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Scientists' Warning to Humanity: Rapid degradation of the world's large lakes

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Review

Scientists' Warning to Humanity: Rapid degradation of the world's large lakes

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ABSTRACT

Large lakes of the world are habitats for diverse species, including endemic taxa, and are valuable resources that provide humanity with many ecosystem services. They are also sentinels of global and local change, and recent studies in limnology and paleolimnology have demonstrated disturbing evidence of their collective degradation in terms of depletion of resources (water and food), rapid warming and loss of ice, destruction of habitats and ecosystems, loss of species, and accelerating pollution. Large lakes

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are particularly exposed to anthropogenic and climatic stressors. The Second Warning to Humanity provides a framework to assess the dangers now threatening the world's large lake ecosystems and to evaluate pathways of sustainable development that are more respectful of their ongoing provision of services. Here we review current and emerging threats to the large lakes of the world, including iconic examples of lake management failures and successes, from which we identify priorities and approaches for future conservation efforts. The review underscores the extent of lake resource degradation, which is a result of cumulative perturbation through time by long-term human impacts combined with other emerging stressors. Decades of degradation of large lakes have resulted in major challenges for restoration and management and a legacy of ecological and economic costs for future generations. Large lakes will require more intense conservation efforts in a warmer, increasingly populated world to achieve sustainable, high-quality waters. This Warning to Humanity is also an opportunity to highlight the value of a long-term lake observatory network to monitor and report on environmental changes in large lake ecosystems.

Contents

Introduction

Fresh waters are the most valuable natural resource on Earth. Lakes provide ecosystem services across four main categories, not only to the human populations directly surrounding them, but also at broader regional and global scales: provisioning, regulating, supporting, and cultural services (Table 1). Large lakes are especially valuable resources in all four categories. They provide drinking water to millions of people, a crucial matter considering that the drinking water insecurity faced by many populations may be exacerbated by increases in drought due to climate change. Food harvested from large lakes is also of cultural and economic importance, and includes fish, invertebrates such as crayfish, and aquatic plants. Fish harvested commercially from large lakes not only provide regional benefits to markets but are also exported around the world. Approximately 1.35 million tons of fish are harvested each year from the 25 largest lakes in the world by commercial or artisanal fisheries, with approximately 95% of this harvest coming from the African large lakes (Sterner et al., 2020). In devel-

Table 1
List of services provided by large lakes, and specific examples of services. Most of these services are provided by lakes of all sizes and are not restricted to large lakes. However, large lakes represent 90% of the total global lake surface area and hence contribute the major portion of these services. Modified from de Groot et al., (2012).

|	Ecosystem services	Examples
1	Provisioning services	Food, drinking water, industrial water and hydroelectricity, water for navigation, genetic resources, medicinal resources
2	Regulating services	Water flow regulation, local climate regulation, water quality regulation, regulation of natural risks, transfers or sequestration of elements . . .
3	Supporting services	Habitats for nursery and reproduction (plant and animal), maintenance of aquatic fauna and flora from micro-organisms to macro-organisms, support of migratory species and wildlife, hot spots of biodiversity
4	Cultural services	Aesthetics, recreation, inspiration for culture and art, spiritual experience, cognitive and scientific development
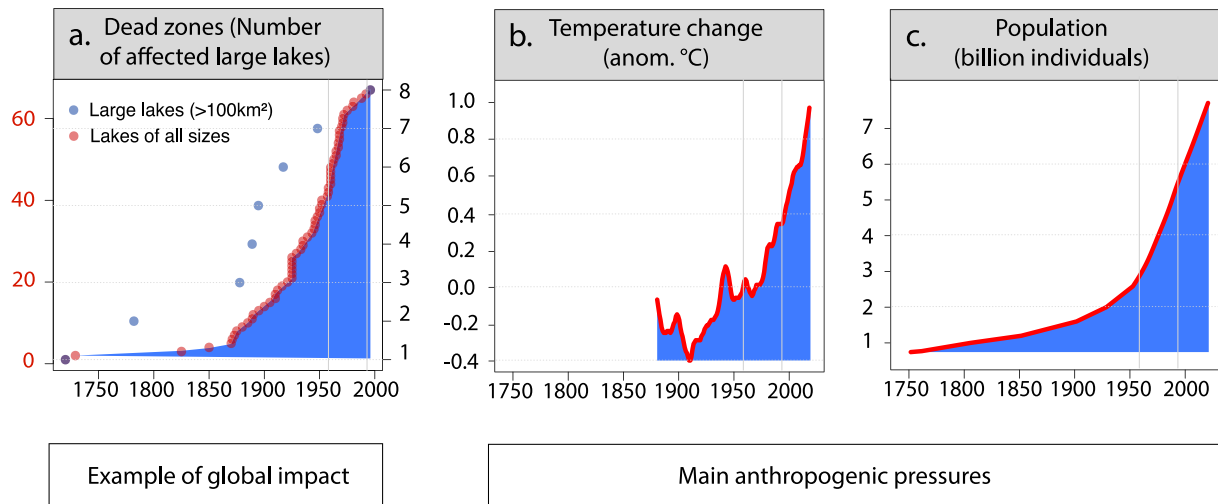
Fig. 1. Trends over time for some environmental issues identified in the 1992 Scientists' Warning to Humanity and extent of dead zones in lakes (left axis) and large lakes (right axis) of the world (Jenny et al., 2016a, 2016b). The number of dead zones were inventoried in lake sediment archives (a). In panel (b), global air temperature change, and in panel (c) (in Ripple et al., 2017).

oping countries and indigenous communities especially, the food provided by large lakes can represent key components of the diet. Aquaculture, a growing industry within the waters of several large lakes (e.g., Jia et al., 2015), also provides a source of protein to a growing human population, along with employment opportunities and economic benefits. Large lakes can offer supplemental resources to human populations, or in some regions the necessary resources to sustain populations (Carpenter et al., 2007). Large lakes also provide important shipping corridors for trade, as is the case with the Laurentian Great Lakes. Regulating services — benefits obtained by regulating ecosystem processes — provided by large lakes include safe harbors (protection from storms), erosion and sedimentation regulation, water storage, hydroelectric power generation potential, water quality regulation, and waste assimilation. In terms of non-material benefits or cultural services, large lakes offer remarkable aesthetic experiences (viewscapes), recreational (boating, fishing, beach use) and tourist opportunities, and places of spiritual respite that humans value immeasurably. As with other ecosystems, the variability in ecosystem services provided by large lakes depends on their underlying ecology and the current state of their environment that is closely connected to the surrounding watershed (Soranno et al., 2010).

Environmental degradation often results in a loss of ecosystem services that support human societies (Chanda, 1996). Degradation of lake ecosystems is evident worldwide, threatening the functioning of these ecosystems and the necessary services they provide at a global scale (Fig. 1, Keeler et al., 2012). Future threats to large lakes include the overexploitation of resources (water and food), inputs of excess nutrients and harmful algal blooms, changing climate, overfishing, species invasions, infectious diseases, expanding hydropower, acidification, contaminants, emerging organic pollutants, engineered nanomaterials, microplastic pollution, artificial light and noise, freshwater salinization, and the cumulative effects of multiple stressors. Lake sediment archives keep track of the extent to which lakes have departed from their so-called pre-Anthropocene status (Keeler et al., 2012), following a dynamics of change synchronized to the "Great Acceleration" phase of human pressures on the Earth since around 1950 (Steffen et al., 2007).

Past alteration of large lakes is also reducing their capability to resist new threats, and degradation of water quality will continue because of the cumulative impact of ongoing local pressures, syn-

ergies between stressors, and the imposition of global stressors (climate, volatile compounds, and invasive species). Even in regions that successfully combatted environmental degradation such as eutrophication, new threats are emerging, with consequences for large lakes and their ecosystem services that are difficult to fully predict. These impacts are altering large lake ecosystems and services in unprecedented ways, causing widespread concern among freshwater scientists.

We believe there is an urgent need to alert world nations about the current state and trajectory of the world's large lakes. In less than a century, the effects of rapid population growth and lack of adequate attention to environmental protection have resulted in striking perturbations to freshwater ecosystems across the planet, including the world's large lakes. More broadly, the initiative follows the joint European Large Lakes Symposium (ELLS)-International Association for Great Lakes Research (IAGLR) 2018 conference "Big Lakes - Small World", held in Evian (France) in September 2018, which brought together scientists working on large lakes around the world. Here, the participating authors make use of their broad expertise and knowledge of these global resources and present an updated assessment of the threats, both long-term and emerging, that confront large lakes of the world today. We begin by summarizing the ecosystem services of large lakes and the long-term and new threats that they are experiencing. We then examine some of the successes, but also failures, in the management of large lakes. We end this article with a set of recommendations on conservation policies and approaches to protect and sustain the world's large lakes.

General characteristics of large lakes

Choice of a quantified definition for "large lakes"

The International Association for Great Lakes Research (IAGLR; http://iaglr.org/lakes/) uses a definition of large lakes based on the analysis by Herdendorf (1982), defining Great Lakes to be inland waters greater than 500 km^2 in area, which encompasses the Laurentian Great Lakes and many other large lakes of the world. Herdendorf did leave open the need for additional input to refine this definition. For the present paper, our aim was to identify a subset of larger waterbodies as a sentinel
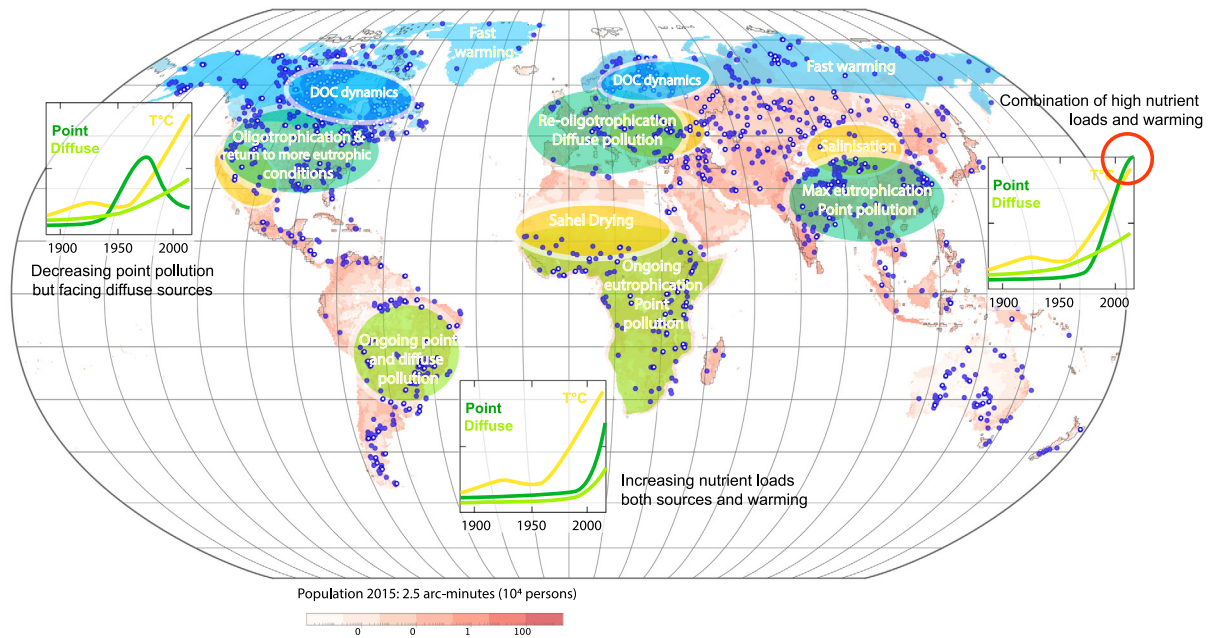
Fig. 2. Stressors in large lake ecosystems of the world are represented by examples of point and diffuse nutrient pollution, and climate forcing. Note the different intensity and the accumulation of climate and warming forcing for different regional contexts. Contrasted situations are presented (for Eastern China, Europe and North America, and for Southern Hemisphere). World distribution of large lakes larger than 100 km² (blue dots), lakes larger than 500 km² (blue open circles) and human population density (background map, Center for International Earth Science Information Network-CIESIN-Columbia University, 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

network to track and assess global change in the past and present. Specifically, we analyzed the global distribution of lakes to identify a size class that would cover gradients of hydrological (Electronic Supplementary Material (ESM) Appendix S1, Fig. S1, S2), geochemical, and climatic conditions (ESM Fig. S3). Based on these criteria, the size class of $\geq$ 100 km² was selected, and is adopted here as a definition of "large lakes". The lakes of this size class encompass a wide range of human and environmental conditions, including a diverse range of biomes, geological origins and salinities, and they are well spread out across the world (Fig. 2 and ESM Fig. S3). As a result of their large size, they share some limnological properties, to varying extents (see next section), and collectively they have enormous economic (ESM Table S1) as well as ecological value. Here we believe that our summary of the issues for large lakes would still apply even if a different size-based definition were used.

Global large-lake characteristics

In total, 1,709 inland waters meet our $\geq$100 km² criterion for large lakes, and their global distribution is shown in Fig. 2. If we consider lakes of all ages and origins, including tectonic, volcanic, alluvial, glacial, moraine, karstic, and human-made waterbodies such as dams and reservoirs, then large lakes represent only 0.2% of the total number of lakes in the world greater than 0.1 km². However, they account for nearly 90% of the total surface area (1,773,306 km²) and volume (178,772 km³) of the world's lakes. These large lakes vary greatly in many of their limnological attributes, but as an overall class of waterbodies, they differ from smaller lakes in terms of the following characteristics, in descending order (ESM Fig. S4): 1) larger water volumes; 2) larger watersheds; 3) greater shoreline length; 4) greater water inflows; 5) greater depth; 6) greater shore development; and 7) greater influence of wind due to a much larger fetch and wave action (ESM Fig. S4, Table S2). These properties have direct and indirect consequences on the exposure to stressors, the intensity of the impacts, the effec-

tiveness of environmental management actions, and the duration of recovery. For instance, the most rapid climate-induced warming for many large, deep, dimictic lakes can be found at the surface of the deepest, offshore waters (*e.g.*, Lakes Superior, Michigan, Huron (Woolway and Merchant, 2018). This is due to the high sensitivity of the date of stratification to climate warming (Austin and Colman, 2007; Zhong et al., 2016) which is a result of the lakes' significant depth. Shallower lakes such as Lake Erie do not show such high sensitivity (Zhong et al., 2016).

A coastal catchment zone extending 10 km inland was selected (Allan et al., 2017) to estimate the spatial extent of services provided around large lakes, and we calculated that this size class of lake ecosystems could directly provide services to 131 million people in their coastal zones (Fig. 3, ESM Fig.S1). Additional support for this 10-km boundary is found in the analysis that shows that 10% of the world's population lives further than 10 km from a surface freshwater body (Kummu et al., 2011). This estimate is likely to be conservative given that many large lakes provide services to populations that reside at distances well beyond 10 km from the lake. For example, Lake Biwa provides drinking water via aqueducts for 15 million people in the Kansai region of Japan, the Laurentian Great Lakes provide drinking water to 48 million people, and Lake Chad provides water to over 30 million people at the edge of the Sahara. Large lakes are present in 105 of the world's 195 countries (Fig. 3), and at least 10 such lakes occur in each of the hydrologic zones defined by Meybeck et al. (2013), indicating that this global network of waters spans a wide gradient of conditions (Fig. S2).

In spite of monitoring issues related to their size, many large lakes are well-monitored ecosystems. Resulting datasets of environmental parameters are shared among networks such as the Great Lakes Observing System (GLOS) and the Global Lake Ecological Observatory Network (GLEON), the latter of which references almost half of their sites as large lakes. This $\geq$100 km² size class of lakes provides an exceptional network of sentinels of environmental change, and the ensemble of these long-term datasets
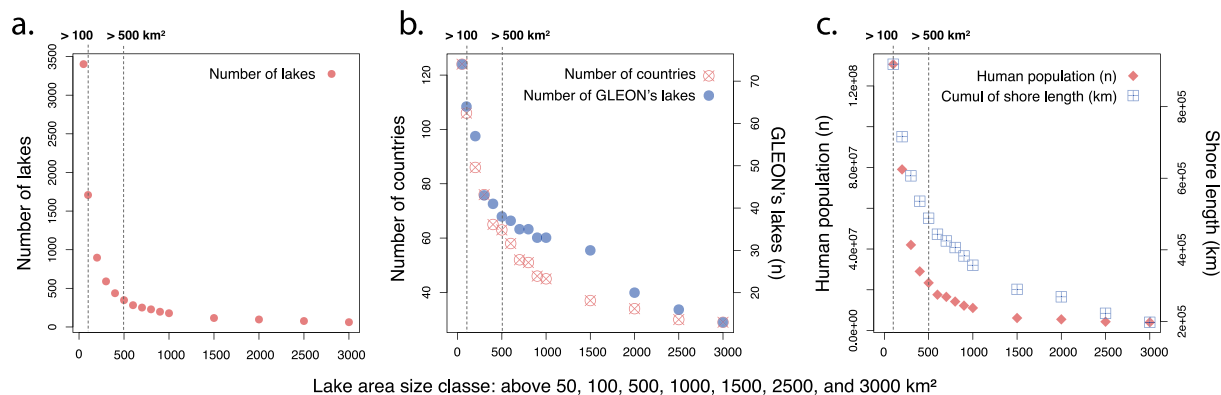
Fig. 3. Effect of different size classes on the spatial distribution and abundance of large lakes in the world. a. Number of lakes by lake size class, b. number of countries and GLEON's lakes by size class (Sharma et al., 2015), and c. sum of shore length and number of human population by size class of lakes. Note the exponential increase in the number of countries and humans affected by lake services as we include lakes of smaller size.

provides a valuable resource to better understand their functioning and vulnerability to global and local threats.

Long-term ecosystem services of large lakes: Their role for humanity

On geological timescales, the rise of human civilization during the Neolithic around 12,000 years ago is concomitant to the proliferation of lakes, a "Lake Age" following a glacial period when most lakes in the Northern Hemisphere were covered by ice or did not yet exist. The contribution of lakes to human resources and to the regulation of biogeochemical cycles is therefore particularly important at the human scale. Over the last few centuries, societal awareness and the value of provisioning, regulating, or cultural ecosystem services (Table 1) provided by large lakes have shifted, often in response to a growing human population and previous ecosystem degradation. Large lakes provide critically important benefits to all humanity (Table 2), and they need increasing care and attention to meet the growing demands for their ecosystem services at a time of increasing threats of ecosystem degradation.

From water samples and sediment records, lakes can provide a detailed record of land, hydrologic, or atmospheric degradation (*e.g.,* Davis, 2015; Jenny et al., 2019; Williamson et al., 2009), thereby yielding insights into human interactions with the environment at multiple spatial and temporal scales. Given their integrative behavior, including as the lowest points in the landscape, the world's lakes may be thought of as a vast, spatially distributed network of sentinels of environmental change (Williamson et al.,

2009), a concept we build upon here by proposing a sentinel network of large lakes. Certain lakes are especially sensitive indicators of environmental change, for example polar and alpine lakes that are strongly influenced by climate warming effects on the cryosphere, and that lie at remote locations where the arrival of long range contaminants can be detected (Bourgeois et al., 2018; Vincent, 2018). Lakes are also sentinels of local human pressure, pollution, and ecological impacts, particularly large lakes, which integrate the impacts of human activities on land use, mass fluxes, pollutant transfers, and management interventions, all extending over large areas. Large lakes therefore provide evidence of socio-ecological resilience and are an integrative measure of humanity's willingness to protect and sustain their environment.

About half of the world's largest lakes are ancient waterbodies that existed before the last glaciation, and sometimes for millions of years (Hampton et al., 2018). These lakes not only record long histories of environmental variation and human activity in their sediments, but also contain very high levels of biodiversity and endemism (Hampton et al., 2018; Vincent, 2018). These ancient ecosystems and other large lakes are natural laboratories for wider understanding, including as model systems to study evolutionary processes.

Surveillance, warning and programs

There is a long history of limnological research on the degradation of large lakes and the causal mechanisms of change. This work

Table 2
List of services provided by large lakes, related lake properties in each service class, and specific examples of services.

	Services related to Observation and warning	Related characteristics	Examples
1	Earth System integrators	Lake area, volume, depth lakeshore length; Lake:watershed; position within fluvial systems, and Earth system, sensitivity to climate variability	Climate and atmospheric regulation (local and regional), mitigation (buffer) of water volumes and quality and hydric-pollution transfer to the sea: storage of particulate matter, biogeochemical reactors (erosion, carbon circulation, water-storage), Mostly equivalent to 'regulating services'
2	Natural laboratories	Depth, age, origin, morphology, basin/ lake ratio; water renewal time, salinity, chemistry, microbiology, endemism, species colonization	Lake system functioning, basic processes (water chemistry interface, chemotrophic microbiota, speciation, paleo-limnology, ecological responses to natural or anthropogenic perturbations etc).
3	Sentinels of global and local changes	Length of hydrological, thermal, chemical and ecological records; position within biomes; paleo-limnological records	Surveillance of climate and human impacts on biota, habitat, physics and geochemical cycles.
4	Natural archives of human history	Riparian population, drinking water supply, other irreplaceable economic resources; documented historical records; evidence of past /present spiritual value, land cover and uses	Anthropocene, witness of human history, Interaction of human with nature, changes in how human value lakes, but also land ecosystems

Table 3
Examples of some international and national frameworks to manage large lakes.

Programs	Year	Countries	Description
International/Multi-national			
Boundary Waters Treaty	1909	Canada (Great Britain), USA	Treaty for comprehensive sharing of waters between these two nations, including the Great Lakes.
Laurentian Great Lakes Coastal Wetland Monitoring Program	1996	US, Canada	Assess coastal wetlands (Cooper et al, 2018; Uzarski et al., 2017, 2019)
EU Water Framework Directive (WFD)	2000	European Union countries	Legislative framework for assessing and protecting ecological status of all aquatic ecosystems (Directive 2000/60/EC; WFD, 2019)
The Great Lakes Water Quality Agreement Protocol (GLWQA)	1972, 1978, 1987, 2012	US and Canada	Commitment to restore and maintain the integrity of the Laurentian GL waters
Commission Internationale pour la Protection des Eaux du Léman (CIPEL)	1963	Switzerland and France	Commission responsible for monitoring the quality of the water in Lake Geneva, in the Rhône and in their tributaries
International Commission for the Protection of Lake Constance (IGKB)	1959	Germany, Austria, Switzerland and Liechtenstein	Observation, recommendation for coordinated preventive measures, and discussion of planned utilization of the lake.
The Great Lakes Basin Compact (GLC)	1955	Eight US states and Ontario and Quebec, Canada	Enable transboundary cooperation on lake management
National/Domestic			
Canada Ontario Agreement (COA)	1994	Canada	Restore, protect, conserve Laurentian Great Lakes water quality and ecosystem health
Great Lakes Restoration Initiative (GLRI)	2010	USA	Restore, protect, conserve Laurentian Great Lakes water quality and ecosystem health
Water Pollution Prevention and Control (WPPC) Law	1984	China	Water management to ensure emergency and back-up water resources are available in cities
Single large lake policies			
Programs	Year	Lakes	Description
Aral Sea Program	1995	Aral Sea	Restoring the Aral Sea to its former level
Convention on the Legal Status of the Caspian Sea	2018	Caspian Sea	How to divide up the potentially huge oil and gas resources
Framework Convention for the Protection of the Marine Environment of the Caspian Sea	2006	Caspian Sea	Protection of the Caspian environment from all sources of pollution
Lake Victoria Environmental Management Program (LVEMP)	2011	Lake Victoria, Africa	Tackle environmental challenges of lake basin over the long-term and improve welfare of inhabitants that depend on its resources
Canada-Ontario Lake Erie Action Plan, under the Great Lakes Protection Act (2015)	2018	Lake Erie	Reducing P loads to the western and central basins of Lake Erie by 40% by 2025
Convention on the sustainable management of Lake Tanganyika	2003	Lake Tanganyika	Objective to ensure the protection and conservation of the biological diversity and the sustainable use of the natural resources

has given rise to public alerts and has stimulated restoration activities and monitoring programs to track the effects of restoration and to detect new and ongoing threats. A wide variety of policy frameworks exist to manage large lakes across the globe, with different levels of maturity and effectiveness. These frameworks are essential to ensure that scientific results are communicated to policymakers and drive management actions that can protect and restore these valuable freshwater ecosystems. Many large lakes are transboundary, necessitating international policy frameworks. Several examples are described in Table 3.

Major disturbances and threats

Due to intense human activities and lake uses, large lakes are exposed to a wide variety of stressors. These stressors can be chemical (heavy metals, nutrients, organic contaminants), physical (temperature, radiation, water budget, habitat alteration), biological (invasive species), or from direct human extraction of resources (harvesting, mining). Stressors are agents that cause disturbance, defined as pronounced changes in the function or structure of an ecosystem, leading to decreased inherent qualities such as losses in biodiversity or a reduced capacity to sustain ecosystem services.

Stressors can directly impact individual performances and life history traits with cascading consequences at species, population, and community levels. Specifically, stressors can change physical and chemical conditions in a lake to promote or decrease photosynthesis and associated plant and animal growth, modify the production of hormones, operate as lethal components by increasing mortality, or change the behavior and seasonal timing of plant and animal development. In addition to the direct effects, stressors can operate indirectly through prey, predation, competition and non-trophic interactions. Those indirect effects may propagate through the network of species interactions and have profound impacts on lake functioning, water quality, and ecosystem services (Fig. 4). The most widespread stressors with strong impacts on human society and a description of the main impacts are summarized below.

Increased nutrient loading as a result of human activities has been found to trigger "cultural eutrophication." Cultural eutrophication is historically associated with an oversupply of phosphorus (P) (Carpenter, 2008; Carpenter et al., 2018; Schindler, 2012, 1977). Most common symptoms of cultural eutrophication also include changes in species composition, decrease in water transparency, increased incidence of anoxia, and biodiversity loss (Carpenter, 2005). Potential outcomes include the development of cyanobacterial harmful algal blooms (CHAB) and an increased release of greenhouse gases such as methane (Wurtsbaugh et al., 2019). Consequently, eutrophication impairs ecosystem services such as fishing, water supply, and recreation. The introduction by the public authorities of regulations to limit eutrophication still is a source of tension and debate on the activities identified as contributing or having contributed decisively to these phenomena (Le Moal et al., 2019).

Internal P loading (i.e., recycling of sedimentary P back to the water column) is often the major reason for a delayed response in improved lake water quality following reduced external nutrient loading (Jeppesen et al., 2005; Schindler, 2012). The mobilization of sedimentary P is usually associated with oxygen depletion that triggers reduction of ferric iron to ferrous iron and the subsequent release of associated P. However, P release has also been observed
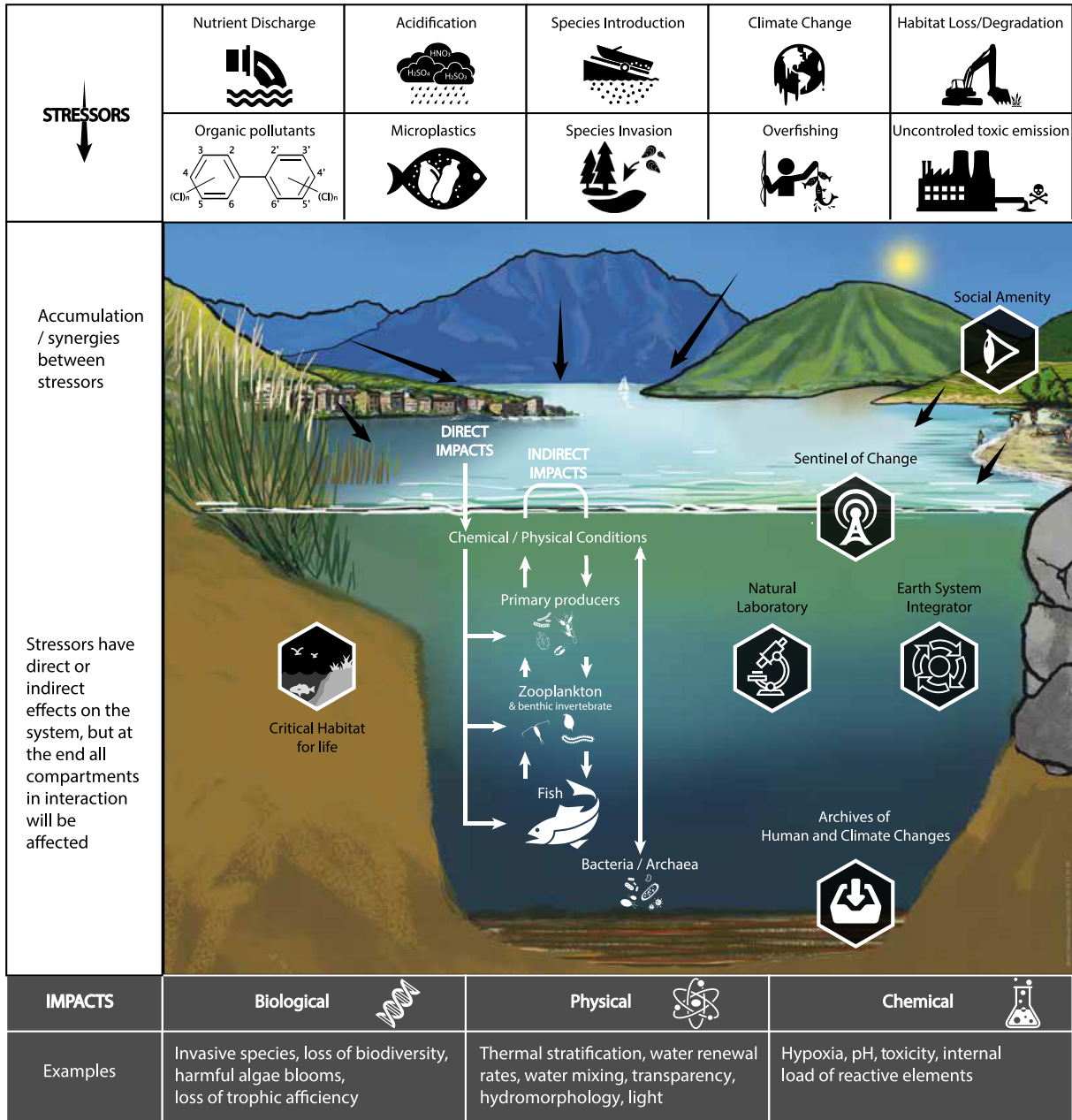
Fig. 4. Overview of services provided by large lakes, of most known stressors, and of the impacts of these stressors on lakes. White arrows highlight direct or indirect impacts on the lake food web.

under oxic conditions, and the mechanism behind P release may be much more complex (Hupfer and Lewandowski, 2008; Tammeorg et al., 2017).

The morphology of large lakes strongly affects their biogeochemical cycles and the mechanisms that control these cycles. Large and shallow lakes, such as Lake Peipsi (Estonia/Russia), Lake Okeechobee (USA), and Lake Taihu (China) are particularly influenced by sediment resuspension due to the high dynamic ratio (square root of lake area to mean depth, Håkanson, 1982). In Lake Erie, by contrast, external loading of nutrients has become a more significant threat, particularly due to increased delivery of soluble reactive phosphorus delivery from nonpoint sources via tributaries (i.e., labile P fractions at the soil surface and transmission of soluble P via subsurface drainage) (Jarvie et al., 2017).

Climate change has been identified as one of the most important problems facing humanity today (Feulner, 2017; IPCC, 2018).

The responses of lakes to climate change are well documented (Woolway et al., 2020), including increases in surface water temperature (O'Reilly et al., 2015; Schneider and Hook, 2010), loss of ice cover (Magnuson et al., 1990; Sharma et al., 2019), changes in stratification and mixing regimes (Woolway and Merchant, 2019), and increased lake evaporation (Wang et al., 2018). Deep lakes, which also tend to be "large" in surface area, are more likely to experience winters without ice cover in a warming climate than shallow lakes at similar latitudes (Sharma et al., 2019). Similarly, the epilimnetic waters of large, deep lakes have often been found to be warming at fast rates, as high as 1.0 °C per decade (O'Reilly et al., 2015; Schneider and Hook, 2010), due in part to the aforementioned high sensitivity of the date of stratification onset to warming air temperatures (Austin and Colman, 2007; Zhong et al., 2016). The rates of warming, however, are generally quite variable among lakes (O'Reilly et al., 2015) and even spatially

variable across large lakes (Woolway and Merchant 2018). Interactions with additional stressors can also lead to ecological surprises (Christensen et al., 2006). For example, changes in precipitation, evaporation, runoff, and consumptive water use have contributed to some lakes experiencing shifts in seasonal water levels (Lenters, 2001), while others have seen historically low / high lake levels (Rodell et al., 2018; Wurtsbaugh et al., 2017), contributing to alterations in water quantity and water quality (Vörösmarty et al., 2000). Feedbacks from large lakes to the atmosphere have also been identified, such as the warming of regional air temperature (Le Moigne et al., 2016).

Changes in lake thermal structure will affect the ecosystem by, for instance, altering the distribution of freshwater fishes, and/or decreasing deep-water oxygen concentrations (Cohen et al., 2016). In addition to modified vertical structure from climate change, some large lakes have also shown changes in *horizontal* temperature structure, such as more rapid warming of offshore surface waters as compared to shallower, nearshore waters (Woolway and Merchant 2018). Such characteristics are important to consider for lake organisms, given that temperatures warmer than a specific threshold can be lethal to some species. This is relevant for coldwater species in a warming climate, for example, if they cannot escape to cooler, deeper waters or groundwater inflow regions (Kangur et al., 2013). The warming-related collapse of coldwater fish populations has already been documented in many lakes in Northern Europe (Jeppesen et al., 2012). Climate change is also expected to amplify the impacts of eutrophication in the future (Moss et al., 2011), in part through changes in stratification. Changes in the length of the growing season within lakes can also have profound impacts on the seasonal timing of population development for organisms within lakes (Winder and Schindler, 2004). The extent to which species phenology is affected by climate change differs among species, which might result in a mismatch between prey and consumers, with consequences in terms of growth rates and survival (Adrian et al., 2006; Thackeray et al., 2008), especially when warming is seasonally heterogeneous (Straile et al., 2015).

Acidification has many negative biogeochemical consequences for species diversity as well as ecosystem health and functioning (Beamish and Harvey, 1972; Malley, 1980; Vinogradov et al., 1987), and it is driven by inputs of acid anions, such as sulfates and nitrates, and/or dissolution of atmospheric CO_2. It implies a decrease in water pH, carbonate ion concentration, and the saturation level of biologically important calcium carbonate minerals. In the 1960s and 1970s, acidification of natural waters was a pressing issue of regional concern because of acid rain and local atmospheric deposition, and it is not clear how pCO_2 in lakes will change in the future (Hasler et al., 2016) as the global atmospheric levels of carbon dioxide (CO_2) continue to rise, reaching unprecedented levels of 400 ppm in the 2010s (Monastersky, 2013). Large lakes typically have a low ratio of watershed area to lake area, which is one of the factors that influences a lake's susceptibility to potential atmospheric driven acidification (Eilers et al., 1983). However, decreasing CO_2 solubility and elevated algal productivity due to increasing temperature may counterbalance the effects of increasing atmospheric CO_2 (Phillips et al., 2015), but future acidification trends are not well understood currently and more research will be needed.

Harvesting of fisheries resources is common in large lakes and includes commercial, recreational, and subsistence fishing. Large lakes tend to experience more commercial fishing pressure than smaller lakes (75% of the freshwater ports inventoried in the *World Food Program logistics global ports* database are located in lakes greater than 19,347 km^2). As a result, they could be vulnerable to over-exploitation without management intervention. Overfishing has led to population collapses and species extirpa-

tions in some large lakes. For example, blue pike (*Sander vitreus glaucus*), a locally endemic subspecies of Walleye, was one of the most heavily harvested commercial species in Lake Erie until their collapse in the 1960s (Brenden et al., 2013). Overfishing continues to be a threat today. In Lake Malawi (Africa's 3rd largest lake), 9% of the 458 species of fish are at high risk of extinction, with 3 out of 4 of the species of chambo – oreochromine cichlids, the lake's most vulnerable fishes – being deemed as "critically endangered" due to unsustainable fishing (IUCN 2018). This overharvest of large-lake fishes threatens food security and livelihoods in some of the most food-deprived countries in East Africa. A newly emerging impact from harvest is the rapid evolution of key yield-determining traits in fish populations, slowing recovery and impacting resilience (Dunlop et al., 2018). Furthermore, the impacts of harvest can spread beyond the target fish species, as critical predator–prey relationships are altered within impacted food webs (Nõges et al., 2018).

Littoral shoreline modification has obviously increased in large lakes with the development of human society. Human settlement on the coast, inputs of nutrients and pollutants, and creation of harbors and beaches strongly influence local shoreline habitats, which constitute hotspots of lake biodiversity (Schmieder, 2004; Vadeboncoeur et al., 2011). In addition to previously described stressors, stressors near the coast include physical alterations that induce changes in the functioning of the whole coastal ecosystem. For instance, shoreline transformations modify the physical influence of waves and littoral slopes and have created sheltered areas with higher nutrient accumulation, enhancing the development of phytobenthos and phytoplankton at the expense of macrophyte communities (Sand-Jensen and Borum, 1991; Weisner et al., 1997). This affects habitats for fishes and macroinvertebrates and can disrupt the trophic relationships of the whole ecosystem. However, the available literature is not yet sufficient to evaluate the effects of human-made structures on fish recruitment (Macura et al., 2019).

Invasive species have drastically altered large-lake ecosystems, causing significant economic losses to human society. For example, dreissenid mussels have changed nutrient pathways in the Laurentian Great Lakes (Hecky et al., 2004), altering benthic invertebrate and plankton communities (Madenjian et al., 2015) and leading to life history and population changes in commercially harvested fishes (Fera et al., 2017, 2015). Water hyacinth, the world's most invasive aquatic weed, has invaded numerous systems, including the African large lakes (Ogutu-Ohwayo et al., 1997). Water hyacinth forms dense mats in shallow waters that alter fish breeding habitat, impair boat traffic and water intake, and provide breeding opportunities for mosquitos acting as disease vectors (Ogutu-Ohwayo et al., 1997). The threat from invasive species will remain into the future as climate change pushes species boundaries to new areas and as globalized trade expands. Furthermore, large lakes connected to transoceanic shipping networks (such as the Laurentian Great Lakes; Holeck et al., 2004), combined with ship ballast introductions, can be gateways for invasive species to expand into other surrounding inland lakes and waterways.

Complexity of interacting stressors: Insights from successes and failures in restoring the ecological state of large lakes

In large lakes, one stressor usually does not act alone. Instead, multiple stressors interact in additive or synergistic ways, and their combined impacts generate complex responses. The examples below highlight this complexity in the response of large lakes and the challenge that such complexity poses to lake management. Hence, the "cocktail" of stressors are generally specific to each lake, making it difficult to generalize environmental diagnostics; but elements of categorization can still be provided at the stressor

level. For instance, the development of wastewater treatment and associated reduction of point pollution varies greatly across the globe. Some countries would therefore still have to conduct policies in this direction, while others need to better manage the diffuse pollution of their intensive agriculture, with great disparities in geographical situations, such as those related to heritage of past uses, soils, drainage, land use, or lake tributary relations (Kayal et al., 2019).

Successful management of eutrophication, but arrival of new problems due to species invasions and warming

Lake Constance recovered from eutrophication due to successful lake management (Güde et al., 1998), with total phosphorus (TP) concentrations dropping by an order of magnitude to current levels (6–8 μg/L) that were typical for the years (early 1950s) prior to massive eutrophication (Jochimsen et al., 2013). Up through recent years, phytoplankton and zooplankton populations responded as predicted, and many food web changes due to eutrophication were reversed. For example, extirpated species (i.e., species with abundances below detection level for a long period) reappeared, including several diatom species (Kümmerlin, 1998) and the cladoceran *Diaphanosoma brachyurum* (Stich, 2004). On the other hand, species that had increased with eutrophication fell into decline (Straile, 2015), and relative contributions of green algae and cyanobacteria also decreased (Jochimsen et al., 2013). Even evolutionary responses to oligotrophication (the return to more oligotrophic conditions) were evident, such as the re-emergence of functional diversity lost during eutrophication (Jacobs et al., 2019). However, overall productivity decreased, which presumably contributed to reduced catches of important fish species such as whitefish (Thomas and Eckmann, 2007). In recent years, Lake Constance has experienced massive changes affecting various trophic levels of the pelagic food chain. Most notably, sticklebacks, a littoral fish present in Lake Constance since the 1950s, underwent a habitat change and is now the numerically dominant fish species in the pelagic zone (Eckmann and Engesser, 2019; Rösch et al., 2018). This habitat shift seemed to have further decreased whitefish growth and also (possibly due to stickleback predation on larval fish) whitefish recruitment (Rösch et al., 2018). Overall increased predation pressure in the pelagic zone seems to have changed the zooplankton community. Furthermore, the cyanobacterium *Planktothrix rubescens* recently increased in abundance despite TP concentrations below 10 μg/L. Presently, it is unclear to what extent climate warming and/or food web alterations due to stickleback invasion of the pelagic zone are causing these new developments. Nevertheless, Lake Constance demonstrates that despite lake managers successfully combatting the eutrophication problem in this lake, the arrival of new species in the pelagic zone possibly in combination with climate change may create new food webs, which could change the ecosystem services that large lakes provide.

Failed management of eutrophication

Since the 1950s, excess nutrient concentrations of nitrogen and phosphorus have been changing the trophic state of Lake Erie's ecosystem, leading to reduced water quality and shifting environmental structures and functions within the lake ecosystem (Steffen et al., 2014; International Joint Commission, 2014). Eutrophication, climate change, and hydrologic dynamics have likely driven naturally occurring genera of cyanobacteria, including dominance by *Microcystis* spp., to multiply at a rapid rate, resulting in harmful algal blooms (HABs). In the mid-1990s, the western basin of Lake Erie, following years of improvement after point source P loading reduction (International Joint Commission, 2014), was confronted

by a shift in planktonic communities from nitrogen-fixing to non-nitrogen-fixing cyanobacteria, especially *Microcystis* species that can produce toxins (Brittain et al., 2000; Chaffin and Bridgeman, 2014; Rinta-Kanto et al., 2005). Although phosphorus has been considered the primary driver of the biological productivity of freshwater ecosystems, including harmful algae (Schindler, 2012, 1977, 1974) such as in Lake Erie (International Joint Commission, 2014), the precise nutrient regime that favors toxigenic, non-nitrogen fixing cyanobacteria is complicated and is becoming better understood (Carey et al., 2012). Indeed, it has been suggested in several studies that nitrogen chemistry may shape the biological diversity of the system (*e.g.,* Wilhelm et al., 2003). Yet the vast majority of current nutrient management is focused on the reduction of phosphorus loads into the watersheds of Lake Erie (International Joint Commission, 2014), not on nitrogen loads (United States Environmental Protection Agency, 2017, 2015), which have also increased in the past two decades (Paerl et al., 2016). As such, management measures may be inadequate in mitigating the recent events of detrimental cyanobacterial blooms of *Microcystis* (Gobler et al., 2016; Harke et al., 2016). However, more agencies now promote a dual strategy to reduce both N and P (Paerl et al., 2018) even though this imputes higher societal costs for wastewater treatment.

Success against invasive species via the use of chemical treatments, while actively seeking alternative control options

The story of sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes is the world's only example of the successful, ecosystem-scale control of an invasive aquatic vertebrate. The sea lamprey, native to the Atlantic Ocean, was first recorded in Lake Ontario in 1835 and, after improvements to the Welland Canal, spread throughout the remaining Laurentian Great Lakes by the 1920s-30s (Christie and Goddard, 2003). This species invasion was catastrophic both ecologically and economically, decimating lake trout stocks and other native species and contributing to the collapse of commercial fisheries (Siefkes et al., 2013). Sea lamprey adults are parasitic, attaching to a fish host with their suction-cup mouth, using a rasping tongue to pierce the host's flesh, and feeding on blood and other body fluids. A breakthrough was made in the 1950s, when it was discovered that a compound, 3-trifluoromethyl-4′-nitrophenol (TFM), could selectively kill sea lamprey larvae (Applegate et al., 1957). Sea lamprey larvae burrow into the soft sediments of tributaries, where they remain vulnerable to pesticide application for up to 7 years before they transform and out-migrate to the open lake to feed. The treatment of the Great Lakes' tributaries with TFM is the cornerstone of an extensive binational, science-based control program administered by the Great Lakes Fishery Commission. Sea lamprey populations have been suppressed by as much as approximately 90% compared to pre-control levels (Heinrich et al., 2003; Smith and Tibbles, 1980), resulting in the recovery of key fish populations and the restoration of the 7-billion-dollar fishery (Siefkes et al., 2013). Barriers blocking the upstream migration of spawning sea lamprey have also contributed to control, but there is increasing pressure to remove some barriers to increase connectivity for native species (McLaughlin et al., 2013). There remains a need for vigilance and the continued search for alternative or supplemental control options in order to reduce reliance on TFM and avoid sea lamprey evolving pesticide resistance (Dunlop et al., 2017, p. 2017). Also, there is a considerable economic cost to treating streams with TFM, and although many exposed aquatic species appear to be unharmed by TFM, there are potential negative effects on some valued species (*e.g.,* lake sturgeon). However, if managers stopped these treatments, then sea lamprey populations would likely rebound. The sea lamprey example highlights the success

of a science-based invasive species control program, but it is also a cautionary tale for the importance of preventing exotic species introductions in the first place to avoid costly control programs to mitigate negative effects.

Failed conservation of lake fauna

In eight southern alpine lakes (including large lakes) non-native species contributed between 4.0% and 71.5% to standardized fish catches by number (Volta et al., 2018). Eutrophication is recognized as the main driver of the decline of coregonid diversity (Vonlanthen et al., 2012). Nevertheless, inappropriate fish management practices can also have strong contribution in diversity loss (Anneville et al. 2015). For instance, fishery management practices such as stocking have also contributed to coregonid diversity loss by different mechanisms (Cucherousset and Olden, 2011), such as competition, predation, habitat modification, or genetic extinction through introgressive hybridization (Winkler et al., 2011). In Africa, the introduction of the Nile perch (*Lates niloticus*) is a major issue in Lake Victoria (Njiru et al., 2018). Introduced in the 1950s to improve the fishery, this big carnivorous fish is famous for its flesh quality. Native fish stocks, however, including several hundred endemic species belonging to the Cichlidae family (Seehausen, 2006), have become depleted as the Nile perch stock increased during the same period. The loss of species diversity is due to several factors, including: 1) eutrophication leading to extension of anoxic layers, increased turbidity, and changes in lake functioning, which contribute to degraded spawning habitat of some endemic species and shifts in food web such as increased shrimp and pelagic fish; 2) new fishing gear and intensive exploitation without regulation, causing decreased fish stocks; and 3) competition for space and resources between Nile perch and endemic fish species (Getabu et al., 2003). The combined effects of these different factors have led to the disappearance of endemic fish species over a relatively short period of time. Management interventions such as pollution regulations and invasive species prevention and control must be investigated as options to preserve fish species diversity in lakes.

An example of how management actions have so far failed to recover an iconic fish stock is the lake sturgeon in the Laurentian Great Lakes, where historical overfishing contributed to the collapse of this previously abundant species (Haxton et al., 2014). In Lake Erie, lake sturgeon is now rare, but the lake had an estimated historic carrying capacity of 23,000 metric tons (Sweka et al., 2018). The collapse of this benthivore from the littoral zone likely had profound effects on the aquatic community (Haxton et al., 2014) and impacted the many indigenous communities around the Laurentian Great Lakes for which the species holds great cultural significance. The government listing of lake sturgeon as a species-at-risk and the protection of stocks from fishing has unfortunately failed to recover the species. This is likely because of the many other factors affecting populations, such as barriers in tributaries blocking spawning migrations, anthropogenic degradation of spawning and nursery habitat, and invasive species that increase the mortality of various life stages, currently limiting the recovery of lake sturgeon (Sweka et al., 2018). However, stocking of young sturgeon has increased sturgeon populations in the Lake Ontario watershed (Jackson et al., 2002), and spawning habitat rehabilitation in the connecting channels shows promise as spawning sturgeon are attracted to these habitats (Detroit, Niagara and St Lawrence Rivers).

Failed hydrologic management in the Aral Sea

The endorheic Aral Sea, the fourth largest lake in the world, has significantly declined in volume and surface area since the 1960s due to water withdrawal from the Amu Darya and Syr Darya rivers for irrigation (Micklin, 2010; Micklin et al., 2014). The resulting strong imbalance between inflow and evaporation led to the separation of the sea into the "Small" and "Large" Aral Seas in 1986–87, with the latter splitting further into three parts (Cretaux et al., 2019, 2013). Salinity increased from 10 g/l during the initial period to 30 g/l in the Small Aral during later years and greater than 100 g/l in the Large Aral, eliminating most of the freshwater species, while many endemic saline species have also been lost due to competition with introduced marine species (Aladin and Potts, 1992). Due to the collapse of commercial fisheries (Ermakhanov et al., 2012), thousands of fishermen lost their livelihoods (Glantz, 1999). The desiccation of the Aral Sea has also created a large desert, the Aralkum (Breckle et al., 2012), exposing unfertile salt and sand contaminated with pesticides (Whish-Wilson, 2002), heavy metals (Ge et al., 2016), and residue from weapons testing (Bennett, 2016). Toxic dust emissions have negatively affected female reproduction and fertility (Gulmira et al., 2018) and infant mortality rates (>100 per thousand, caused mostly by acute respiratory and diarrheal diseases), and high levels of salts in drinking water have increased incidences of kidney and liver disease (Whish-Wilson, 2002). Long-distance transport of salt and dust (Xi and Sokolik, 2016) has caused soil salinization and acceleration of the melting rate of glaciers and snow, changing the water balance of rivers in downwind areas (Abuduwaili, 2010). Loss of the climate-moderating role of this previously large water body has increased both diurnal (Roget and Khan, 2018) and seasonal temperature ranges (Sharma et al., 2015). A dike was built in 1992 to allow the water level to be raised in the Small Aral, maintain its salinity below 20 g/L, and restore fishing activities (Aladin et al., 2008), but conflicting interests between the countries sharing the basin have so far prevented efficient efforts toward rational water management (Bennett, 2016).

Unexpected consequences of lake restoration

Europe's sixth largest lake – Lake Vättern – is another example of a lake where efficient phosphorus reduction in the 1970s through improved treatment of wastewater in the catchment area resulted in a rapid decline of algal biomass in the lake (Willén, 2001). The outcome of the reduction was, however, different in this large lake compared to other, smaller lakes. Because of a very long water retention time (58 years), the successful phosphorus reduction continued over decades, and in conjunction with a natural phosphorus concentration decline that was observed across Sweden in nutrient-poor reference lakes (Weyhenmeyer and Broberg, 2014), phosphorus concentrations in this large lake are now exceptionally low, averaging only 4.6 ± 0.3 µg L^{-1} in 1992–2010 (Sandström et al., 2014). Together with overharvesting, climate change, and introduced species, the reduced nutrient loading was suggested as the reason behind a collapse of the Arctic char in the lake. Thus, the final outcome of a successful restoration program might have contributed to a mismatch in the food web, causing the collapse of a piscivorous fish (Jonsson and Setzer, 2015).

New challenges and future threats to large lakes

Ecosystem health and ecosystem services provided by large lakes are vulnerable to emerging threats such as microplastics, micropollutants, and the cumulative effects of threats including climate change, eutrophication, over-harvesting, and invasive species. An evaluation of 50 potential stressors in the Laurentian Great Lakes suggested that invasive species and climate change had the greatest potential impacts on large lakes, in contrast to the long-standing emphasis on eutrophication and bioaccumulation of

contaminants (Smith et al., 2015). Nonetheless, eutrophication remains a major concern in specific areas of the Laurentian Great Lakes (*e.g.,* western Lake Erie. Green Bay, Saginaw Bay) as well as in many other places in the world. Here, we highlight key emerging threats and the challenges associated with cumulative effects of multiple stressors in the world's large lakes.

Eutrophication in a changing climate

Phosphorus loadings to largest lakes of the world increased in 50 out of 100 lakes between 1990 and 1994 and 2005–2010 (Fink et al., 2018). Furthermore, multiple stressors, under the lens of climate change, are an emerging challenge to freshwaters worldwide (Smith et al., 2019). Climate change may act synergistically with nutrients to amplify eutrophication and further degrade ecosystem health and related ecosystem services provided by large lakes, including provisioning of clean drinking water and recreational opportunities (Moss et al., 2011; Paerl and Huisman, 2008). With a changing climate, future nutrient loading will likely need to be reduced to lower levels than needed in the past if we are to maintain water quality in lakes.

Climate change will have substantial effects on lake ecosystems irrespective of their size. Higher temperatures will: 1) advance the onset and enhance the strength and duration of stratification, creating a higher risk of oxygen depletion in bottom waters and subsequent release of nutrients stimulating eutrophication, 2) enhance the risk of temporary or permanent stratification in polymictic lakes (even in large lakes such as Lake Taihu), and shift some lakes from dimictic to monomictic (Woolway and Merchant, 2019), creating risk for temporary or longer-term oxygen depletion and nutrient release, and 3) shift species composition, with a projected enhancement of dominance by potentially toxic cyanobacteria or dinoflagellates, and 4) promote expanding ranges of invasive species, resulting in new species introductions and enhanced impacts to aquatic food webs.

In more arid climate zones, eutrophication might be further exacerbated through reduced water levels, and in wet areas by increasing external loading of nutrients. In temperate zones, climate change–induced precipitation changes will substantially increase riverine total nitrogen loading by the end of the century, such as within the continental United States (Sinha et al., 2017, p. 201). The interactions between climate and nutrients might induce major changes in the trophic structure by shifting dominance to small omnivorous fish, leading to higher predation on zooplankton and benthic animals and subsequently less chances of controlling nuisance algae (Moss et al., 2011). Furthermore, in large lakes with extensive shipping, climate change may enhance the risk of species invasion and more importantly dominance of these invasive species.

Shoreline modification and wetland loss in the catchment

Wetland loss in catchments and shoreline modifications are likely to be an emerging threat in large lakes, particularly in areas experiencing human population growth. Although the loss of coastal wetlands in the Laurentian Great Lakes was first documented in 1982 (Whillans, 1982), there are few studies that quantify wetland loss, due to the difficulty in quantifying dynamic baseline conditions in the presence of naturally fluctuating water levels. Whillans (1982) estimated that 57% of coastal wetlands were lost along the Canadian shoreline of Lake Ontario, and losses approached 100% in heavily settled areas.

Coastal wetlands of large lakes support essential ecosystem services, including wildlife habitat, fisheries, and water quality improvement, which can all be substantially degraded as a result of wetland loss (Sierszen et al., 2012, 2019; Trebitz and Hoffman, 2015; Uzarski et al., 2017). Coastal wetlands are essential to integrating the pelagic habitats of large lakes with the surrounding landscape, and in the process provide areas of high biodiversity and nutrient cycling (Uzarski, 2009). For instance, coastal wetlands of large lakes support a diverse assemblage of fishes, including both permanent residents and migratory species (Cooper et al., 2018; Jude and Pappas, 1992; Trebitz and Hoffman, 2015).

Coastal wetland loss and shoreline modification are expected to interact with other environmental stressors in the Laurentian Great Lakes (Kovalenko et al., 2018; Smith et al., 2019). Few studies assess interactions among multiple stressors, highlighting an important research area. For example, wetland loss is expected to exacerbate nutrient loading due to reduced trapping and removal of nutrients (Smith et al., 2019). Changes in water levels as a result of climate change could exacerbate or alleviate shoreline modification because higher water levels often will result in the hardening of shorelines (i.e., wetlands loss), whereas lower water levels may allow wetlands to recover and develop between the water and hardened shoreline (Smith et al., 2019).

Microplastics

Since the start of plastics mass production in the 1940s, microplastic contamination of aquatic environments has been a growing problem, especially over the last decade. Microplastics can be ingested by organisms, accumulate in specific tissues, and be transported along the food chains. Moreover, they may act as a medium to concentrate and transfer chemicals and persistent, bioaccumulative, and toxic substances to organisms (Eerkes-Medrano et al., 2015). As these polymers are highly resistant to degradation, quantities of microplastics in aquatic environments will most likely continue to increase over time; and, consequently, microplastics represent a problem that future generations will have to face (Galloway and Lewis, 2016).

The presence of microplastics in aquatic environments is widely recognized, and various ecological consequences have been reported (Eerkes-Medrano et al., 2015; Mani et al., 2015). Rivers and effluents have been identified as major pathways for microplastics of terrestrial origin (Fischer et al., 2016; Mani et al., 2015). Recent research now shows large lakes also contain microplastic pollution, with the highest concentrations in heavily urbanized regions, such as Toronto (Canada) and Detroit (USA) (Eriksen et al., 2013). For example, Castañeda et al., (2014) found that a liter of sediment from the St. Lawrence River contained up to 1,000 spherical microplastics – on par with the world's most polluted marine sediments. Volunteer beach cleanups show that typically more than 80% of anthropogenic litter along the shorelines of large lakes is comprised of plastics (Driedger et al., 2015). Plans to combat and curtail plastic debris pollution (i.e., by reducing debris input, but also tracking and removal efforts) in large lakes will come at a significant economic cost, likely in excess of $400 million annually (Driedger et al., 2015).

Micropollutants

In the past decade, micropollutants, i.e., chemicals that occur in the environment at trace levels mostly from anthropogenic sources, including heavy metals, pesticides, pharmaceuticals, and cosmetics have become recognized as key threats for aquatic ecosystems (Blair et al., 2013; Chèvre and Gregorio, 2013; Codling et al., 2018; Metcalfe et al., 2019; Schwarzenbach et al., 2006). For example, certain synthetic and natural compounds, collectively known as endocrine-disrupting compounds, could mimic natural hormones in the endocrine systems of animals and human-beings. Pharmaceuticals and personal care products (PPCPs) consumed by humans are discharged into surface waters, as they are

not degraded by wastewater treatment plants (Kümmerer, 2008). These products have been collectively grouped under the term "Chemicals of Emerging Concern" and are receiving attention owing to their potential adverse effects on animals and humans at trace concentrations in large lakes (Huerta Buitrago et al., 2016; Rahman et al., 2009; Snyder et al., 2003). There are some natural sources for these compounds (*e.g.,* Rogers et al., 2011). While we do not have a way to clearly distinguish anthropogenic from natural sources at this juncture, it is clear that some populations favored by eutrophication and climate change (*e.g., Microcystis* spp.) produce some of these chemicals.

Micropollutants can have wide-ranging impacts on freshwater organisms, in particular because some compounds bioaccumulate along the trophic chain (Mazzoni et al., 2018; McGoldrick and Murphy, 2016; Rajeshkumar and Li, 2018; Visha et al., 2018). Micropollutants can affect the survival and behavior of aquatic species (Amiard-Triquet et al., 2015; Chèvre and Gregorio, 2013), alter the reproductive system of aquatic organisms, and promote the development of resistant bacterial strains, representing a health risk to humans (McGowan et al., 2007; Uslu, 2012). The occurrence of a combination of micropollutants is particularly concerning, even if the concentrations of the micropollutants alone are below the national or international threshold for freshwater systems; the mixture of micropollutants may synergize effects, engendering the "something from nothing" effect (Chèvre and Gregorio, 2013).

Conclusions and perspectives

The demands of a growing global population with rapidly changing consumption patterns for food, mobility, and energy are exerting ever-increasing pressure on the Earth's ecosystems and their life-supporting services (GMT 8, 2015). In combination with climate change, these changes raise concerns about the current ecological status of large lakes and the services they can provide. These changes require limnologists and paleolimnologists to evaluate and warn about the current state of ecosystems and their ability to provide ecosystem services that support humanity during its societal, technological, and demographic transitions.

Lessons learned from past management practices

Some large lakes are ecosystems that humans have employed enormous efforts over the last decades to sustain critical services such as drinking water. Some generalizations of lessons can be drawn from our synthesis on lake management, but the following conclusions are far from exhaustive:

Restoration efforts have often achieved success: Catastrophic degradation of lakes occurred in the past, such as acidification or eutrophication, but humans have achieved restoration of many of these impacted large lakes. Success in mitigating eutrophication in European large lakes or the Laurentian Great Lakes include strong examples for other countries facing a current increase in nutrient loading of their waterbodies. International treaties have been signed for many large lakes with shorelines that belong to multiple countries (see examples in Table 3).

Complete restoration to historic or pristine conditions is hard to achieve and sometimes even fails, but our examples show that the worst can be avoided. The questions are still open in terms of what can be a balanced target? And how do we help recover self-functioning for freshwater ecosystems through restoration? And who decides? While lakes can be restored to reinvigorate degraded ecosystem services, past lake degradation always has lingering implications; ecologically the systems are weakened, with increased vulnerability to new threats, and economically, these restoration and resiliency-enhancing programs require increased human capital and financial investments. Establishing systems for efficient management is expensive and is generally the privilege of wealthier countries with more stable governance institutions and greater access to capital. But the future cost of inaction is too high, perhaps especially for developing countries, and action has to be taken.

Current efforts are challenging because of the continuous arrival of new threats; Future developments may hold many ecological surprises (Filbee-Dexter et al., 2017) because of climate change, legacy of past perturbations, and combined stressors. Thus, large lakes will require more intense conservation efforts in a warmer and more anthropic world to achieve acceptable water quality. Major challenges remain to reduce pollution (diffuse nutrient inputs, but also micro-pollutants and micro-plastics). Moreover, the lack of knowledge can also limit the diagnosis of causes and therefore lead to misapplied management. It is time for humanity to pay close attention to the signals from lakes, to correctly diagnose problems, and to design actions to preserve and/or recover lake systems. Thus, the programs to restore large lakes should be maintained and strengthened.

Plans to combat and curtail emerging threats, such as plastic debris pollution in large lakes, will come at significant economic cost (Driedger et al., 2015). The large costs associated with conservation efforts are legitimate concerns by the citizens who bear those costs, and who need to understand the pertinence and sustainability of such programs. Furthermore, decisions about long-term strategies will have to be supported by future generations. As such, lake managers need to consider if these strategies can be supported in the future and at what cost, and they should be able to demonstrate the value of such costs as well as the social, cultural, economic, and ecological implications from temporary or permanent interruptions in ecosystem services due to inadequate investment in policies and programs for large lake monitoring, restoration, and protection.

Each lake has its own history of anthropogenically-induced change, requiring strategies that are tailored to its particular circumstances. For instance, point sources of nutrients were a leading cause lake degradation in more industrialized nations, causing for instance a historical degradation of oxygen conditions in Europe (Jenny et al. 2016b). Treatment plans have been reducing these nutrient supplies in many cases over the last decades, but point sources are now progressively increasing to affect the quality of the environment for various systems in developing nations, where population is growing (*e.g.* Fig. 2). On the opposite, industrialized nations are facing today high and still growing diffuse supplies of nutrient principally due to agricultural fertilisation, whereas fertilisation is still low (but growing) in developing nations.

Another example concerns lake degradation in emerging economies which is occurring in a warmer climate than similar earlier degradation in Europe and North America where management programs started decades ago; a case in point is the recent alarm about eutrophication in China, while it was already 60 years ago that eutrophication became a severe concern in Europe (Vollenweider, 1968).

Conservation policies for the world's large lakes

Large lakes are an important category of ecosystems that need to be more explicitly integrated into international as well as local policy instruments. Their global conservation in the face of ongoing change, as well as recovery of the services provided by these valuable ecosystems, requires attention to policy actions in four main categories: mitigation of multiple stressors, adaptation to change, conservation measures to protect and restore environmental values, and knowledge production and dissemination.

Mitigation policies include ongoing work to restrict the production and release of long-range contaminants such as persistent organic pollutants and increased global attention to limiting the discharge of microplastics, nanoparticles, pharmaceutical products, nutrients and other emerging pollutants into natural waterways.

Adaptation policies for sustained environmental stewardship of large lakes must consider the multiple stresses that are imposed on these ecosystems, including the arrival of new species and the overarching effects of rapid climate warming. Many regions are changing so rapidly that local policy decisions are urgently needed to address the present and near-future challenges posed by climate warming (Vincent, 2020).

Conservation areas play a key role in protecting species and ecosystems from some of the additional stresses that are superimposed on the rapidly warming climate, and policies that support their maintenance and expansion are now more important than ever (Vincent, 2018). For large lakes, such areas include regional, municipal, and national parks, ecological reserves, protected watersheds, wetland refuges, and managed riparian zones that act as buffers between human activities on land and the associated freshwaters.

Finally, the long-term stewardship of large lakes requires policies that enable knowledge acquisition and transfer, including the promotion of education, outreach, and research programs, as well as the dissemination of observations to the public, environmental managers, policy makers, and others with influence such as local conservation groups.

Contribution list

Conceived and designed the experiments: JG, OA, JPJ, JMD, MM, VP, WFV. Performed the experiments: JPJ, TN. Analyzed the data: JPJ. Coordinated the writing of the sections: OA, SJ, SS, WFV, JPJ, MM, JG, ID, IG-E, M−EP, VP, CR, DU, AJ, GAW. Wrote the paper: VP, DU, FA, CR, PN, ZJ, GK, OA, SJ, SS, WFV, JPJ, MM, NC, JG, ID, IG-E, M−EP, VP, CR, OT, DU, AJ, GW, DS, ED, GAW, SÅW, SWW. Critically revised, improved, and approved the final manuscript: All Authors. The authors declare that no competing interests exist.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2020.05.006.

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