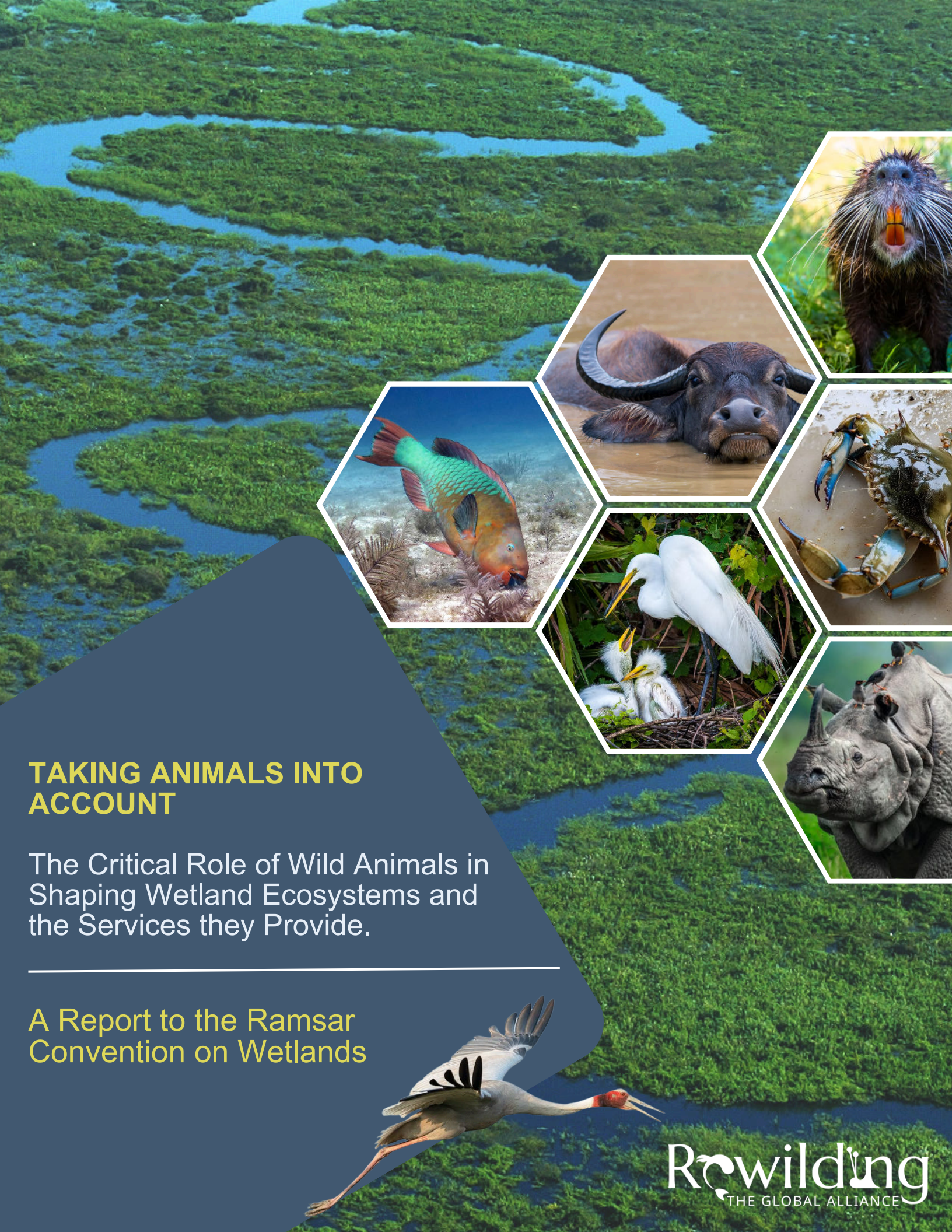

TAKING ANIMALS INTO ACCOUNT

The Critical Role of Wild Animals in Shaping Wetland Ecosystems and the Services they Provide.

A Report to the Ramsar Convention on Wetlands

Rewilding
THE GLOBAL ALLIANCE

TAKING ANIMALS INTO ACCOUNT

A Report to the Ramsar Convention on Wetlands:
The critical role of wild animals in shaping wetland ecosystems and the services they provide.

Geneva, January 2025

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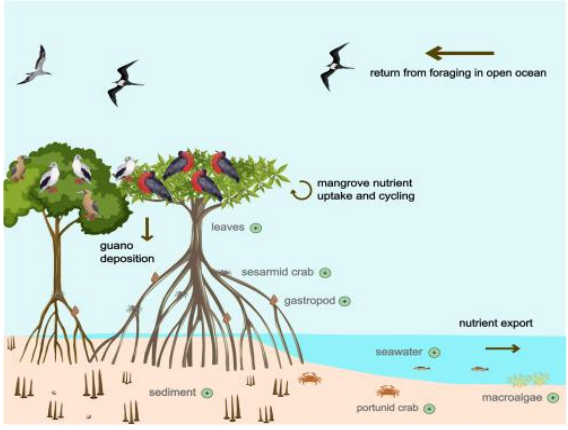

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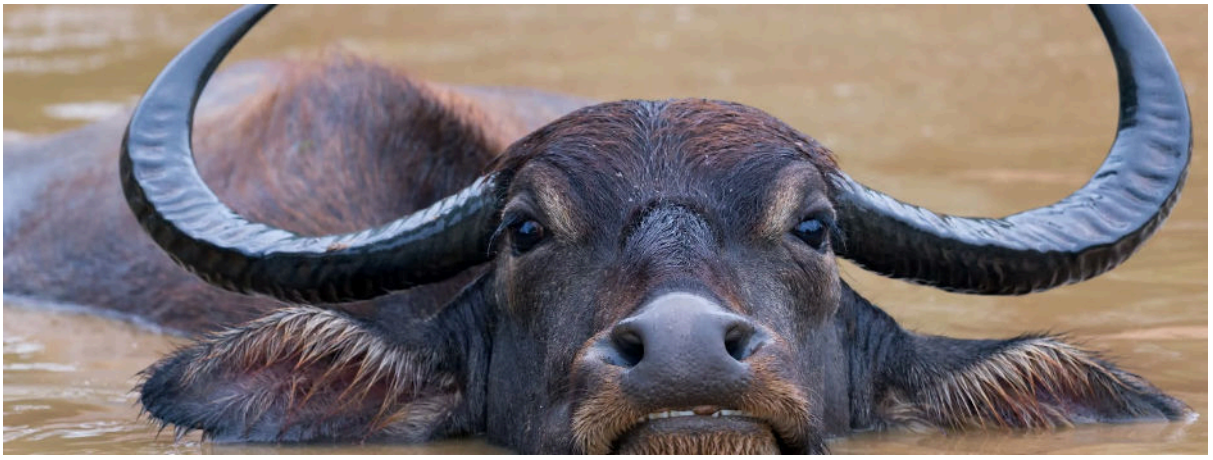
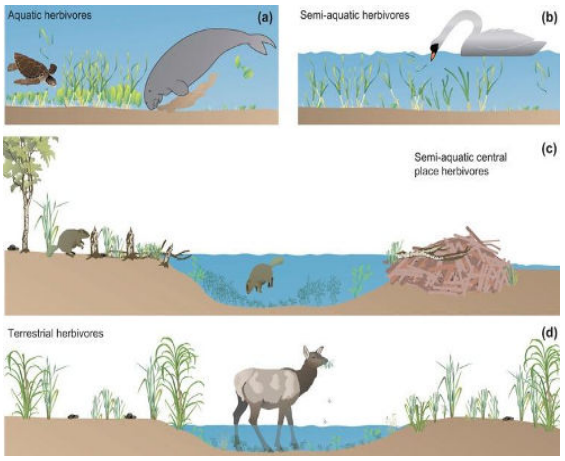
"This report will be a significant value for those implementing the Ramsar Convention, summarising very many scientific studies that demonstrate the multiple ways in which large animal species not only depend on wetlands, but also contribute to the maintenance of wetland ecological character through a wide range of different ecological roles and interactions. It demonstrates that maintaining species diversity should be central in the mission to sustain and conserve wetlands across the world."

David Stroud, Emeritus Senior AdvisorScientist, JNCC, UK; Honorary Patron of the AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds), Warmington, UK & Chair of Ramsar, STRP, 2019-20212019



"Overall, the report is a compelling reminder of the need to consider ecosystem services in the context of the whole ecosystem including the full complement of species, the interactions of animals, and feedback loops, of which animal populations are important drivers. Given the alarming loss of large animals in many wetland types, this report is also valuable in thinking about restoration practices, and planning to enhance/restore ecosystem services and biodiversity in restoration programs. I see real value here in setting restoration projects in the river basin and landscape context."

Siobhan Fennessy, Philip and Sheila Jordan Professor of Environmental Studies and Professor of Biology, Kenyon College, Ohio, USA & Vice-Chair of Ramsar, STRP, 2022-2024



Executive summary

As part of efforts to mainstream a rewilding perspective in science, policy and practice, the Global Rewilding Alliance undertook a preliminary analysis of how mammals, birds, fish, reptiles & amphibians, macro-crustaceans (especially crabs and crayfish) and molluscs shape lakes, rivers and streams, as well as saltmarshes, seagrass meadows, estuaries, coastal lagoons, deltas and mud flats, mangroves, coral reefs, and kelp forests. The work consisted of an extensive literature review combined with the compilation of eleven case studies: ten drawn from the practical work in Asia, Europe, and Latin America, and two derived from summaries of published studies. The studies serve to illustrate and contextualize the findings of the review.

The initial information highlights the dramatic declines of wild animal populations and the widespread negative impacts of trophic downgrading of the Earth system, including the negative ecological impact of megafauna downsizing. Examples are also provided to illustrate how "fishing down the food web" affects coastal and inland fish populations, as well as how ocean warming and deoxygenating through climate change is anticipated to accelerate the overall decline of marine vertebrates, with impact also on coastal wetlands. There is also an urgent need to take into account the critical contributions to population dynamics and ecosystem processes and services provided by old and wise individuals in long-lived species of mammals, birds, freshwater and marine fish, reptiles, amphibians, crustaceans, and molluscs.

In the following two sections, examples are provided to illustrate how wild animals shape inland and coastal ecosystems, with an emphasis on the ecological roles played by various animal groups. The summary is as follows:

- *Fish and waterbirds are reported to play a particularly important role in **lakes**.*
- *In **rivers and streams**, migratory fish, large mammals such as beavers, muskrats and hippos, and the freshwater pearl mussel have been found to act as keystone species or ecosystem engineers. Other species including water buffaloes, tapirs, crocodylians, anacondas, large freshwater turtles, and pond breeding amphibians may also play important roles.*

- *Predatory crabs, terrapins, geese, and sea otters exert important top-down effects on **saltmarshes**.*
- *In **seagrass meadows**, tiger sharks, fish, and herbivorous geese (brent goose) and ducks (wigeons) are important for maintaining the vegetation.*
- *In **estuaries, coastal lagoons, deltas and mud flats**, macro-crustaceans (e.g., crabs), fish, stingrays, birds (especially colony breeders and shorebirds), deer (e.g., Père David's deer), Neotropical otters, seals, and cetaceans (e.g., bottlenose dolphins) facilitate sediment formation, nutrient exchange, primary production, carbon capture, and enhanced biodiversity.*
- *Aquatic molluscs (bivalves), slugs & snails (gastropods), shipworms (teredinid bivalves), predatory fish, colony-breeding seabirds, crab-feeding birds, and ants that protect the trees from insect damage have been found favourable for **mangroves**.*
- *Seabirds and reef sharks enhance the nitrogen levels and **coral reef** productivity and functioning. Grazing by parrotfish prevents algae establishment, thereby increasing coral productivity. Through 'seascapes of fear', reef sharks also positively influence the abundance of seaweeds and carbon sequestration.*
- *Sea otters, sea stars, lobsters, and predatory fish prevent the expansion of sea urchins, fostering favourable conditions for **kelp forests** and supporting a diverse community of fish and other marine organisms to thrive.*

A detailed account is provided on how different species of mammals, birds, fish, reptiles, amphibians, and macro-crustaceans interact with wetlands.

*Subsequently, information from the previous sections is contextualized within ecosystem services. The different animal species are categorized under the following 9 "**supporting services**":*

- *Ecosystem engineering & habitat modification for other organisms,*
- *Nutrient cycling & ecosystem productivity,*
- *Sediment/soil formation,*
- *Seed dispersal,*
- *Mediating cross-ecosystem linkages,*
- *Biodiversity enhancement,*
- *Food webs & trophic cascading,*
- *Water distribution & flow,*
- *Ecosystem heterogeneity.*

*And the following four "**regulating services**":*

- *Carbon dynamics, climate regulation & adaptation,*
- *Flood regulation,*
- *Water purification,*
- *Invasive species control.*

This section also gives some quantitative information on the role of animals in carbon cycles across different wetland ecosystems and includes an example of the cultural services illustrated through a crane species.

Four case studies are presented to illustrate how knowledge of the ecological roles of wild animals can or should be applied in practice. An overview of the situation in India indicates that only a few wetlands in the country support a more complete set of ecologically important animal species, with less than nine percent of the current Ramsar Sites hosting near-intact megafauna assemblages. An example from Argentina, where the Ramsar Site constitutes less than 2% of the total wetland area, illustrates the need to adopt a broader planning perspective.

Finally, the findings are contextualized within the implementation framework of the Ramsar Convention, with some specific recommendations for changes needed to achieve the overall objectives of the convention in its future work.

In the concluding section, keystone species for each of the eight wetland ecosystem categories are highlighted as part of a summary of the main findings.

While this study represents only an initial effort to summarize current knowledge on wildlife-ecosystem connections for wetlands, the results underscore the need to place wild animal species at the core of the ecological functional agenda of the Ramsar Convention on Wetlands.

Rewilding, as defined by the Global Charter for Rewilding the Earth, is an ecological restoration strategy focused on restoring nature by returning wildlife so they can play their critical role in shaping their natural habitats on land and in the seas, always with a human co-existence perspective. This process allows natural dynamics to foster vibrant and self-sustaining ecosystems put into a wider societal perspective. This paper supports the Charter's twelve guiding principles by illustrating the vital roles wild animals play in wetland ecosystems.

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1. Background

The Ramsar Convention on Wetlands is the oldest of the modern global multilateral environmental agreements. The treaty was negotiated through the 1960s by countries and NGOs concerned about the increasing loss and degradation of wetlands for migratory waterbirds. The Convention was adopted in the Iranian city of Ramsar in 1971 and came into force in 1975. The wise use of wetlands that conserves the fundamental ecological functions of wetlands is one of the foundational cornerstones of the convention:

"CONSIDERING the fundamental ecological functions of wetlands as regulators of water regimes and as habitats supporting a characteristic flora and fauna, especially waterfowl;

Wetlands are indispensable due to the countless benefits or ecosystem services that they provide to humanity as well as biodiversity. Key services include freshwater supply, food and building materials, biodiversity, flood control, groundwater recharge, and climate change adaptation and mitigation.

The Convention uses a broad definition of wetlands: "wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres." This includes all lakes and rivers, underground aquifers, swamps and marshes, wet grasslands, peatlands, oases, estuaries, deltas and tidal flats, mangroves and other coastal areas including coral reefs. It also includes all human-made sites such as fishponds, rice paddies, reservoirs, and salt pans.

By January 2025, 172 countries had joined the convention ("contracting parties"), with 2,525 wetlands designated, covering a total area of 257 million hectares.

At the 26th meeting of the Scientific and Technical Review Panel (STRP) in Gland, Switzerland, 5th-8th February 2024, the Global Rewilding Alliance[16] (GRA) offered to undertake a study on "Wild animals & Ramsar Convention", which was accepted. This is the report.

The analysis consists of two main sections, integrated into an overall report:

- Providing an overview of academic literature on the importance of wild animals for the functions of wetlands, including their contributions to various ecosystem services.
- Summarizing and sharing the practical experiences of the GRA network on how wild animals help to shape wetlands.

[16] As of January 2025, the GRA consisted of a network of 220+ small to large conservation organisations working to protect and rewild 2.5 million km^2 of land (incl. freshwater) and 5 million km^2 of sea across Africa, Asia, Europe, Latin America, Middle East, North America, and Oceania (incl. Australia). Inland and coastal wetlands are included.

In conclusion, the study offers best-practice recommendations for how wild animal species could add value in achieving the convention's overall objectives, including management practices.

The report is a non-systematic review and provides an introduction based on a selection of published and practical experiences. Its primary aim is to highlight the importance of incorporating wild animal species into plans for enhancing wetland functionality under the Ramsar Convention thereby supporting one of its foundational objectives.

Throughout this report, the information provided is referenced with help of hyperlinks, allowing for quick access to the various sources. Some of the case studies provide traditional literature references.

2. Study approach (methodology)

The following nine functional aspects are included:

- Ecosystem engineering and habitat modification for other organisms (a process by which organisms create and modify habitats through changes in their abiotic and biotic environment),
- Sediment/soil formation & control (e.g., reduced erosion)
- Seed dispersal,
- Nutrient cycling (including scavenging/decomposition),
- Mediating cross-ecosystem linkages (e.g., water-terrestrial), such as of seeds and nutrients,
- Biodiversity enhancement,
- Trophic cascading (keystone species), controlling food webs,
- Water distribution & flow, and
- Ecosystem heterogeneity.

The following six animal groups are considered:

- Mammals,
- Birds,
- Fish,
- Reptiles & amphibians,
- Macro-crustaceans, and
- Molluscs

The following sub-set of the wetland types addressed by Ramsar were selected.

- Lakes, rivers, and streams,
- Saltmarshes, and seagrass meadows,
- Estuaries, deltas (inland and coastal) and mud flats,
- Mangroves,
- Coral reefs, and
- Kelp forests.

No human-made wetlands were considered.

The literature review was helped by a set of existing overviews covering different animal groups and geographical areas:

- Fengzhi, H. et al. 2024: "Freshwater megafauna shape ecosystems and facilitate restoration", Biol. Rev. 99:1141-1163, https://onlinelibrary.wiley.com/doi/epdf/10.1111/brv.13062
- Rodrigues-Filho, J.L. et al. 2023: "From ecological functions to ecosystem services: linking coastal lagoons biodiversity with human well-being", Hydrobiologia 850:2611-2653, https://link.springer.com/article/10.1007/s10750-023-05171-0
- Bakker, E.S. et al. 2015: "Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems", Ecography 39:162-179, https://nsojournals.onlinelibrary.wiley.com/doi/epdf/10.1111/ecog.01651
- Green, A.J. & Elmberg, J. 2014: "Ecosystem services provided by waterbirds", Biological Reviews 89:105-122, https://onlinelibrary.wiley.com/doi/10.1111/brv.12045
- Pelicie, F.M. et al. 2023: "Ecosystem services generated by Neotropical freshwater fishes", Hydrobiologia 850:2903-2926, https://link.springer.com/article/10.1007/s10750-022-04986-7
- Hammerschlag, N. et al. 2019: "Ecosystem Function and Services of Aquatic Predators in the Anthropocene", Trends in Ecology & Evolution 34 (4):369-383, https://www.sciencedirect.com/science/article/abs/pii/S0169534719300205
- Green, A.J. et al. 2023: "Dispersal of aquatic and terrestrial organisms by waterbirds: A review of current knowledge and future priorities", Freshwater Biology 68:173-190, https://onlinelibrary.wiley.com/doi/10.1111/fwb.14038

Web-based search engines (Google & Yahoo) were used to find additional publications.

An analysis of the ongoing work within the Global Rewilding Alliance partnership network using web-based information, led to the selection of 21 organisations to provide case studies out of a larger group of 56 working on various wetland issues. Of the 21 organisations, ten provided case studies, which are incorporated throughout the report to illustrate the findings of the literature review.

3. Results

3.1 Dramatic declines of animal populations and the trophic downgrading of the coastal & freshwater environment

"Until recently, large apex consumers were ubiquitous across the globe and had been for millions of years. The loss of these animals may be humankind's most pervasive influence on nature. Although such losses are widely viewed as an ethical and aesthetic problem, research reveals extensive cascading effects of their disappearance in marine, terrestrial, and freshwater ecosystems worldwide. This empirical work supports long-standing theory about

the role of top-down forcing in ecosystems but also highlights the unanticipated impacts of trophic cascades on processes as diverse as the dynamic of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles." Estes, J.A. et al. 2011, Trophic Downgrading of Planet Earth

Over the past 50 years (1970–2020), the average size of monitored wildlife populations has shrunk by 73%, as measured by the Living Planet Index (LPI) (ref). The finding is based on almost 35,000 population trends and 5,495 species of amphibians, birds, fish, mammals, and reptiles. Freshwater populations have suffered the heaviest declines, falling by 85%, followed by terrestrial (69%) and marine populations (56%) (*Figure 1*). Freshwater fish, in particular, are often threatened by alterations to their habitat, which can block essential migration routes. For example, the updated LPI for migratory freshwater fish shows a decline of 81% between 1970 and 2020. The steepest overall declines are seen in Latin America and the Caribbean, Africa and Asia and the Pacific. Habitat degradation and loss are the most frequently reported threats to vertebrate populations, followed by overexploitation, invasive species, disease, climate change, and pollution.

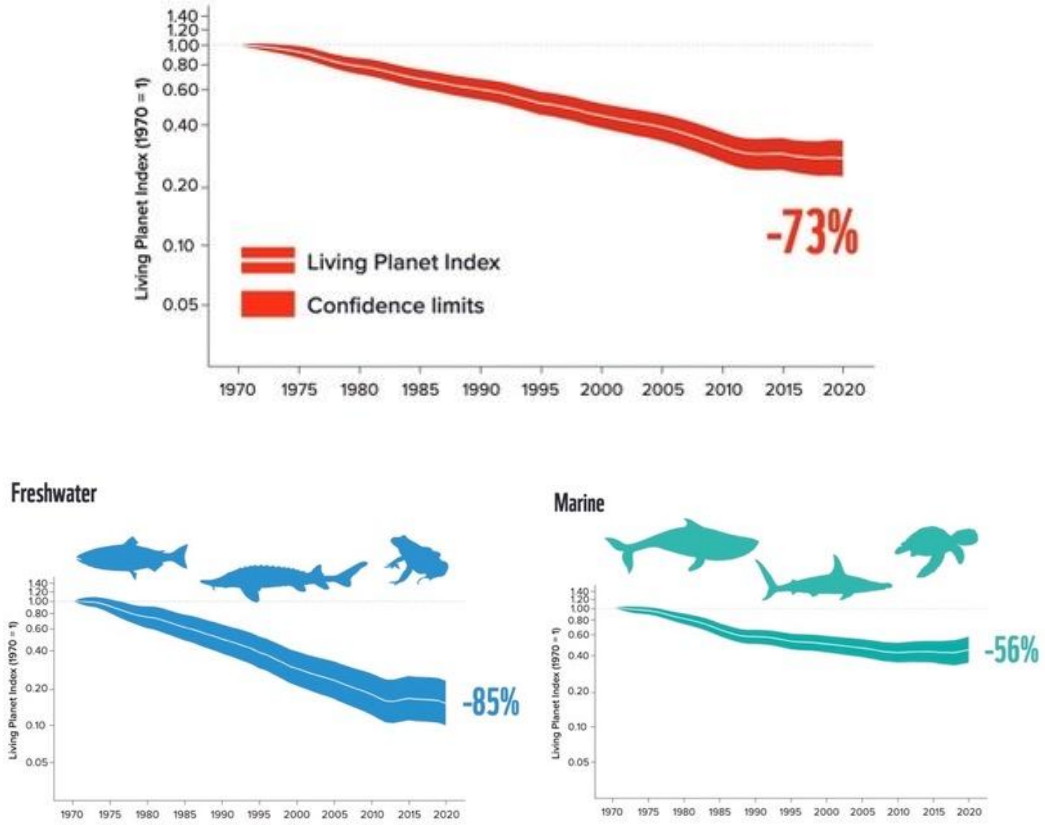


***Figure 1**: Development of the Living Planet Index (LPI) during the period 1970-2020 across all global ecosystems (top) as well as for freshwater and marine species specifically. Image source.*

Trophic downgrading - the disproportionate loss of species high in the food chain - has had far-reaching effects on ecosystem function (ref). One of humankind's most pervasive effects on ecosystem function has been changes to biodiversity at higher trophic levels. The biosphere has undergone significant trophic downgrading (ref). Compared to the extensive

megafauna extinction in terrestrial ecosystems in the Late Pleistocene and Early Holocene, megafauna in aquatic systems were likely less affected until a few hundred years ago. This changed with the onset of intensive commercial harvesting and large-scale habitat modification, which began to alter marine and freshwater ecosystems (ref). Below are some examples of extinct aquatic species:

- *Chinese river dolphin or Baiji (Liotes vexillifer)*
- *Schomburgk's deer (Rucervus schomburghi),*
- *Chinese paddlefish (Psephurus gladius),*
- *Steller's sea cow (Hydrodamlis gigas),*
- *Caribbean monk seal (Neomonachus tropicalis),*
- *Japanese sea lion (Zalohus japonicus),*

Figure 2 provides some examples of landscape-level effects of trophic cascades.

***Figure 2**: Landscape-level effects of trophic cascades from five selected freshwater and marine ecosystems. (A) Shallow seafloor community at Amchitka Island (Aleutian archipelago) before (1971) and after (2009) the collapse of sea otter populations. Sea otters enhance kelp abundance (right) by limiting herbivorous sea urchins (left). (B) A plot in the rocky intertidal zone of central California before (September 2001, right) and after (August 2003, left) exclusion of the seastar (Pisaster ochraceous). Pisaster increases species diversity by preventing competitive dominance of mussels. (C) Long Lake (Michigan) with largemouth bass present (right) and experimentally removed (left). Bass indirectly reduces phytoplankton (thereby increasing water clarity) by limiting smaller zooplanktivorous fishes, thus causing zooplankton to increase and phytoplankton to decline. (D) Coral reef ecosystems of uninhabited Jarvis Island (right, unfished) and neighboring Kiritimati Island (left, with an active reef fishery). Fishing alters the patterns of predation and herbivory, leading to shifted benthic dynamics, with the competitive advantage of reef-building corals and coralline algae diminished in concert with removal of large fish. (E) Pools in Brier Creek, a prairie margin stream in south-central Oklahoma with (right) and without (left) largemouth and spotted bass. The predatory bass extirpate herbivorous minnows, promoting the growth of benthic algae. Image source.*

Defaunation is a pervasive component of the planet's sixth mass extinction and a major driver of global ecological change (ref). Extinction and endangerment vary with body size, with larger-bodied species showing a greater vulnerability (*Figure 3*).

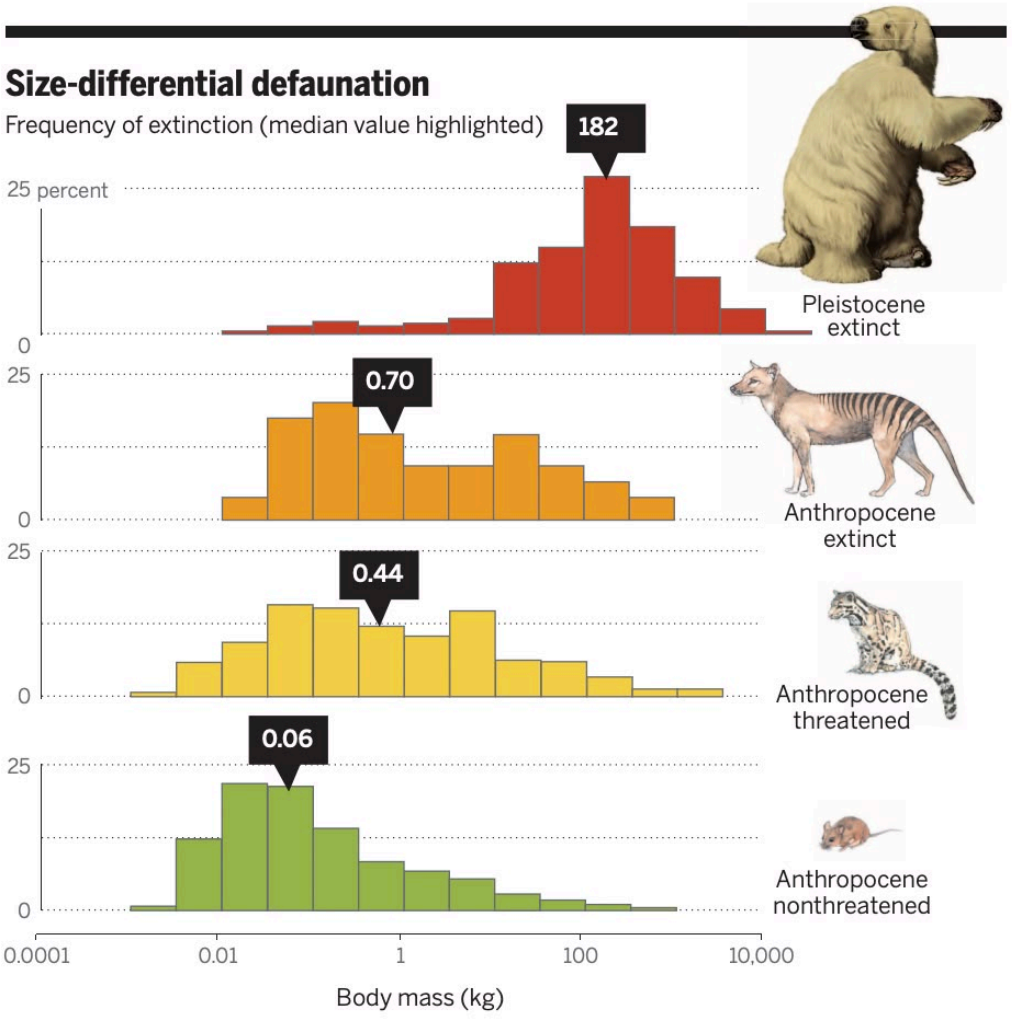


***Figure 3**: Comparing data on body size (kg) of all animals that are known to have gone extinct in Pleistocene or are recently extinct shows selective impact on animals with larger body sizes (median values denoted with black arrow). Differences in body masses between distributions of currently threatened and non threatened species suggest ongoing patterns of size-differential defaunation. Image source.*

Anthropocene defaunation has been predominantly documented in terrestrial ecosystems; however, indicators suggest defaunation has been more severe in freshwater ecosystems (*Figure 4*). While, marine defaunation is in a more incipient stage, pronounced effects are already apparent, and its rapid acceleration seems likely (ref).

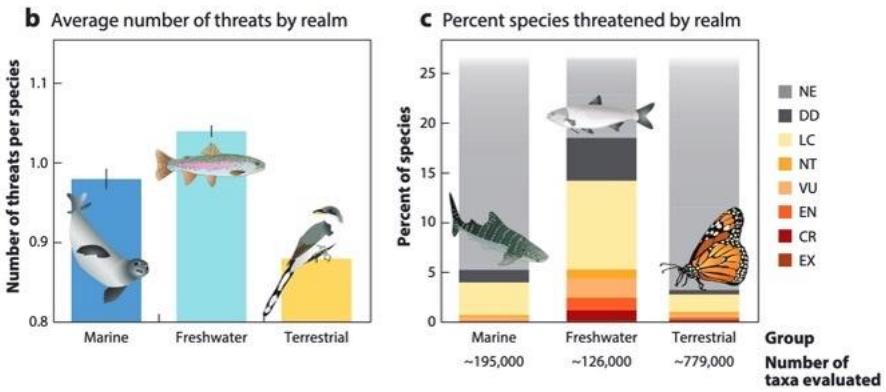


***Figure 4**: The threats to animals across the marine, terrestrial, and freshwater realms. (b) Only species in freshwater ecosystems have, on average, more than one stressor reported per species. (c) The freshwater realm also has the highest proportion of animal species listed as threatened, although this may be partially due to having a higher proportion of species evaluated. Image source.*

In marine systems, recent studies (ref) have investigated how ocean warming and deoxygenation are expected to influence fish populations, projecting dramatic declines in the future (*Figure 5*). These changes will also have substantial effects on coastal wetlands covered by the Convention on Wetlands, further accelerating the general decline of marine vertebrates worldwide. Historically, this decline has included an average reduction of 89% in populations of large marine mammals, birds, reptiles, and fish (ref).

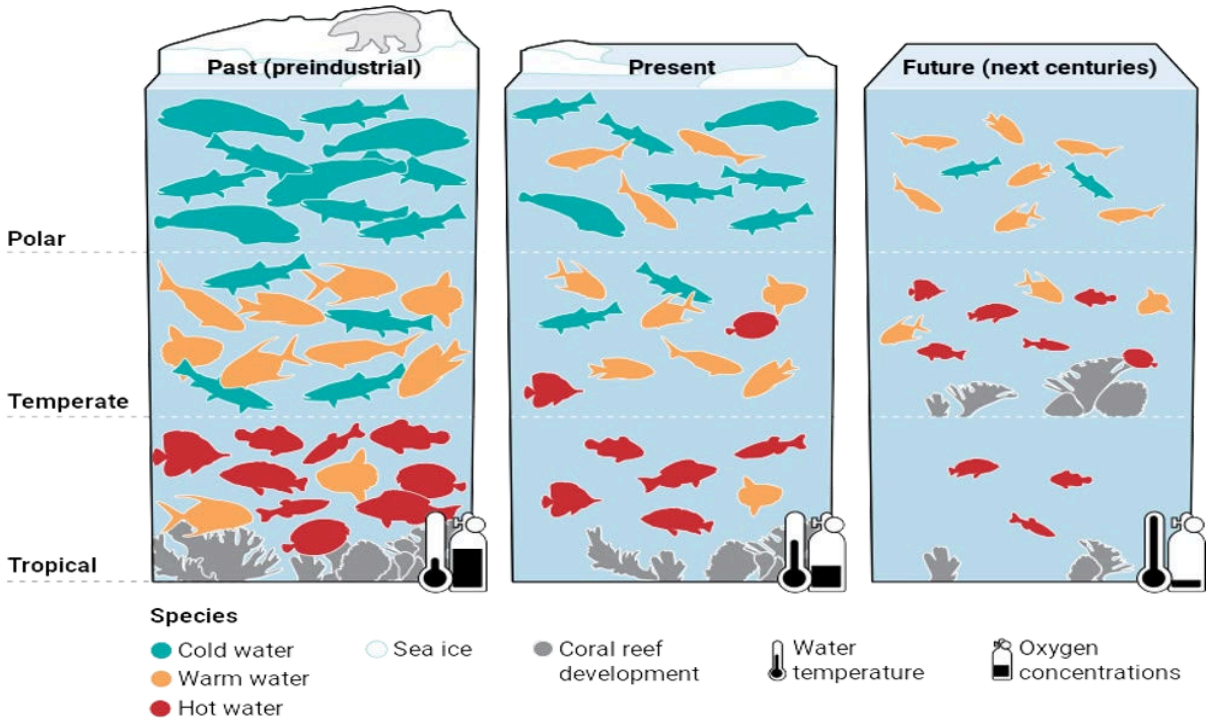


***Figure 5**: The future of ecosystems in tropical, temperate, and polar oceans - A warming and deoxygenating ocean will make species smaller and push them from the tropical zone to the temperate zone, from the temperate zone to the polar zone, and from the polar zone to extinction, resulting in a loss of biodiversity in the tropics and higher biodiversity in higher latitudes. Overexploitation and other direct human impacts are not considered in this conceptual model. Image source.*

In addition to the impacts of climate change, the phenomenon of "fishing down" marine and inland waters – characterized by a gradual shift in landings from long-lived, high trophic level, piscivorous bottom fish to short-lived, low trophic level invertebrates and planktivorous pelagic fish (*Figure 6*) - poses a significant challenge for the future management of aquatic ecosystems as well as a challenge/ threat to livelihoods and food security (ref). The historic development of the Wadden Sea area along the North Sea coasts of the Netherlands, Germany and Denmark provides an illustration of what "fishing down the foodweb" has meant in practice (ref).

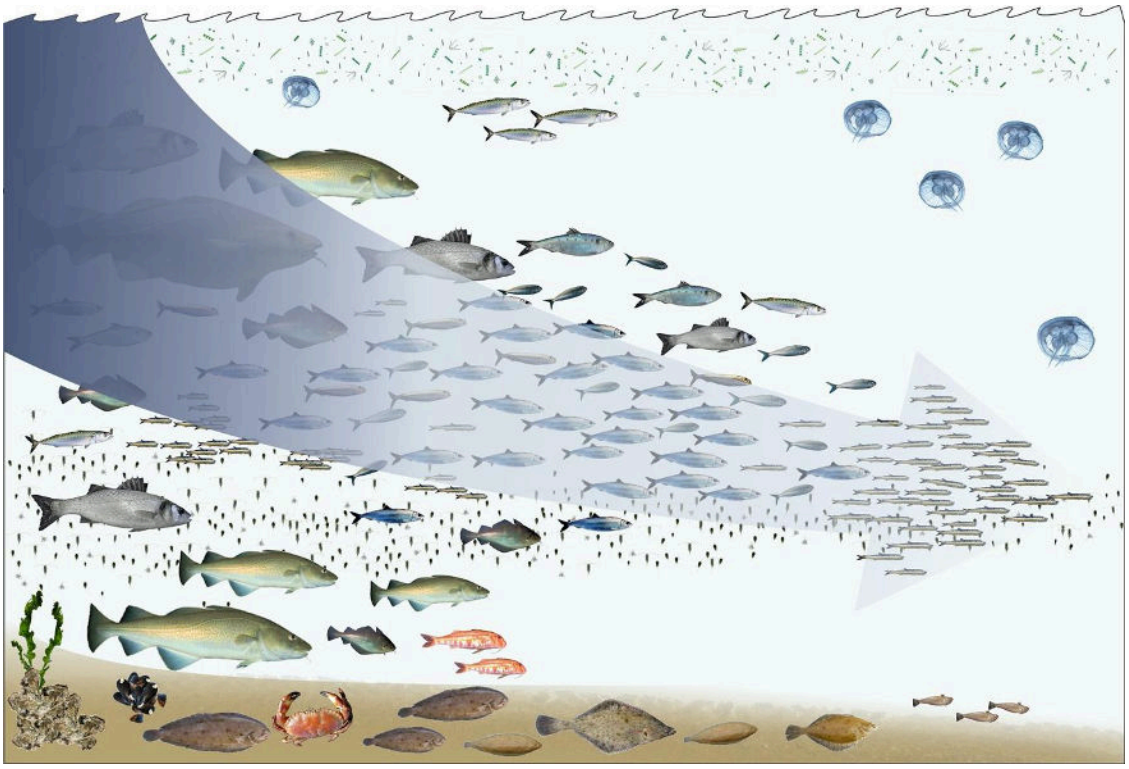


***Figure 6**: A characteristic regime shift in aquatic systems involves an abrupt increase in the dominance of lower trophic level groups within aquatic food webs. This regime shift involves a change from an ecosystem with high numbers of predatory fish to one dominated by pelagic planktivorous. The shift is often initiated by high fishing pressure on top-predators followed by a trophic cascade but can also be brought about by other environmental factors like global warming and upwelling increase. In extreme cases, the food web is shortened due to disappearance of top predators and the carbon transfer pathways are dominated by microbial webs instead of the classic trophic chain. The new regime can be enforced and maintained by biological mechanisms including minimum population biomass, competition and dietary relations, or environmental conditions. Despite there being some mechanisms that often dissipate the trophic cascade, food web regime shifts do have substantial impact on commercial fisheries, as well as increase the vulnerability of an ecosystem to eutrophication, hypoxia, and invasion by non-native species. Image source.*

Defaunation has a significant impact on ecosystem functioning (ref). Assessments have shown that defaunation negatively impacts several ecosystem services, including: (i) pollination, (ii) pest control, (iii) nutrient cycling and decomposition, (iv) water quality, and (v) human health (ref). Again, the Wadden Sea area provides an illustrative case study (ref). Through experimental manipulation, defaunation has been found to have substantial effects on biodiversity, ecological processes, and ecosystem functioning and services. For example, it has been associated with generating higher fire intensity, decreased mycorrhiza fungi activity, and lower photosynthesis and transpiration (ref).

3.2 Size matters – The negative ecological impact of megafauna downsizing

Few organismal traits are as profoundly important as body size, given its role in reproductive fitness, physiology, demography, predator-prey dynamics, carbon cycle, and value for human use (ref). Declines in body size have influenced the trophic interactions and ecosystem

services. A widespread size decline in four Pacific salmon species has been documented over a 60-year period (*Figure 7*) (ref). For Chinook salmon specifically, the decline has been estimated to result in a 16% reduction in egg production, a 28% decrease in nutrient transport, a 21% decline in fisheries value, and a 26% reduction in meals for rural communities.

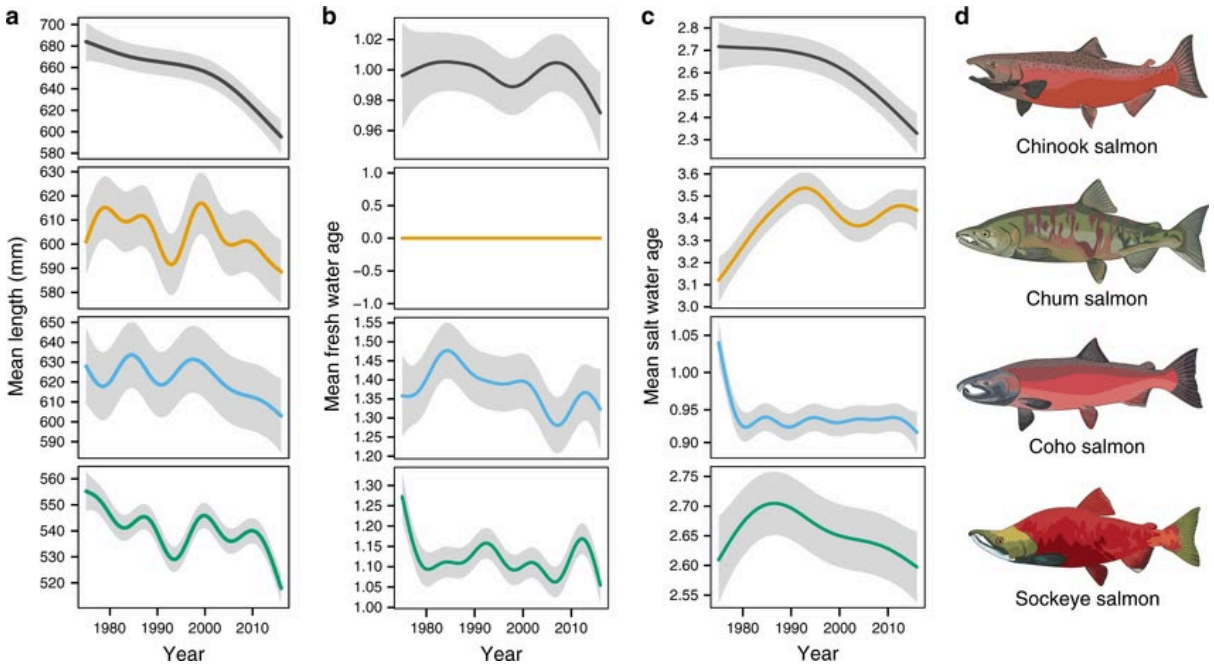


***Figure 7**: Decline in mean fish length for four Pacific salmon species (a). With the exception of the Chum salmon, the age of salmon living in both freshwater (b) and salt water (c) also declined. Image source.*

A size-dependent decline in reproduction has also been reported for the Red snapper (*Lutjanus campechanus*) along the North Atlantic coast of the USA (*Figure 8*) (ref).

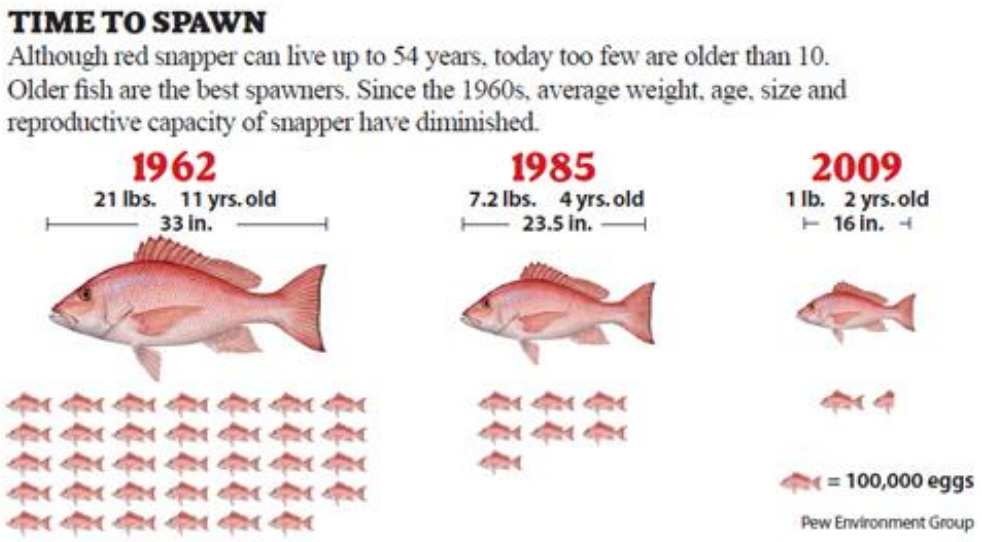


***Figure 8**: Image source.*

Today, individuals of freshwater megafauna species often fail to reach their potential maximum body size due to the preferential harvesting of large individuals (ref). The reduced abundance of large predators, for instance, decreases predation pressure on smaller planktivorous and algivorous fish, altering the trophic dynamics and ecological processes in ocean ecosystems, rivers and lakes (ref). A clear body-size reduction in large freshwater fish species has been observed in many regions (ref).

Size also matters when it comes to seed dispersal. Size-selective overfishing has drastically depleted and downsized populations of tambaqui (*Colossoma macropomum*) (*Figure 9*), a key species in the natural regeneration of Amazonian floodplain forests by dispersing seeds of more than 100 species of trees. Due to gape limitations, only large-bodied tambaqui can disperse large-seeded fruits, and consequently, the downsizing of tambaqui has diminished their key ecological function as a seed disperser (ref). Reduced establishment of young trees may also negatively impact carbon stocks in Neotropical rainforests. Large-seeded floodplain trees are usually disperser-limited and do not float, relying on large-sized fish to disperse their seeds. These taxa significantly contribute to carbon stocks in Neotropical rainforests (ref). In conclusion, dwindling abundances and the loss of large individuals are likely to reduce complexity and stability of the food webs in local ecosystems (ref).

***Figure 9**: Tambaqui (Colossoma macropomum) play a key role in the ecological functions of Neotropical floodplain rainforests. Downsizing of the individuals due to overfishing may also negatively impact on the positive climate impacts these forests have since the larger-seed trees dependent on larger fish will dwindle. Image source.*

3.3 The importance of age - longevity conservation

Old age-classes of many animal populations have declined or been eliminated due to human impacts (ref). Across five ocean areas, the oldest age-classes of fish have been depleted in 79-97% of populations (ref). Due to overharvesting, the same applies to river systems, like in Western Europe, North America and Australia (ref). Old animals play a vital role in the maintenance of biodiversity, population dynamics, and ecosystem processes and services (ref). The largest and most experienced, old individuals often contribute critically to reproduction, information acquisition and cultural transmission, trophic dynamics, and resistance and resilience to natural and anthropogenic disturbance. Reproductive output increases with body size and age in many fishes, reptiles, amphibians, crustaceans, and molluscs. Social learning and experience provided by “Elders” may facilitate effective

responses to environmental change also in mammals and birds (ref). The loss of old animals may also have important consequences for ecosystem structure and function. Consequently, there is an urgent need for a "longevity conservation" approach "to better understand and protect the functions and ecosystem services provided by old animals" (ref).

3.4 How different wetland types are shaped by wild animals.

Here follows an overview for eight wetland types.

3.4.1 Lakes

Through cascading trophic interaction, **fish** are the dominant functional organism group when it comes to lakes: "Simply put, a rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass" (*Figure 10 & 11*) (ref). Fish can also outcompete waterbirds like the goldeneye *(Bucephala clangula)* for common prey (ref).

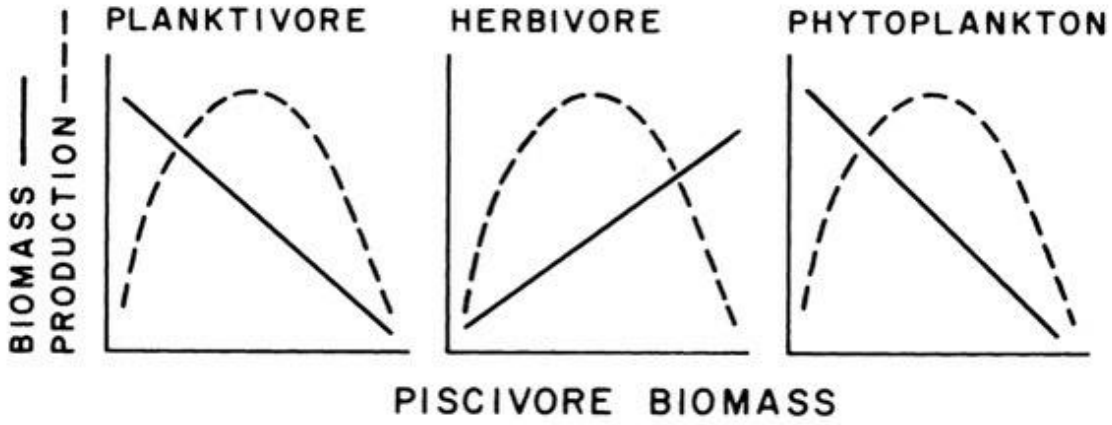


***Figure 10**: Piscivore biomass in relation to biomass (solid line) and production (dashed line) of vertebrate zooplanktivores, large herbivores, and phytoplankton. Image source.*

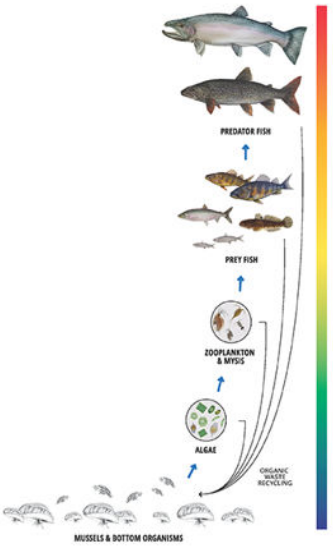


***Figure 11**: The principal trophic structure of fish in lake systems in the northern hemisphere. Image source.*

Grazing by **waterbirds** has been found to increase the diversity of submerged macrophytes (ref). In oligotrophic systems, productivity and fish production are likely to be enhanced by the input of nutrients by colonial waterbirds (ref). Large birds such as swans and flamingos create bioturbation effects while feeding and can drastically change the distribution of sediments. This may negatively affect some submerged macrophytes, but by increasing spatial heterogeneity this may benefit invertebrates (annelids, dipteran larvae, etc.) exploiting the benthic environment. Cormorants likely act as apex predators in marine, brackish, and freshwater ecosystems, while fish species function as meso-predators, feeding on smaller fish species or individuals, phytoplankton, and zooplankton (ref). However, a meta-analysis of published data on the relationship between cormorants and various fish species provided no conclusive results on the impact on fish populations in general, but it could have significant negative effects on certain species, such as cyprinids (*Cyprinidae*), Sander spp. (*Pericidae*), and European perch (*Perca fluviatilis*). The analysis offered no additional insights into cascading effects, likely due to the scarcity or absence of relevant studies and the complexity of methodological approaches required.

3.4.2 River catchments, including streams

Fish migrations play a critical role in ecosystem subsidies—that is, landscape-scale flows of energy, materials, and organisms that influence local food web and ecosystem dynamics. Two general categories of subsidies are distinguished: material subsidies and process subsidies. Material subsidies are the transfer of energy, nutrients, and other resources resulting in direct changes in resource pools within ecosystems (ref). Material subsidies occur under only a subset of life history strategies and ecological settings, and the potential for migratory fish to represent major material subsidies is greatest when:

- *The biomass of migrants is high relative to the size of the recipient ecosystem,*
- *The availability of nutrients and energy is low in the recipient ecosystem (i.e., oligotrophic),*

- *There are effective mechanisms for both liberating nutrients and energy from migratory fishes and retaining those materials within the food web of the recipient ecosystem.*

For example, anadromous semelparous Pacific salmon (*Oncorhynchus spp.*) with a mass programmed spawning migration and senescence in oligotrophic Pacific Northwest streams can be large material subsidies. It has been estimated that anadromous fish species, including large salmonids and sturgeons, annually moved 140,000 tons of phosphorus between the oceans and freshwater systems prior to human exploitation of water courses (e.g., dams & overexploitation), which generated a population decline of 96% (*Figure 12*) (ref). Evidence shows that nutrients transported by anadromous fish increase riparian productivity and biodiversity (ref). In the western US salmon streams, the lack of returning salmon is referred to as a 'carcass famine' for the ecosystems (ref). After the collapse of salmon stocks due to overfishing it can also be difficult to reestablish populations because juvenile survival is poor without the nutrient subsidies (Brett K. Sandercock, *pers.com.)* Potamodromous fish[17], like catfishes, carps and some sturgeons, that move between different river sections or between lakes and rivers (e.g., feeding in downstream river reaches and moving upstream for spawning), also redistribute nutrients between different habitats, although there is limited quantification (ref).

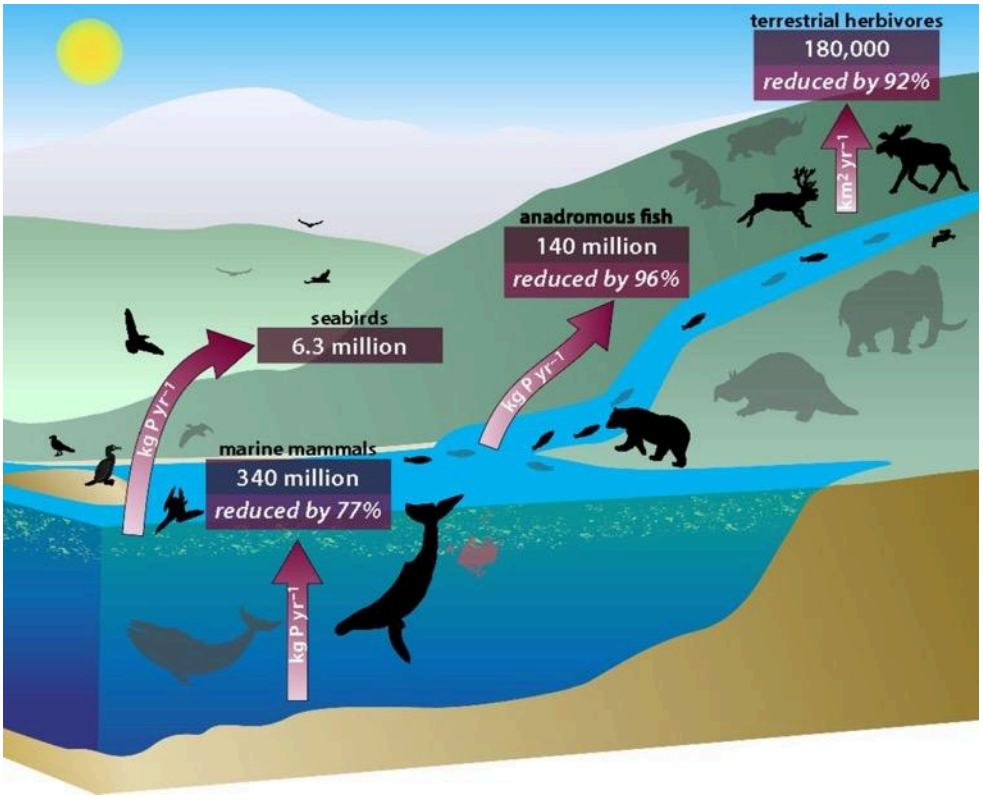


***Figure 12**: Potential interlinked system of recycling nutrients. The diagram shows a potential route of nutrient (phosphorus) transport of the planet in the past. Red arrows show the estimated fluxes or diffusion capacity of nutrients (kg/y). Grey animals represent extinct or reduced population densities of animals. Image source.*

[17] Potamodromous fish are migratory fish that spend their whole life in fresh water.

The freshwater pearl mussel (*Margaritifera margaritifera*) is considered a keystone species in riverine ecosystems, creating habitats for other species, and contributing significantly to ecosystem services (Case study #1). As filter feeders, these mussels can purify up to 50 litres of water per day. This process not only helps water purification but also produces nutrient-rich mucous lumps that serve as food for bottom-dwelling animals, which, in turn support juvenile fish populations, including salmon and trout.

Large animals can significantly modify the structure and function of river corridors (ref). For example, beavers can increase the surface area of open water by more than an order of magnitude compared to conditions prior to beaver modifications (ref). Beavers also excavate canals to expand access to new resources, increasing the wetland perimeter by up to five times its original length (ref). Native to North American temperate wetlands, the common muskrat (*Ondatra zibethicus*) is an ecosystem engineer that alters its environment through herbivory, house and structure building, creation of activity networks as well as enhancing plant biodiversity (ref). Similarly, hippos and crocodylians create channels, while hippos, crocodylians, water buffaloes and tapirs increase the size of freshwater habitats through wallowing. The increasing area and depth of natural puddles and pools over a long period provide important habitats for small aquatic and semi-aquatic species, especially in dry seasons (ref). Beavers and hippos also alter flow dynamics, reducing flow velocities and flood peaks, while creating favourable conditions during low water seasons (ref). Rivers, floodplains, and wetlands associated with megafauna typically exhibit more heterogeneous geomorphological and vegetation characteristics than those where megafauna have been extirpated (ref).

Hippos feed on land but spend extensive periods of time resting in water, where they discharge faeces and urine, providing a significant amount of carbon, nitrogen, and phosphorus to river ecosystems (ref). Beavers also increase nutrients and woody biomass input to freshwater systems (ref). Diet analysis of reptiles such as anacondas, caimans, American and Nile crocodiles and large freshwater turtles (e.g., alligator snapping turtle & Arrau turtle) indicate a transfer of nutrients from terrestrial to water systems (ref). Pond breeding amphibians have been found to mediate nutrient fluxes across aquatic-terrestrial boundaries of wetlands (ref).

3.4.3 Saltmarshes

In salt marshes, top-down control of community structure seems to be a feature of these ecosystems (ref). The control of grazing snails (e.g., periwinkle, *Littoraria irrorate*) by predatory crabs (*Callinectes sapidus*) and terrapins, (*Malaclemys terrapin*) is critical to the persistence of some salt marshes. The loss of predators can lead to the complete degradation of salt marshes, resulting in the loss of carbon sequestration (*Figure 9*). In New England salt marshes, reductions in predatory blue crabs have led to an increased abundance of bioturbators such as sesarmid crabs. This shift has reduced the carbon sequestration capacity of the ecosystem (*Figure 13*) (ref). Research indicates that goose grazing can promote nitrogen cycling in saltmarshes (ref), but overabundant geese populations can also cause degradation and habitat loss of saltmarshes (ref).

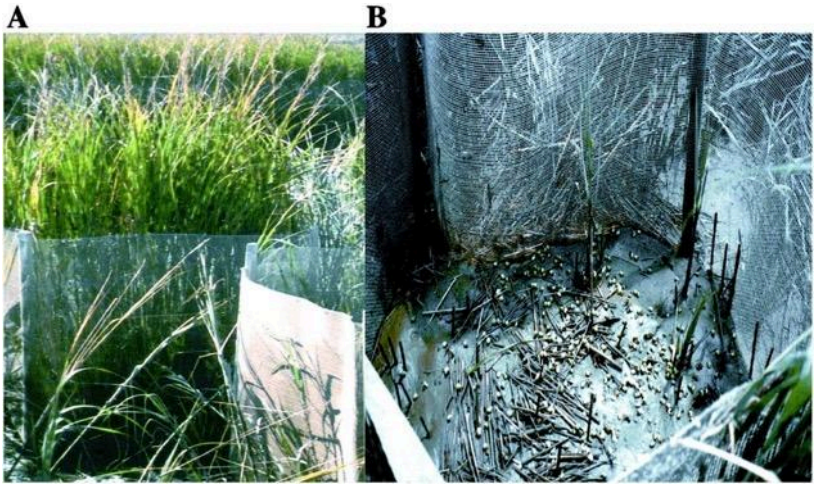


***Figure 13**: Effects of periwinkle grazing on Spartina standing crop and canopy structure in the tall zone after 8 months in Western Atlantic saltmarshes, USA. (A) Low-density plot. (B) High-density plot. After 20 months, cordgrass in all medium-density plots was reduced wholesale, and the marsh substrate was completely denuded (B). Image source.*

Predator-exclusion experiments in saltmarshes have revealed that sea otters suppress the abundance of burrowing crabs, a top-down effect that cascades to both increase marsh edge strength and reduce marsh erosion (*Figure 14*) (ref). Crabs eat salt marsh roots and dig into the soil, which can cause parts of the salt marsh to collapse. These results show that trophic downgrading could be a strong but underappreciated contributor to the loss of coastal wetlands and suggest that restoring top predators can help to re-establish geomorphic stability.

***Figure 14**: Through feasting on burrowing crabs, sea otters help to reduce the erosion of saltmarshes and building resilience against sea level rise. Image source.*

3.4.4 Seagrass meadows

Relaxed predation on herbivores, such as green turtles, in seagrass meadows can result in the removal of 90-100% of the aboveground vegetation (ref). In subtropical seagrass ecosystems in Western Australia, large tiger sharks influence the foraging behavior of

dominant grazers including dugong and green turtles by inducing shifts in their habitat use and foraging tactics (ref). The non-consumptive effect of the sharks creates a landscape of fear where sea turtles and dugongs preferentially forage in seagrass microhabitats that are low in predation risk. Seagrass habitats associated with high predation risk have higher carbon stocks than those with low predation risk (*Figure 15*). Another example of the top-down impact of predators on herbivory comes from a study on eelgrass in Sand Diego Bay, USA, where the exclusion of micro-carnivorous fishes resulted in a 300-1000% increase in seagrass epifauna (tube-building crustaceans and limpets) and a 50% reduction in eelgrass production (ref).

An interesting example of the link between the seagrass (*Zostera marina*) food web is linked and fish abundance comes from Sweden. Overfishing of cod, a top predator in the coastal ecosystems, led to an 80% decline in the population. This reduction generated an increase of 8-11 times in intermediate predatory fish (gobies and sticklebacks) and the near-total disappearance of meso-herbivores (idoteids and gammarids) which feed on the epiphytes of seagrass. Epiphytes and filamentous ephemeral algae out-compete the seagrasses for light and water column nutrients. The lack of grazers in concert with eutrophication contributed to the overgrowth by filamentous algae, which reduces seagrass growth, and the disappearance of the seagrass from the Swedish west coast (ref).

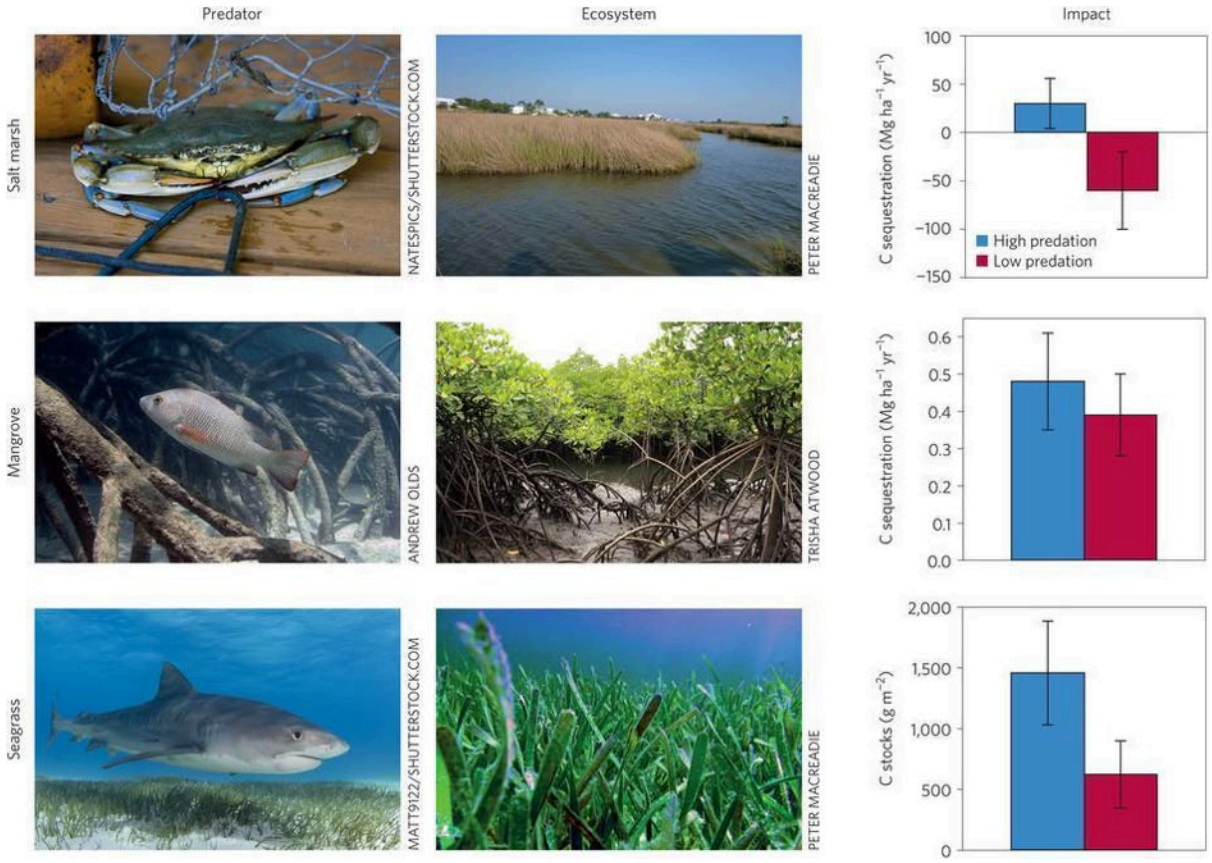


Figure 15*: Reductions in predatory blue crabs in New England saltmarshes (top panel) and in predatory fish (mangrove jack) in Australian mangroves (middle panel) resulted in increased abundance of bioturbators (for example Sesarmid crabs) and a reduction in the carbon sequestration capacity of these ecosystems. Non-consumptive effects of tiger sharks (bottom panel) in Shark Bay,*

Western Australia, create a "landscape of fear" in which sea turtles and Seagrass microhabitats associated with low predation risk have lower C stocks than do microhabitats associated with high predation risk. Image source.

Grazing on seagrasses by brent geese (*Branta b. bernicla*) and wigeon (*Anas penelope*) can have a positive long-term effect on intertidal seagrass beds (*Zostera noltii* and *Z. marina*) due to reduced mud accretion in grazed beds (ref). It was concluded that in the sheltered upper intertidal zone, seasonal erosion caused by herbivorous geese and ducks is necessary for the persistence of *Z. noltii*.

3.4.5 Estuaries, coastal lagoons, deltas & mud flats

Macro-crustaceans: The complex life histories of macro-crustaceans (e.g., crabs, freshwater prawns, isopods, and amphipods) are linked to evolutionary adaptation processes and high environmental heterogeneity, playing essential functions in energy flow and nutrient cycling in food webs (ref). Burrowing behaviour in soft sediments is widespread among decapod crustaceans and has been classified as ecological engineering. This bioturbation involves creating sediment movement and resuspension which supports oxygen penetration into sediment, enhancing microbial processes and nutrient transport and cycling (nitrogen & phosphorus) through the sediment-water interface. These processes are vital for sediment formation.

Fish assemblages are composed of species that occupy a wide range of trophic levels in the food chain and assist with the regulation of trophic structure and ecosystem resilience in coastal lagoons (ref). Many fishes move between freshwater and marine environments, which assist with sediment formation (i.e., bioturbation), nutrient exchange (i.e., migration) and primary production through excretion and carcass decomposition. Through their consumption and trophic cascades, all fishes feed and interact with other organisms, generating regulation of food web dynamics and other processes. This, in turn, can assist with carbon exchange regulation and contribute to global carbon dynamics and climate regulation. Coastal lagoons can become sources or sinks of carbon depending on the feeding activities of fishes:

- *Feeding on zooplankton promote the primary producers (carbon fixers), and*
- *Feeding on other fish can suppress the abundance of fish feeding on zooplankton, allowing the zooplankton community to grow, reducing the primary carbon fixers.*

Fish feeding activity on phytoplankton can assist with the regulation of eutrophication processes, providing a water purification service. By consuming other organisms, fishes help the recycling of nutrients, making the nutrients available for primary production.

Through feeding on buried invertebrates, stingrays enable oxygen and organic matter to penetrate deeper into sediments, supporting biogeochemical cycling and the associated microbial assemblages that drive these processes (ref).

Birds comprise a diverse group with a broad range of diets and foraging behaviour. Coastal lagoons support a high diversity of resident and migrating birds due to their high biological productivity and habitat heterogeneity, which provides sites for nests, roosting, and foraging

(ref). Birds feeding on aquatic organisms create a direct link between terrestrial and aquatic systems, facilitating the exchange of nutrients between habitats through the birds' excretion. Colony breeding birds, such as gulls, terns, cormorants, herons, and ibises are particularly important. Bird predation generates top-down effects on the food chain that shape fish and invertebrate communities, promoting the coexistence of species from different taxa, like fish, shrimps, and crabs.

Aquatic mammals are not a common component in coastal lagoons, however, when they occur, they can modulate the structure and stability of the habitats, particularly by their feeding activity (ref). Their high trophic levels and prey consumption rate regulate the abundance of prey populations, and their decline could trigger a series of cascading events through lower trophic levels. Due to their high metabolic rates, aquatic and semi-aquatic mammals consume a significant amount of biomass and release high amounts of nitrogen in their faecal plumes, enhancing primary production. They also increase the cycling of nutrients through their horizontal movements between different seascape ecosystems.

Examples of predators are:

- *The Neotropical (river) otter (Lontra longicaudis) found in wetland systems from Mexico and Central America through mainland South America to northern Argentina. It feeds on crabs and freshwater and marine fish species.*
- *The Bottlenose dolphin (Tursiops truncatus) is a generalist predator that feeds on fish and molluscs in coastal lagoons and estuarine ecosystems,*
- *Beluga whales (Delphinapterus leucas), and*
- *Harbour seals (Phoca vitulina).*

The (Case Study #2) document the functional role of shorebirds/waders and a deer species (Père David's Deer, *Elaphurus davidianus*) in shaping coastal wetlands and their ecological functions.

3.4.6 Mangroves

Bivalves (aquatic molluscs) and gastropods (slugs & snails) as primary consumers and detritivores ensure direct releases of faecal matter enriching the sediment, ensuring other animal forms gradually congregate and form complex food webs (Sevvandi Jayakody, pers. com). Substantial amounts of dead wood in the intertidal zone of mature mangrove forests are tunnelled by teredinid bivalves ("shipworms"), which serves as refuges for a large number of animals, ranging from animals found in terrestrial ecosystems including centipedes, crickets and spiders, and animals found in subtidal marine ecosystems such as fish, octopods and polychaetes - hence, teredinid bivalves acting as ecosystem engineers (ref). Shore crabs (Carcinus spp.), especially sesarmid crabs (Neosarmatium smithi) and fiddler crabs (family Ocypodidae) (ref), appear to be a major driver of recruitment, tree density and distribution, and size structure in mangrove and other coastal tropical forests. They also serve as a primary food source for stingrays, shorebirds/waders, and fish (ref). However, mangrove ecosystems with large crab populations have lower carbon sequestration rates than those with no or fewer crabs. Small-bodied predators, such as predatory ants and birds, can directly and indirectly protect mangroves from insect and crab herbivory, which would negatively affect the photosynthesis of mangroves (ref). Under

certain circumstances, predatory fish seem to have a positive impact on carbon sequestration through the decline of bioturbators, such as crabs (Figure 16).

Mangroves are often referred to as nursery grounds for coral reef fishes, but this only holds true when coral reefs are located near the mangrove forests and under low amplitude tidal conditions (ref). Nonetheless, mangrove habitats appear to provide important habitat for coastal and estuary fish across tidal ranges and regions (ref).

Through their roosting or nesting in mangroves, seabirds have been found to play an important role in mangrove ecosystems (ref). Nutrients from seabird guano enrich mangrove plants, reduce nutrient limitations, enhance mangrove invertebrate food webs, and are exported to nearby coastal habitats through the tidal flow. Conserving seabirds is therefore vital to preserve and enhance their role in mangrove productivity, resilience, and provision of diverse functions and services.

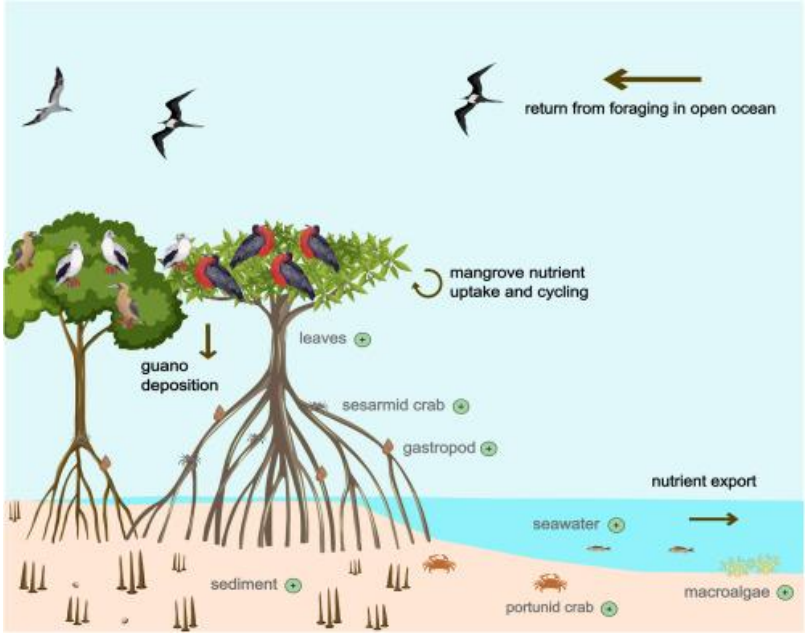


***Figure 16**: Seabirds forage at sea and deposit nutrient-rich guano in their mangrove breeding colonies, which enrich mangroves and their associated invertebrate fauna, and are exported to adjacent habitats by tidal flow. Image source.*

3.4.7 Coral reefs

Coral reefs are among the most productive ecosystems living in oligotrophic waters. In addition to the symbiotic relationship between the coral animals and dinoflagellates, corals can also extract nutrients from the surrounding seawater (ref). External nutrients that elevate local nitrogen conditions in waters surrounding corals can increase the density of zooxanthellae, enhancing photosynthesis and coral growth rates. Seabirds have been found to transfer nutrients via a sea-land-sea system, enhancing coral reef productivity and functioning (ref). From their feeding in highly productive marine waters and the deposit of guano around their nests, roosting sites and island shores, nutrients leak back to nearby marine areas (*Figure 17*). It has been estimated that seabirds feed on food webs supported by net primary production that is 2-5 orders of magnitude higher than the net primary

production of coral reefs (ref). Invasive rats have been found to drastically reduce breeding sea bird numbers on islands, but also reduce nutrient flow to surrounding coral reefs with lower values of nitrogen in macroalgae, filter-feeding sponges, turf algae and fish. Coral reefs surrounded by intact island systems without invasive rats, have been found to have much healthier fish populations with higher biomass across trophic feeding groups, with 48% greater overall biomass (ref). Nitrogen enrichment is higher in corals near seabird colonies decreasing linearly with distance from land. In one experiment, the dominant reef-building species (*Acropora formosa*) grew up to four times faster near the seabird site than others disconnected from seabird influence. Increased seabird-derived nutrients caused a doubling of coral growth rates both within individuals and across entire reefs (ref). Following an extreme marine heatwave, corals near seabirds demonstrated rapid recovery, indicating that seabirds enhance coral reef resilience (ref). Thus, non-native mammal (cat, mice and others) eradication on oceanic islands should also be a high conservation priority for coral reef management.

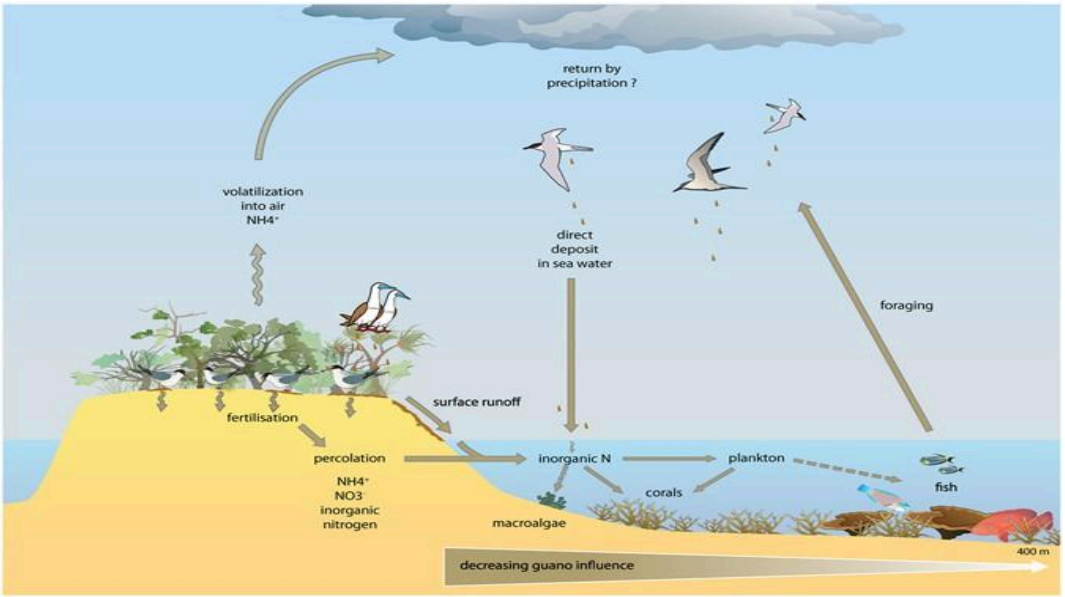


***Figure 17**: Conceptual diagram showing the different pathways for guano-derived nitrogen to enter seawater and marine food webs (brown arrows) with hypothetical transfers to fish and macroalgae in broken lines. Image source.*

Grey reef shark (*Carcharhinus amblyrhynchos*) populations have been estimated to deposit an estimated 95 kg of nitrogen daily into the nutrient-limited reef ecosystem, supporting coral health in the 15,000 acres (6,070 hectares) Altyra Atoll Wildlife Refuge. Approximately 86% of this is likely derived from pelagic resources. These results suggest that sharks may contribute substantially to nutrient transfer from offshore waters to near-shore reefs, providing subsidies that are important for coral reef health (ref). However, overfishing has reduced storage and resupply of fish-derived nutrients on coral reefs by nearly 50%, resulting in diminished coral growth and primary productivity (ref).

Herbivory is a vital ecological process on reefs globally. Intense grazing by herbivores prevents the establishment and accumulation of algae, which can suppress coral growth, survival, and reproduction (ref). Parrotfishes (Figure 18) are among the most abundant and

ecologically important herbivorous fish, providing unique grazing and bioerosion function (ref). The removal of herbivorous fishes from coral reefs has led to state shifts in many regions, particularly in the Caribbean, where decades of overfishing, temperature-induced coral bleaching, and disease events have fostered algal dominance (ref). Due to overfishing of the main predators and nutrient pollution, the crown-of-thorns starfish (*Acanthaster planci*) has contributed greatly to declines in coral cover on Australia's Great Barrier Reef, and remains one of the major acute disturbances on Indo-Pacific coral reefs (ref).

Even at low levels of subsistence fishing, combined with increased nutrient delivery, has been shown to erode resilience of coral reefs and cause transitions from healthy coral-dominated reefs to degraded algal-dominated systems (ref). When parrotfish are overfished and their populations decline, algae can overgrow and outcompete corals for space, light, and nutrients. This can lead not only to a decline in coral health and diversity, but also the decline of many other species that rely on the coral reef for habitat and food. Removing the parrotfish reduces the productivity of the coral, decreases the number and size of populations of other species it can support, and weakens its ability to withstand additional stressors such as climate change, pollution, and disease. This leaves coral reefs more vulnerable to further degradation and potential collapse.

***Figure 18**: With about 100 species, parrotfishes is a highly diverse group. Image source.*

Cascading interactions between reef sharks/herbivorous fish: The tidal conditions and the presence of sharks determine the behaviour of herbivores and the distribution of seaweeds (ref). Both key browsers (Clown unicornfish**,** *N. lituratus and Bluespine unicornfish, N. unicornis*) and the grazer Pacific daisy parrotfish (*C. spilurus*), which are potential prey species of reef sharks, were abundant in lagoons at low tide but were scarce (*N. lituratus and N. unicornis*) or half as abundant (*C. spilurus*) throughout the backreef at high tide

(*Figure 19*). This behaviour likely indicates that these species migrate, or shelter out-of-sight, presumably to minimize exposure to predators hunting in the area during high tide. This is an example of how reef sharks create 'seascapes of fear' and herbivorous fish avoid areas patrolled by sharks which in turn influences the spatial distribution of seaweeds. Seaweed biomass on the reef top ('fear hotspots') was 20 times greater than in hard-bottom lagoons where the herbivorous fish aggregated during low tide and where seaweeds were virtually absent. Based on information from the Heron Island in the Great Barrier Reef Marine Park, Australia, it has been estimated that the net carbon balance could be 0.74 million tons of CO_2 annually for the entire park (2,063 km^2) (ref). Protecting sharks across the world's coral reefs (301,000 km2) could sequester 108 MtCO2/y, which corresponds to the total of fossil fuel emissions by Kuwait in 2022 (109 MtCO2/y) (ref).

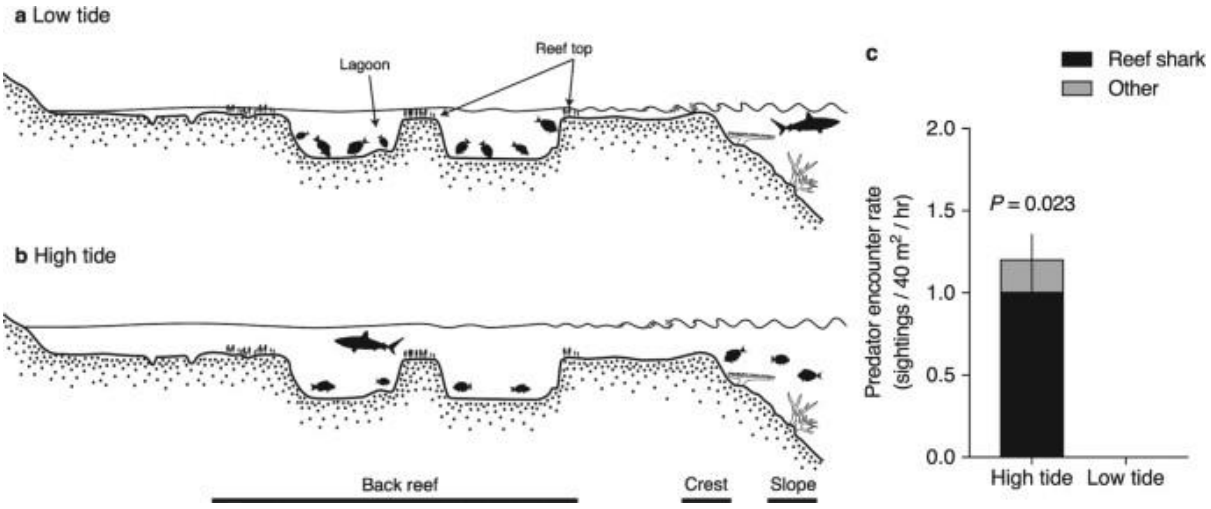


Figure 19: *Reef topography and predation risk as a function of tide. The backreef at (**a**) low tide and (**b**) high tide. Deep, hard-bottom lagoons are habitable to large herbivorous and piscivorous (predatory) fishes throughout the tidal cycle. The upper surface of the reef ("reef top") is not accessible to these fishes at low tide. At high tide, the entire backreef becomes deeper, allowing all fishes, including large predators, access to all reef features. (**c**) Predator encounter rate in the backreef at high vs. low tide each day, with most predator sightings being sharks. Image Source*

3.4.8 Kelp

Kelp forests (*Order Laminariales*) form key biogenic habitats in coastal regions of temperate and Arctic seas worldwide, providing ecosystem services valued in the range of billions of dollars annually (ref). These habitats provide complex three-dimensional habitats with modified sub-canopy conditions. The effect of this supports a trophic foundation of coastal food-webs by providing food for a suite of grazers, carnivores, detritivores, and microbes. Kelp forests play an important role as nurseries for juvenile fish, including economically important species like salmon and rockfish (ref). These effects can reach adjacent reef, seagrass, and sediment communities as well as to deep sea waters beyond the continental shelf (ref). Trophic cascades play a critical role in kelp conservation. The loss of predators such as sea otters, sea stars, lobsters, and predatory fish results in the expansion of sea urchins, (*Figure 20 & 21*), often linked to the loss of the kelp habitat (ref). A recent experiment in northern/ central California and Oregon evaluating the predation on purple sea urchins (*Strongylocentrotus purpuratus*) by the sunflower sea star (*Pycopodia*

helianthoides) in northern/ central California and Oregon, USA, demonstrated a strong top-down control in favour of kelp comeback (ref). It was concluded "that Pycnopodia recovery may be an effective and long-lasting method to control sea urchin populations and restore kelp forest ecosystems" and that the sea star "may serve as a complementary secondary predator to the much more voracious sea otter".

***Figure 20**: This is how the previous kelp forest looks after the Pacific purple sea urchins coat the seafloor, creating an "urchin barren". Image source.*

***Figure 21**: This is how a kelp forest would look like after the return of sea urchin predators, like the sea otter (Enhydra lutris) and the sunflower sea star (Pycopodia helianthoides). Image source.*

3.5 Which roles do different animal groups play?

This section provides examples of how mammals, birds, fish, reptiles, amphibians, and macro-crustaceans (such as crabs and crayfish) interact with different aquatic ecosystems. It has been written in a way to provide complementary, more generic information to the wetland types section.

Mammals: Sediment disturbance caused by mammals can benefit freshwater ecosystems by releasing nutrients and creating habitat heterogeneity which enhances biological diversity (ref). Examples include hippos, tapirs, water buffalos, marsh deer and southern lechwe (ref) as well as moose (ref). Through feeding on aquatic plants, with less cellulose than in terrestrial plants and therefore more digestible, manatees, dugongs, marsh deer, lechwe, sitatunga (*Tragelaphus speki*), musk rat, nutria, moose and water buffalo profoundly influence vegetation composition and growth.(ref). Although aquatic plants are generally a supplementary food source for beavers, hippos and capybaras, their feeding activities still cause considerable changes in the community compositions of aquatic vegetation (ref).

Through their size, feeding, metabolic requirements, social behaviour, and movement patterns, many large herbivores act as ecosystem engineers with the ability to change grazing plant communities, habitat structure, nutrient flows, and trophic dynamics (ref). This role is evident in both terrestrial and aquatic ecosystems. An assessment of the role of large herbivores in structuring and functioning within freshwater and marine angiosperm ecosystems (*Figure 22*) (ref), led to the following conclusions:

- Aquatic (e.g., dugongs, manatees, turtles) and semi-aquatic herbivores (e.g., swans) have been found to consume between 30-80% of the primary production. However, large grazers have also been reported to increase primary production by up to 40% by removing heavily epiphytized seagrass blades, which reduce light limitation and facilitate the production of new, fast-growing shoots.
- Large aquatic herbivores (including waterfowl) also affect the vegetation structure, both above and below ground, and/or increase the patchiness as well as the species composition. Deer and hippos create grazing lawns on land while green turtles, dugongs, and swans do so in aquatic environments. At extreme, high population densities, green turtles, dugongs, and manatees overgraze, which also negatively impact other animal species.
- One of the most significant effects of large aquatic herbivores is the modification of sedimentation, which can influence primary production, increase plant burial rates, or reduce transparency. Beavers, for instance, modify channel geomorphology and hydraulic conditions through their dam building, creating habitats that are structurally more diverse and productive, supporting a wide variety of aquatic and terrestrial animals and plants, and acting as carbon stores.
- Large aquatic herbivores modify nutrient cycling and the transport of nutrients in or out of the system. Sustained grazing in both aquatic and terrestrial systems has been shown to enhance nitrogen content through compensatory growth, benefitting other herbivores and decreasing nutrient limitations. In contrast to land-based systems, large aquatic herbivores do not fertilize the benthic primary production, as their

urine and dung quickly disperse through the water movement due to the animals' often-large home ranges.

- Through their foraging activities, certain large herbivores, such as hippos, swans, green turtles, beavers, and moose, facilitate the transfer of nutrients between terrestrial and aquatic systems.
- Some aquatic birds, such as ducks and swans, have been found to transport seeds of aquatic plants and resting stages of numerous invertebrates over longer distances.

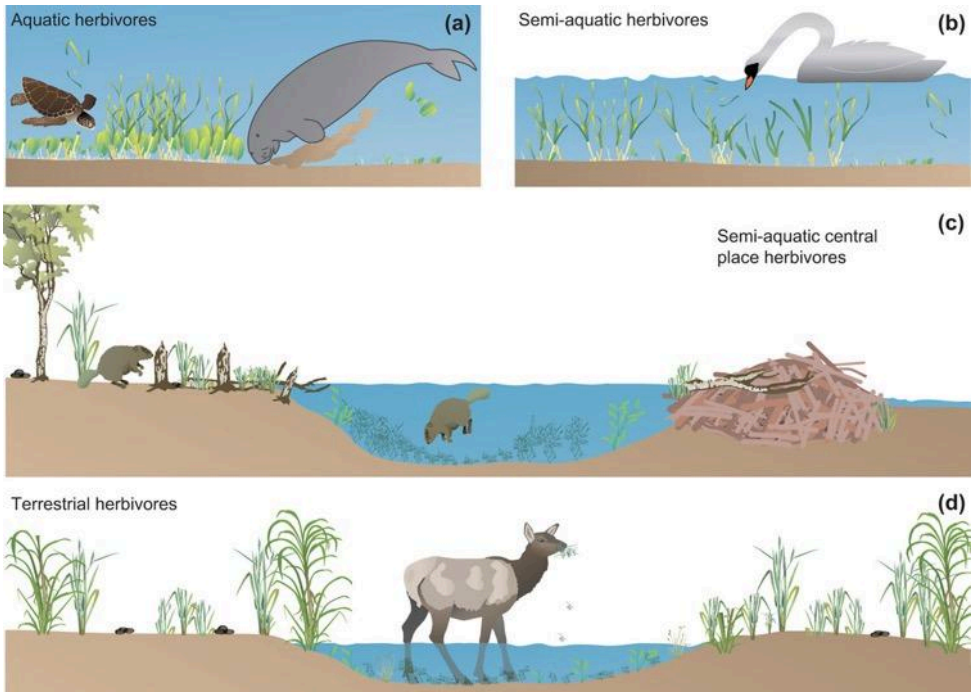


***Figure 22**: Large aquatic herbivore categories: (a) fully aquatic herbivores (dugongs, turtles, and manatees) that live and forage under water. They may be resident or migrant. They strongly impact plant beds, especially if resident. They may transport nutrients and plant material within their large home range. (b) semi-aquatic species (swans) adapted to life on water, but that frequent both water and terrestrial habitats. They usually display migration behaviour. (c) semi-aquatic central place foragers (hippopotamus, beaver, capybara). They are residents and have strong impacts on plants within their core areas. (d) terrestrial species that frequent aquatic habitats (cervids, water buffalos, lowland tapir) in search of food supplements/complements (e.g., sodium). Image source.*

As illustrated in (Case Study #3), large herbivores are vital to the health of wetland ecosystems. Their presence ensures diverse, open landscapes that benefit both plant and animal life, as seen in the successful rewilding efforts in Kaziranga National Park in India and Saeftinghe area, in the Netherlands. Sustainable management of these herbivores is key to maintaining these ecological benefits.

One case study on the Eurasian beaver from Scotland (Case Studies #4) highlights how the animals have reshaped former straightened farm drainage ditches, increased the wetland area, the landscape complexity and overall biodiversity, generating a threefold increase in plant richness and aquatic invertebrates. The tree felling improves the structure and regeneration of riparian forests. How precisely beavers influence nutrient cycling is currently

investigated, with some preliminary indications that beaver dams process agricultural pollution. Sediments retained by beaver dams store carbon.

The re-introduction of the European otter (*Lutra lutra*) in an area of the UK triggered a significant and rapid reduction in the densities of the invasive alien American mink (*Mustela vison*), which may, in turn, have potential benefits for native species threatened by this invasive predator.(ref). Similarly, in Chile, the southern river otter (*Lontra provocax*) has been found to affect the feeding pattern of the invasive American mink in coastal areas, mitigating its impact (ref).

Even a smaller aquatic mammal, such as the platypus (*Figure 23*) has been found to affect the functioning of stream ecosystems. In an experiment, it was shown that the species had a strong, suppressive effect on invertebrate populations, especially detritivores and omnivores, while having less impact on invertebrate taxon richness and composition. Contrary to expectations, the platypus had less impacts on lake ecosystems (ref).

Figure 23*: Through its feeding, the elusive platypus affects invertebrate populations in streams where it lives. Image source.*

Carnivores have been found to play a secondary role in seed dispersal by preying on primary seed dispersers or seed predators, inadvertently consuming seeds contained in their prey's digestive tracts and later depositing viable seeds elsewhere (ref). The European otter (*Lutra lutra*) has been identified as a primary seed disperser for riparian vegetation in Iberian fresh waters by feeding preferentially on elmleaf blackberry (*Rubus ulmifolius*) (ref). Similarly, Neotropical otters (*Lontra longicaudis*) have been observed in this role within a Brazilian Atlantic forest (*Figure 24*). This suggests that otters may serve as disperses for plants in a wider set of riparian ecosystems.

***Figure 24**: Neotropical otter. Image source.*

Birds: Waterbirds play a vital role in maintaining connectivity among communities in isolated aquatic systems and, thus, maintaining species and genetic diversity (ref). By acting as passive dispersal agents, waterbirds are known to be vectors of a whole range of aquatic invertebrates including crustaceans, bryozoans, dipterans, molluscs, rotifers, and annelids as well as aquatic and terrestrial plants, and fish eggs (*Figure 25*).. Many of these organisms are incapable of moving between lakes or river catchments on their own, making waterbirds crucial for facilitating gene flow between communities (ref). It has also been proposed that waterfowl are the principal vectors for marshland plants, a function originally dispersed by large, migratory mammals that are now extinct. However, "they probably offer only a pale shadow of what once had been a massive seed flow by large herbivores" (ref). Ducks and other waterfowl also play a vital role in the colonisation and regeneration of new and restored wetlands by aquatic flora and fauna (ref).

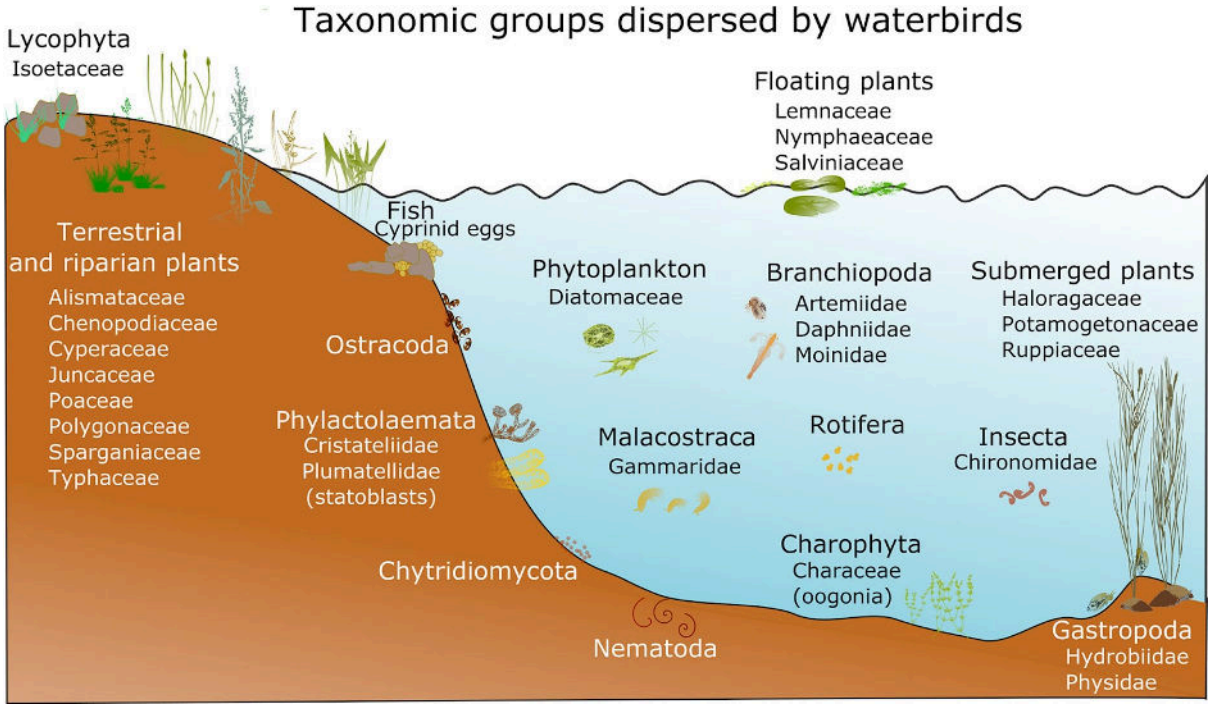


***Figure 25**: Land–water transition zone from terrestrial to littoral to pelagic habitat, illustrating organisms dispersed by waterbirds - ducks (Anatidae) and/or rails (Rallidae). Major taxonomic groups are indicated by the larger font, and key families known to be dispersed in the smaller font. Blue represents aquatic habitats, brown represents terrestrial habitat and lake sediments. Image Source*

Fish are a key component of aquatic biota with ecological roles that are essential for the stability of their ecosystems (*Figure 26*) (ref). They make significant contributions to nutrient cycling, with feeding strategies that span all levels of the food web, ranging from detritivorous up to apex predators. Within fish assemblages, functional diversity, rather than species richness alone, plays a pivotal role in maintaining the stability of aquatic ecosystems. The diversity of species functional attributes adds another important dimension to ecosystem understanding and could buffer ecosystems against disturbances.

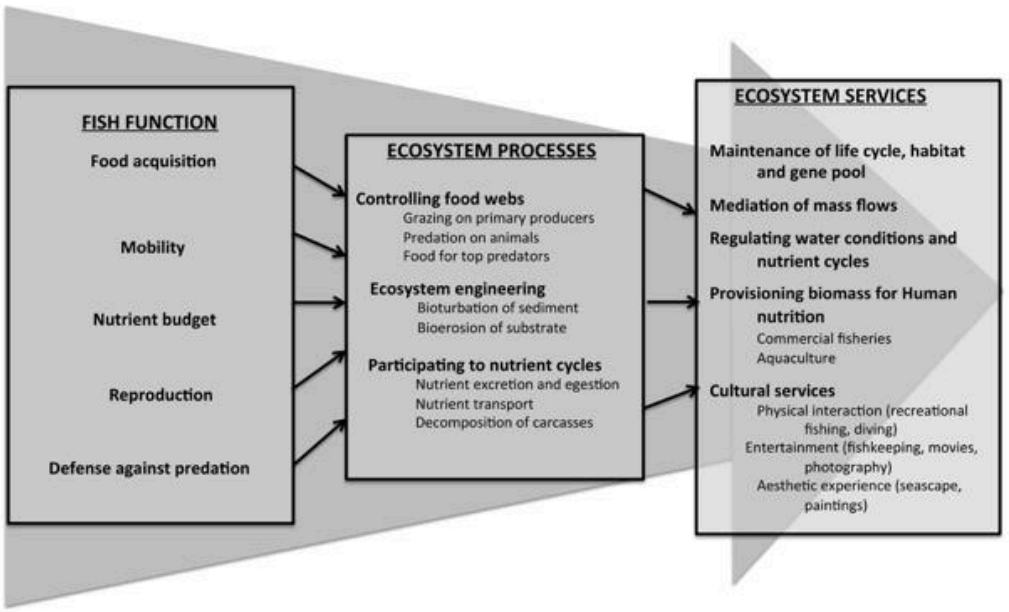


Figure 26*: Overview of how facets of fish ecology determine the services aquatic ecosystems supply. Image source.*

Fish contribute to various functional aspects within aquatic ecosystems. For example, Eastern freshwater cod (*Maccullochella ikei*) and chinook salmon (*Oncorhynchus tshawytscha*) create breeding sites that could have favourable impacts on habitat heterogeneity and the release of nutrients, especially at high population densities (ref). Foraging activities of grass carp (*Ctenopharyngodon idella*) directly alter the abundance and composition of aquatic vegetation (ref). American paddlefish (*Polydon spathula*), smallmouth buffalo (*Ictiobus bubalus*) and bighead carp (*Hypophthalmichthys nobilis*) feed on zooplankton, thereby reducing grazing pressures on certain phytoplankton and inducing trophic cascades (ref). Other potential trophic cascades through top predators include species of *Arapaima* spp*., Brachyplatystoma spp., Esox spp.,* and *Maccullochella spp* (ref).

With approximately 6,000 described species, representing one third of all freshwater fish species on the planet, Neotropical freshwater fish in particular play a critical role in the functioning of water and riparian systems (ref). A significant proportion of these species are frugivorous, contributing to seed dispersal and the maintenance of riparian vegetation (*Figure 27*). Many species also contribute to the decomposition of organic matter through feeding on detritus and decaying organic matter, which is beneficial for the nutrient cycle (*Figure 27*). Fish also control filamentous algae and periphyton, affecting nutrient dynamics, habitat quality, carbon cycling, and system state. Due to their abundance and widespread distribution across South America, these species are expected to have a strong impact on ecosystem functioning and dynamics. Experimental evidence even suggests that freshwater fish can indirectly facilitate the reproduction of terrestrial plants by reducing the abundance of dragonfly larvae in lakes, which prey on pollinating insects as adults. The Neotropical realm stands out as the region with the highest functional diversity of freshwater fish (ref).

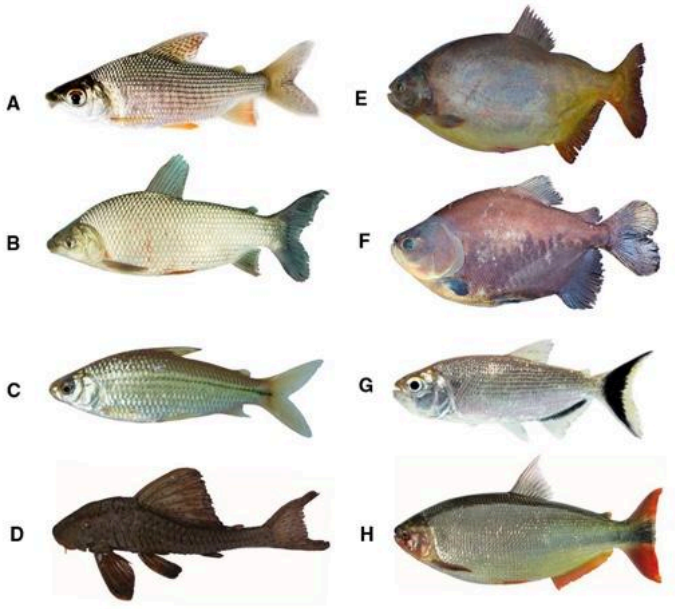


***Figure 27**: Detritivorous Neotropical fish that scrape substrates and contribute to decomposition, nutrient cycling, and environmental quality are represented by: Prochilodus nigricans (A), Prochilodus lineatus (B), Steindachnerina brevipinna (C), and Hypostomus cochliodon (D). Frugivorous and omnivorous fish that contribute to seed dispersal are: Piaractus mesopotamicus (E), Colossoma macropomum (F), Brycon falcatus (G), and Brycon microlepis (H). Image source.*

The larvae of freshwater pearl mussel, considered a keystone species in riverine ecosystems, require host fish to develop, with Atlantic salmon and brown trout being the only suitable hosts (Case Study #1).

Reptiles and amphibians: *Crocodylians* (27 species of true crocodiles (family *Crocodylidae*), alligators and caimans (family *Alligatoridae*), and the gharial and false gharial (family *Gavialidae*) are a widely distributed group of primarily freshwater-dwelling, large-bodied predators (ref). Although crocodylians are often believed to have significant ecological roles, much of this is based on limited evidence. Many claims about their roles as apex predators, keystone species, ecosystem engineers, and nutrient transfer agents are speculative. Future research should focus on filling these gaps with targeted, hypothesis-driven studies (Case Study #5).

Of the 356 species of turtles, tortoises, and terrapins, many are associated with the aquatic environment (ref). The group plays an important ecological role. Many turtle populations make or made significant contributions to the biomass of their environment. Turtle standing crop biomass is generally very high in comparison with other vertebrates, often surpassing that of all other reptiles. Biomass values for turtles are typically at least an order of magnitude higher than those of other reptiles and similar to those of large schools of fish. The high biomass of turtles is related largely to the high population densities they can achieve. Turtles also contribute substantially to secondary productivity in some ecosystems. Because of their overall secondary productivity and biomass, turtles have a disproportionate influence on processes in many wetland and terrestrial environments. As a result of their numerical dominance, turtles have played important roles as significant bioturbators of soils,

infaunal miners of sea floors, dispersers and germination enhancers of seeds, nutrient cyclers, and consumers. Breeding sea turtles make a significant contribution to energy flow within and between ecosystems (*Figure 28*). However, the collapse of turtle populations on a global scale has greatly diminished their ecological roles.

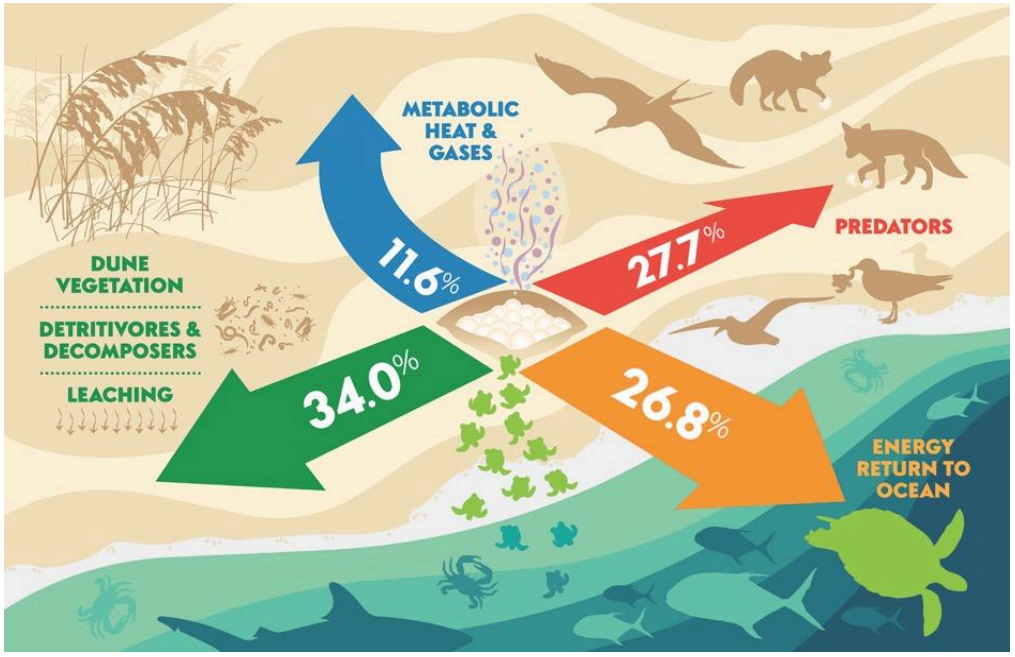


***Figure 28**: This figure shows the projected transfer of energy from 14,305 loggerhead sea turtle (Caretta caretta) nests with an estimated 1.6 million eggs on a 21-kilometer stretch of Florida beach in 1996. Only about one quarter of total energy transferred to beaches returned to the marine environment in hatchlings. Image source.*

For nesting, Chinese (*Figure 29*) and Japanese giant salamanders create sediment depressions that can release nutrients and create habitat heterogeneity which could be favourable for biodiversity (ref).

***Figure 29**: The Chinese giant salamander (Andrias davidianus) is one of the largest salamanders and one of the largest amphibians in the world. It is fully aquatic, and is endemic to rocky mountain streams and lakes in the Yangtze river basin of central China. Image source.*

Macro-crustaceans (*decapods*): This group includes shrimp, prawns, lobsters, crayfish, hermit crabs, and crabs, with most species found in the coastal and marine environment. Crabs are primarily tropical, while crayfish are predominately temperate, with the highest diversity in North America. As bioturbators, macro-crustaceans are considered ecosystem engineers because they alter resource availability to other species through the physical changes they make to their environments. The complex life histories of macro-crustaceans are related to evolutionary adaptation processes and high environmental heterogeneity, playing essential functions in energy flow and nutrient cycling in food webs (ref). This overview will report on the ecological role of a few crab species as well as freshwater crayfish.

Crayfish are the dominant decapods in many freshwater ecosystems, playing an important ecological role through their large size, mobility, and omnivory (ref). Size and density affect their ecosystem impacts. Crayfish have been described as keystone controllers of trophic webs and as ecological engineers. Species in streams with a high biomass of invertebrates are at a higher trophic position and have higher growth rates than crayfish living in streams with low biomass of invertebrates. Most studies show that feeding crayfish impacts on vegetation, invertebrates, or both, with the largest impacts in streams and the littoral areas of ponds. Crayfish eat salmonid eggs and juvenile fish and could negatively impact on salmonid recruitment, like the European cisco (*Coregonus albula*). They also serve as an important food source for amphibious predators like newts, otters, and herons. Through their movement and feeding activities, crayfish also affect sediment accumulation in forested streams thus acting as ecosystem engineers, influencing habitat quality and, ultimately, impacting the resource abundance to other coexisting species, such as chironomid larvae, harpacticoid copepods, and mayfly larvae. (Case Study #6)describes the restoration programme of the white-clawed crayfish in the Central Apennines, Italy.

3.6 Ecosystem services

Sections 3.1 to 3.4 provided information on how wild animal species contribute to two of the four principal components of ecosystem services (*Figure 29*), namely supporting and regulating services of wetlands. In this report the following services are included:

Supporting services:

- *Nutrient cycling,*
- *Sediment/soil formation & control (e.g., reduced erosion*
- *Seed dispersal*
- *Mediating cross-ecosystem linkages*
- *Biodiversity enhancement*
- *Ecosystem productivity*
- *Food webs*
- *Water distribution & flow*

- *Ecosystem heterogeneity*

Regulating services:

- *Climate regulation & carbon sequestration*
- *Flood control*
- *Water purification*
- *Invasive species control*

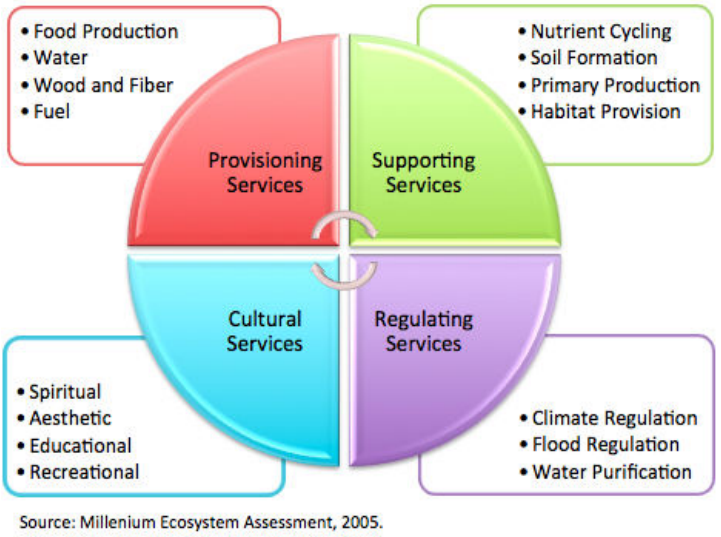


***Figure 29**: The four main elements of ecosystem service provided by nature. Image source.*

The below table provides a snapshot of how different animal groups contribute to the supporting and regulating services.

SUPPORTING SERVICES	
Ecosystem engineering & habitat modification	Beavers, hippos, crocodylians, water buffalo, tapirs, capybaras, deer, rhinos, elephants, turtles, giant salamanders, fish (salmons, paddlefish, etc.), parrotfishes, crabs, crayfish
Nutrient cycling & ecosystem productivity	Fish, sharks (coral reefs), birds, hippos, beavers, turtles/tortoises/terrapins, crabs, crayfish, freshwater pearl mussel
Sediment/soil formation & control (e.g., reduced erosion)	Bivalves, gastropods, fish, birds (ducks & geese), macro-crustaceans, stingrays, hippos, tapirs, water buffalo, deer, beavers, crabs, crayfish, sea otter
Seed dispersal	Neotropical fish, swans & ducks, otters, turtles

Mediating cross-ecosystem linkages	Fish (e.g., salmons, neotropical species), colony breeding birds (islands/coral reefs), waterbirds (plant & invertebrate dispersal), crocodylians, anacondas, turtles, hippos, beavers, moose & amphibians
Biodiversity enhancement	Fish, birds, large mammals (including beavers), reptiles (e.g., turtles, giant salamanders), freshwater pearl mussel
Food webs & trophic cascading	Bivalves, gastropods, fish, birds, crabs, otters, sharks, dolphins, sea stars, lobsters, platypus, crayfish
Water distribution & flow	Beavers, hippos
Ecosystem heterogeneity	Large mammals, turtles/tortoises/terrapins, giant salamanders, fish
REGULATING SERVICES	
Carbon dynamics, climate regulation & adaptation	Fish, sharks, shorebirds, sea otters, beavers, predatory crabs
Flood regulation	Beavers
Water purification	Predatory fish, freshwater pearl mussel, beavers
Invasive species control	Père David's deer, otters

Carbon sequestration is an important service provided by terrestrial, freshwater, and marine ecosystems. Coastal wetlands – seagrass meadows, tidal marshes, mangroves, and kelp forests – sequester more carbon, known as 'blue carbon', per unit area than any other habitat worldwide (ref). In the blue carbon ecosystems, the climate mitigation impacts of fish, sharks, sea otters, and predatory crabs have been quantified (see text box). Additional information on beavers is also provided in the text box.

Additional information on the role of animal species in the carbon cycle of wetlands

Here are some examples of enhancement (in % or tons of carbon dioxide) in 'Blue Carbon' ecosystems with and without predators:

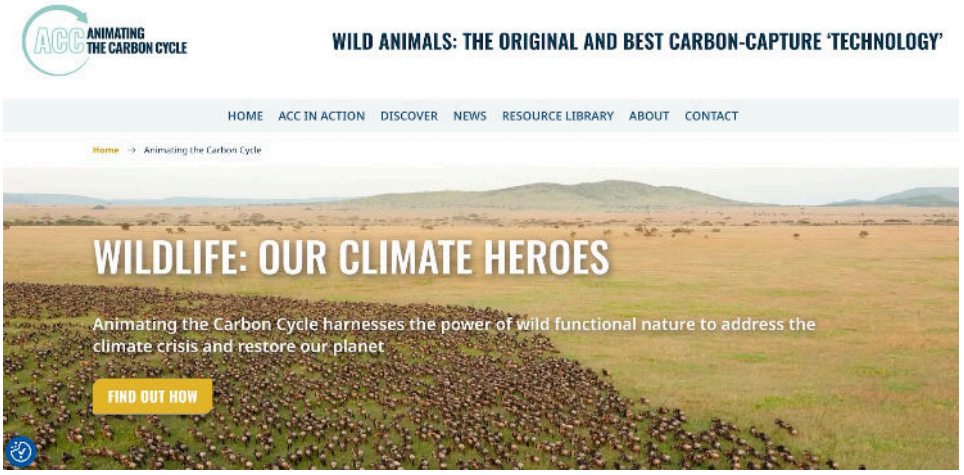
- Saltmarshes (Cape Cod, Atlantic coast, USA), Predatory blue crabs – grazing crabs: +300%,
- Seagrass meadows (Shark Bay, Western Australia), Tiger sharks – Dugongs & green sea turtles: +134%
- Mangroves (Queensland, Australia), Mangrove jack (and other predatory fish) – shore crabs: +20%
- Kelp forests (southern British Colombia to the Aleutian Islands, Canada/USA), Sea otters – sea urchins: net ecosystem carbon balance increased by 5.2 million tons of CO_2 per year through 78,000 sea otters - or 12 times more than without sea otters.
- Coral reefs (Heron Island, Great Barrier Reef Marine Park, Australia), Reef sharks (tiger, black-tipped & lemon sharks) limiting the spatial extent of

herbivory: net ecosystem carbon balance increased by 0.74 million tons of CO2 per year through 1.27 million sharks over 2,063 km^2 of reef systems.

(Saltmarshes, seagrass meadows & mangroves: source; Kelp forests & coral reefs: source)

In the boreal and temperate zones, beavers may enhance carbon storage through engineering the landscape to create wetlands. By building dams with aquatic reservoirs, they alter the biophysical properties of forest ecosystems, collecting organic material and creating dams that act as sediment carbon storage pools. It has been calculated that beaver ponds globally contain 380 million tons of carbon, which can remain for millennia (ref).

For those who would like to learn more about how wild animal species facilitate carbon sequestration in ecosystems, a phenomena that has been called "animating the carbon cycle", please visit the following website: https://animatingcarbon.earth/.



No systematic efforts were made to assess how wild animal species contribute to the Provisioning and Cultural Services, but a description from India of the ecosystem services provided by the Sarus crane (*Antigone antigone*) – a species often associated with wetlands - is included (*Figure 30*) (Case Study #7).

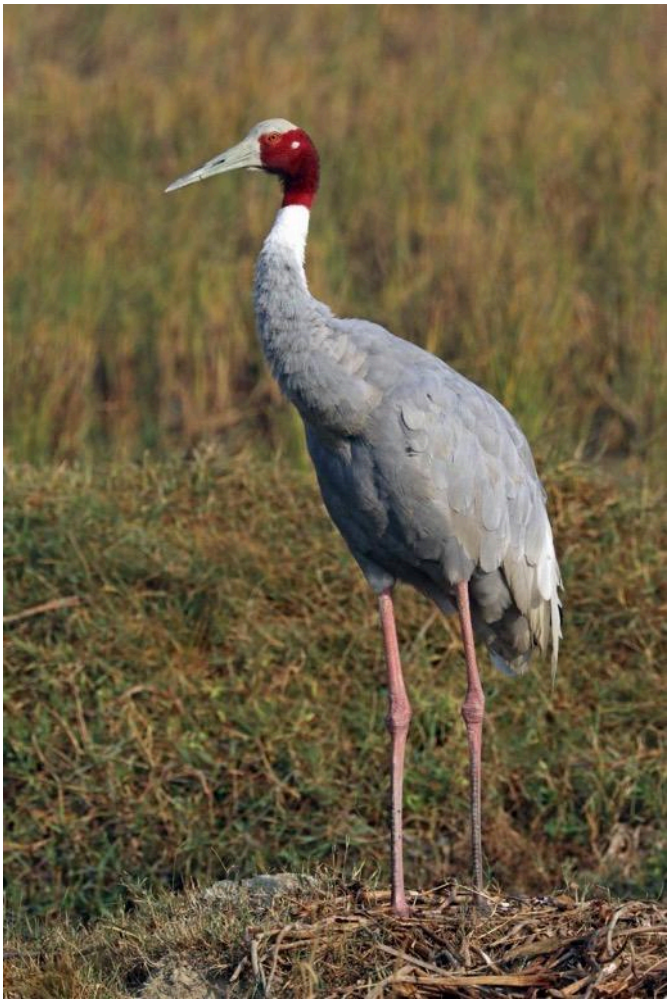


***Figure 30**: During breeding, the Sarus crane is associated with wetlands. The nest platforms have been found to benefit small-scale farming, providing foundations for pioneer grasses instead of the typical reed and sedge stages of natural succession, which allow the farmers to till, plough, and sow crops earlier. Image source.*

The Ramsar Convention has identified the following ten ecosystem services:

- *Flood control*
- *Groundwater replenishment*
- *Shoreline stabilisation & storm protection*
- *Sediment & nutrient retention and export*
- *Water purification*
- *Reservoirs of biodiversity*
- *Wetland products*
- *Cultural values*
- *Recreation & tourism*
- *Climate change mitigation and adaptation*

The wild animal species covered by this report likely contribute to all ecosystem services. However, the focus of this report relates to only six services: flood control, shoreline stabilization and storm protection, sediment and nutrient retention and export, water purification, reservoirs of biodiversity, and climate change adaptation.

3.7 Management considerations

While mammals, birds, reptiles, amphibians, and macro-crustaceans contribute positive ecosystem effects, the actual impact of these species is strongly influenced by their population density (ref). Below are some examples provided by the Global Rewilding Alliance network, emphasizing the importance of incorporating various wild animal species into wetland management strategies. (Note: for the full case studies, go to the case study document.)

Case Study #8, India

Dr. Nachiket Kelkar of the Wildlife Conservation Trust, India, undertook a comprehensive assessment on how large fishes, reptiles, birds, and mammals affect India's riverine, estuarine, and other wetland ecosystems. The overview included the Ganges and Indus River dolphins, three species of crocodiles (the gharial, *Gavialis gangeticus*, marsh crocodile, *Crocodylus palustris*, and saltwater crocodile, *Crocodylus porosus*), three species of otters (Eurasian otter, *Lutra lutra*, smooth-coated otter, *Lutrogale perspicillata*, and small-clawed otter, *Aonyx cinereus*), approximately twenty species of freshwater turtles and aquatic birds, large catfish and carp species (> 1 m in captured size), as well as other carnivore and ungulate species that depend heavily on wetlands and rivers ecosystems. Many of these species are in decline and are classified as threatened. The study considered a total of 122 protected wetlands, riverine, and estuarine protected areas along with 85 Ramsar Sites highlighting the impacts of species reintroductions, invasions, and loss of megafauna on ecological functions.

Among these, the National Chambal Sanctuary in north-central India, stands out as "unique and intact freshwater habitat". Spanning 425 km of the Chambal River, this sanctuary supports an impressive diversity of functionally important aquatic megafauna species, such as gharials, marsh crocodiles, several turtle species, otters, and river dolphins.

***Figure 31**: The National Chambal Sanctuary is one the most ecologically functional wetland areas of India, hosting a large set of key wildlife species. Image credit: Anish Andheria/WCT.*

***Figure 32**: The National Chambal Sanctuary hosts 85-90% of the world's critically endangered gharials. Image credit: Anish Andheria/WCT.*

Another significant location is the Kaziranga National Park, situated along the Brahmaputra River in Assam, North-east India. This park supports a thriving assemblage of megaherbivores, including the Indian elephant (*Elephas maximus indicus*), greater one-horned rhino (*Rhinoceros unicornis*), wild water buffalo (*Bubalus arnee*), barasingha or swamp deer (*Rucervus duvaucelii*), muntjak (*Cervus muntjac*), sambar deer (*Rusa unicolor*) and Indian hog deer (*Axis porcinus*) exists in good numbers together with the tiger as the predator. The persistent ecosystem functions and impacts of these species are extraordinary (more information on ecological role of large herbivores in Kaziranga is provided in (Case Study #3).

Figure 33*: Wild buffalos and the great one-horned rhinos are key species in maintaining the ecological functionality of the Kaziranga National Park floodplains. Image credit: Anish Andheria/WCT.*

Of all the listed Ramsar sites assessed, only a small proportion (~8.5%, n=7) appear to have near-intact megafauna assemblages. Interestingly, most of these sites are estuarine or brackish-water areas with mangrove forests, or relatively well-protected but small stretches of rivers. Bird and waterfowl-dominated wetlands, which are the bulk of the Ramsar sites, need to be surveyed fully for assessments of groups such as turtles and native fishes, for which comprehensive data are currently required.

Case Study #9, Iberá wetlands, Argentina

The Iberá Wetlands, situated in the Iberá Basin of Corrientes province, north-eastern Argentina, represent one of the largest freshwater subtropical wetlands in South America, covering approximately 1.3 million hectares (ha) – 600,000 ha declared as a provincial nature reserve, 168,0000 ha as national park, and 25,000 ha as Ramsar Site. During the 20th century, the ecosystems underwent intensive human exploitation including rice farming, cattle ranching, and forestry, the latter represented particularly by exotic pine plantations. These activities added up to heavy hunting that had substantially impacted on native wildlife, eroding the functional system of the wetlands. In 2007, Rewilding Argentina started to rebuild the ecological system of Iberá through reintroducing lost species, protection of key species (e.g., Marsh deer, *Blastocerus dichotomus*), and through habitat restoration. The jaguar was brought back to help control the capybara (*Hydrochoerus hydrochaeris*) population and restore natural trophic cascades that balance ecosystem dynamics. This is expected to positively increase plant structure and function, increase landscape heterogeneity, modify nutrient cycling, enhance carbon sequestration, and potentially change the fire regimes. Plans are also underway to bring back the giant otter (*Pteronura brasiliensis*) as a freshwater apex species on fish, which is expected to affect primary production and the detritus dynamics. Recently reintroduced collared peccaries (*Dicotyles*

tajacu) are expected to positively impact plant species richness, habitat heterogeneity as well as soil nutrient properties - an effect the peccaries share with the marsh deer. In addition, Rewilding Argentina has promoted the return of giant anteaters (*Myrmecophaga tridactyla*) and the pampas deer (*Ozotoceros bezoarticus*), which are more associated with the drier parts of the area. The ultimate aim of the rewilding efforts is to recreate a network of functional ecosystems, which ensures the long-term health and resilience of the Iberá Wetlands system.

Figure 34*: The reintroduction of the jaguar started in 2021 and through affecting the capybara population is expected to have positive impacts on the vegetation and overall landscape of the Iberá Wetlands in northern Argentina. Image credit: Matías Rebak/Rewilding Argentina.*

Case Study #10: The Danube Delta

The 6.2-million-hectare Danube Delta on the border between Romania, Ukraine and Moldova is the largest river delta wetland in Europe and a designated Ramsar Site (Romania). During the 20th century the delta went through significant changes with embankments and other habitat changes, which affected its ecology. A reduction in grazing pressures due to the decline of natural herbivores and the collapse of large-scale livestock farming, resulted in a decline in the biodiversity of the delta's grasslands, meadows, and salt marshes. To turn these negative developments, Rewilding Europe launched initiatives in 2015 in efforts to rebuild the large herbivore community in some key areas of the delta in combination with restoring the natural water flow. The reintroduction of free-living horses (Hutsul & Konik horses), domestic water buffalo, cattle (Ukrainian grey cattle), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) has already increased plant diversity and habitat complexity, recreating favourable conditions for a wide range of invertebrates,

amphibians, and birds. These megaherbivores also served as new attractions for tourism developments, generating new income opportunities for local communities.

***Figure 35**: In addition to creating favourable ecological conditions in the Danube Delta, domestic water buffalos attract tourists, generating new sources of income for local communities. Image credit: Mykhailo Nesterenko/Rewilding Ukraine.*

Case study #11: U Minh wetlands, Vietnam

The U Minh Wetlands in southern Vietnam are a seasonally inundated ecosystem within the Greater Mekong Subregion. Historically dominated by Melaleuca forests, reed meadows, and swamps, these wetlands faced significant degradation over recent decades due to forest fires, poor management, and human activities like agriculture and plantations. In 2016, U Minh Thuong National Park was designated as the eighth Ramsar Site in Vietnam. Efforts to control peat degradation and fire risk, such as canal systems, have disrupted natural hydrology, drying some areas, and concentrating water in others, worsening fire risks. Native forests have largely been replaced by plantations of acacia, guava, and banana, with remaining Melaleuca forests recovering slowly and becoming fragmented.

The conservation and restoration efforts in the U Minh wetlands have been actively carried out through various ecological assessments since the 2000s, primarily focusing on species status, population distribution, and impact analysis. In this case study, an analysis is provided on the ecological role of different species groups when it comes to (i) ecosystem engineering, (ii) seed dispersal, (iii) nutrient cycling, and (iv) potential top down/bottom-up processes. This kind information will be used for developing a restoration and management plan.

***Figure 36**: Original vegetation is meeting a banana plantation along one of the many canals in the U Minh Wetlands in southern Vietnam, which is a Ramsar Site. Image credit: VNA/Re:wild.*

4. Findings put into the Ramsar Convention context.

The "Strategic Framework and guidelines for the future development of the List of Wetlands of International Importance of the Convention on Wetlands (Ramsar, Iran, 1971)", adopted at COP11 in 2012 and updated at COP14 in 2022, serves as a key instrument for the practical implementation of the Ramsar Convention. The following is an initial assessment of how the findings of this study align with this framework.

The proposed approach of maintaining or upgrading highly functional wetland systems, with most of the key animal species at ecologically significant population levels, supports the overall Vison[18] of the Ramsar List and aligns with three of the five objectives, namely:

- Objective 1: To establish national networks of Ramsar Sites in each Contracting Party that fully represent the diversity of wetlands and their **key ecological and hydrological functions**,
- Objective 2: To contribute to the maintenance of **global biological diversity** through the designation and management of appropriate wetland sites,
- Objective 5: To use national Ramsar Site networks to provide **essential ecosystem services/benefits**, particularly those related to water, which contribute to human health, livelihoods, and well-being.

By considering the key role of animal species in the management of Ramsar Sites, this approach contributes to maintaining the "**ecological character**", defined as "the combination

[18] "To develop and maintain an international network of wetlands which are important for the conservation of global diversity and for sustaining human life through the maintenance of their ecosystem components, processes and benefits/services."

of the ecosystem components, processes and benefits/services that characterise the wetland at a given point in time".

Under the "guidance for Ramsar Site descriptions", the importance of indicator, flagship, and keystone species is emphasized for Contracting Parties to consider. This report provides strong arguments for the **keystone species** concept. It also highlights the need for both descriptions and designation to include "underwater species such as **fish and other aquatic fauna and flora**", while advocating also for a broader perspective that incorporates species influencing the terrestrial/aquatic interface when it comes to descriptions, designations as well as management/restoration.

The report also provides evidence for the importance of **connectivity and ecological interdependence**, supported by numerous examples. Trophic interactions include the connections between mangrove forests and coral reef fish, the terrestrial/aquatic interface of many large herbivores (e.g., beavers), birds, crocodylians, migratory fish, waterbirds which act as vectors for seed and invertebrates' dispersal. Fish are also critical for seed dispersal of riparian plant species.

When it comes to the criteria for the designation of Ramsar Sites, emphasis is placed on Criterion 2 "vulnerable, endangered, or critically endangered species or threatened ecological communities" and Criterion 3 related to maintaining the biological diversity of particular biogeographic regions . Although waterbirds (in Criteria 5 and 6), fish (in Criteria 7 and 8) and non-avian wetland animal species (in Criterion 9) are considered, the "ecological functions" of sites are primarily targeted toward specific species. There seems to be a general lack of recognition regarding the critical role some animal species play in shaping the composition and functionality of various wetland categories and associated ecosystem services. To address this challenge, the inclusion of additional criteria, addressing the critical role animal species play in the ecological status of wetlands could be one possibility. Another option would be to provide enhanced guidance on this issue in the Strategic Framework, to explicitly encompass a diverse range of organisms, including mammals, birds, reptiles, fish, and macro-crustaceans, while reflecting the distinct differences between wetland categories, as illustrated throughout this study.

It is recommended that a much stronger recognition be given to the essential role of wild animal species in the conservation of inland and coastal wetlands. This recognition is urgently required to achieve the overall aspirations of the Ramsar Convention.

5. Conclusions & recommendations

The initial part of the study showed that today's wild animal populations are a fraction of their historical numbers. This decline, combined with the trophic downgrading of global ecosystems, such as the negative ecological impacts associated with megafauna downsizing, demonstrates that most ecosystems require significant restoration to function as they once did. Without such efforts, our ability to manage climate change, disease outbreaks, invasive alien species, wildfires, and other challenges will be seriously compromised.

With numerous examples of the ecological roles of mammals, birds, fish, reptiles, and macro-crustaceans (especially crabs and crayfish) in shaping lakes, rivers and streams, saltmarshes, seagrass meadows, estuaries, coastal lagoons, deltas, tidal areas, mangroves, coral reefs, and kelp forests, it is essential to prioritize wild animal species in the management of Ramsar Sites. Now is the time to restore all ecosystems, to reinstate trophic cascading as a key mechanism for securing and enhancing biodiversity and secure the critical ecosystem functions that inland and coastal wetlands provide.

Evidence from India indicates that only a few Ramsar Sites currently are managed with the goal of creating more holistically functional systems, which often requires a large-scale approach. The examples from the Iberá Wetlands in Argentina, where the Ramsar Site constitutes less than 2% of the total wetland area, illustrates the need to upscale the planning perspective. This is also demonstrated by the connection between mangrove forests and coral fish, the terrestrial/aquatic interface of many large herbivores (including beavers), birds, crocodylians, migratory fish, waterbirds as vectors for seed and invertebrate dispersal. Additionally, even fish play a critical role in the seed dispersal of riparian plant species, displaying the need for a connectivity perspective. And, as illustrated by fishing in Amazonia, the selective exploitation of large-sized animals and old-aged individuals must be considered when designing strategies for the sustainable use of species.

As discussed, wild animal species provide a wide range of ecosystem services. As ecosystem engineers, they play a critical role in essential supporting services, such as nutrient cycling, ecosystem productivity, sediment and soil formation and control, seed dispersal, enhancing biodiversity, controlling food webs, and mediating cross-ecosystem linkages. These “supporting services” act as the basis for important “regulating services”, such as carbon cycle, climate regulation and adaptation, flood control, water purification, and control of invasive alien species.

The literature overview, supported by the practical case studies, indicate the following connections between wetland ecosystems and the keystone role of wild animal groups:

- Lakes: fish & waterbirds,
- Rivers & stream: migratory fish, large mammals (beavers, hippos, muskrats, water buffalos, tapirs), reptiles (crocodylians, anacondas & large freshwater turtles), crayfish, freshwater pearl mussels, and pond breeding amphibians,
- Saltmarshes: predatory crabs, terrapins, sea otters & geese
- Seagrass meadows: sharks, fish, herbivorous geese & ducks
- Estuaries, coastal lagoons, deltas & mud flats: crabs, fish, stingray, birds (especially colony breeds & shorebirds), otters, deer & cetaceans
- Mangroves: aquatic molluscs, slugs & snails, shipworms, predatory fish, colony breeding birds, crab feeding birds & ants
- Coral reefs: parrotfishes, sharks & seabirds
- Kelp forests: sea otters, sea stars, lobsters & predatory fish

Time has come to put wild animal species at the centre of the ecological functional agenda of the Ramsar Convention on Wetlands!

6. References

The information provided in the main report is referenced with help of hyperlinks, allowing for quick access to the various sources. Some of the case studies provide traditional literature references.

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