gulf Sturgeon (*Acipenser oxyrinchus*)¹²³. An increasing amount of research has reported that organic pollutants (e.g. organochlorine) and heavy metals from pesticide and industrial waste were detected in tissue and eggs of numerous crocodylians, including American Alligator¹²⁴, Salt-water Crocodile (*Crocodylus porosus*)¹²⁵, American Crocodile (*Crocodylus acutus*)¹²⁶, Morelet's Crocodile (*Crocodylus moreletii*)⁵⁹ and Nile Crocodile¹²⁷, which could lead to further population declines of these already threatened species. In addition, endocrine disrupting organic pollutants are reported to alter the hormonal balance of aquatic animals, inducing developmental and reproductive abnormalities¹²⁸⁻¹³⁰ and ultimately leading to a population decline. For example, estrogenic pollution from industrial, agricultural and waste water treatment plant effluents contributed to the occurrence of intersex Sharptooth Catfish (*Clarias gariepinus*) individuals in South Africa^{131, 132}.

Species invasion

The introduction of non-indigenous species often produces predatory or competitive impacts on native species, therefore influencing local animal assemblages and ecosystem processes¹³³. Species invasion is regarded as a major threat to global biodiversity, although its relative contribution to species decline and extinction is debatable as native species and their habitats are usually also subject to various other anthropogenic threats simultaneously^{134, 135}. Due to their large body size, adult freshwater megafauna individuals are not likely to become the prey of invasive species, however, they are at risk during hatching and juvenile periods. Bezuijen et al.⁶⁶ showed that introduction of the Wild Pig (*Sus scrofa*) posed a serious stress to the False Gharial in Sumatra due to predation of eggs. Invasive species can directly increase the mortality of native freshwater megafauna populations. For example, the invasion of Cane Toads (*Bufo marinus*) has led to the massive mortality of Australian Freshwater Crocodiles (*Crocodylus johnstoni*) as they consume the toads which contain powerful toxins in their parotid glands⁶⁴. Less directly, Lake Trout (*Salvelinus namaycush*) populations in Ontario lakes declined following introductions of Smallmouth Bass

(*Micropterus dolomieu*) and Rock Bass (*Ambloplites rupestris*) that led to a decline in their key food source, native littoral prey fishes through competition¹³⁶. Introduced Comb Jellyfish (*Mnemiopsis leidyi*) posed a serious risk to Kilka (*Clupeonella cultriventris*), the main prey of Caspian Seal in the central and the southern Caspian Sea, by depleting Kilka's food base (e.g. zooplankton) and also through predation on their eggs and larvae^{137, 138}. In most cases, invasive species affect freshwater megafauna through competition for resources or through induced profound changes to local food webs, however, hybridization with invasive species is also a significant threat. For example, the hybrid of Broadhead Catfish (*Clarias macrocephalus*) and the introduced African Catfish (*Clarias gariepinus*) is capable of breeding with both species, which can result in genetic introgression, thus leading to the local extinction of native Broadhead Catfish⁶³. In addition, the hybrids grow faster than the native Broadhead Catfish and are highly tolerant towards degraded water quality, giving them a competitive advantage¹³⁹.

In the last few decades, managed relocation, of species to areas outside of the native ranges has become a common practice for reducing their risk of extinction¹⁴⁰; however, it can also lead to unintended negative effects. For instance, the Hump Backed Mahseer (*Hypselobarbus mussullah*), an endemic species in the Western Ghats of India, has been pushed to the edge of extinction due to the successful establishment and spread of the non-native Blue-finned Mahseer (*Tor khudree*), which was introduced for conservation purposes⁶⁵. Likewise, the invasive monogenean gill fluke, carried by Stellate Sturgeon (*Acipenser stellatus*) and was inadvertently introduced from the Caspian Sea and played a significant role in the extirpation of Ship Sturgeon (*Acipenser nudiventris*) in the Aral Sea⁶²

OUTLOOK: FILLING THE FRESHWATER MEGAFUNA INFORMATION GAP

Freshwater megafauna, but also freshwater ecosystems in general, are globally at risk from overexploitation, dam construction, habitat degradation, pollution and species invasion. At the same time, freshwaters contain a disproportionately high biodiversity and provide vital goods and services to humans. Conversely, freshwater ecosystems are underrepresented in conservation research and management actions^{76, 141-143}.

Though there is a general consensus that freshwater biodiversity is declining rapidly, the effective coverage of freshwaters by protected areas remains low, especially for large rivers¹⁴⁴. The lack of public awareness towards biodiversity in freshwaters could largely stem from the invisibility of freshwater species hidden in turbid waters¹⁴⁵. Subsequently this may lead to a shift in the baselines, where many people forget the previous existence and abundance of such species as they are rarely encountered, further impeding awareness and knowledge of these species⁸. Highlighting freshwater megafauna as potential flagship and umbrella species is recommended here as a potentially powerful tool to help raise public awareness and support freshwater conservation. Freshwater megafauna species such as river dolphins, hippopotamuses, sturgeons and paddlefishes are considered to have significant potential as both flagship and umbrella species¹⁴⁶ (Table 2). Furthermore, conservation strategies based on freshwater megafauna may provide major benefits for a wide range of lesser known but cohabiting species as well as of key ecosystems processes and functions. Darwall et al.¹⁴⁷ cautioned, however, that those taxonomic groups for which there is better knowledge (most often terrestrial species) should not be utilized as surrogates for the

distributions of less known freshwater taxa where it has been shown that there is low congruence between terrestrial and freshwater species distributions. Research focusing on charismatic species in freshwaters could improve their surrogacy effectiveness (i.e. benefit a larger set of less charismatic species via their umbrella effects)¹⁴⁸.

TABLE 2. Focal species concepts ^{7, 149, 150}, with examples from freshwater megafauna

Type	Description	Examples
Flagship	Charismatic species that could act as ambassadors for broad-scale conservation, used to raise conservation funding, and to attract public attention.	River dolphins, giant salamanders, hippopotamus, sturgeons and paddlefishes
Keystone	Species that play critical and unique ecological roles to local ecosystems, and have disproportionate importance relative to their abundance.	Beavers, crocodilians, Hippopotamus
Umbrella	Species with large habitat requirements for which conservation action potentially benefits other sympatric species.	River dolphins, hippopotamus, sturgeons and paddlefishes

To conclude, our knowledge of large-scale distribution and risk patterns of freshwater megafauna is still lacking for large parts of the world. Future research should focus on these large animals in order to fill knowledge gap by: (i) collating information on their spatial distributions; (ii) exploring the potential of freshwater megafauna to act as flagship and umbrella species; (iii) compiling data to quantify the seriousness of each type of threat and their impacts to each taxonomic group; (iv) identifying potential regions of conflict between the requirements of freshwater megafauna biodiversity and human activities; (v) examining correlations between biological and ecological traits of freshwater megafauna and extinction risk; and (vi) tracking the global population dynamics of freshwater megafauna. Such a comprehensive understanding of freshwater megafauna will assist in the development of more effective conservation strategies and better consideration within development planning, in order to protect these species and to raise public awareness and support for overall freshwater biodiversity conservation.

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