Emerging threats and persistent conservation challenges for freshwater biodiversity

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ABSTRACT

In the 12 years since Dudgeon *et al.* (2006) reviewed major pressures on freshwater ecosystems, the biodiversity crisis in the world's lakes, reservoirs, rivers, streams and wetlands has deepened. While lakes, reservoirs and rivers cover only 2.3% of the Earth's surface, these ecosystems host at least 9.5% of the Earth's described animal species. Furthermore, using the World Wide Fund for Nature's Living Planet Index, freshwater population declines (83% between 1970 and 2014) continue to outpace contemporaneous declines in marine or terrestrial systems. The Anthropocene has brought multiple new and varied threats that disproportionately impact freshwater systems. We document 12 emerging threats to freshwater biodiversity that are either entirely new since 2006 or have since intensified: (*i*) changing climates; (*ii*) e-commerce and invasions; (*iii*) infectious diseases; (*iv*) harmful algal blooms; (*v*) expanding hydropower; (*vi*) emerging contaminants; (*vii*) engineered nanomaterials; (*viii*) microplastic pollution; (*ix*) light and noise; (*x*) freshwater salinisation; (*xi*) declining calcium; and (*xii*) cumulative stressors. Effects are evidenced for amphibians, fishes, invertebrates, microbes, plants, turtles and waterbirds, with potential for ecosystem-level changes through bottom-up and top-down processes. In our highly uncertain future, the net effects of these threats raise serious concerns for freshwater ecosystems. However, we also highlight opportunities for conservation gains as a result of novel management tools (e.g. environmental flows, environmental DNA) and specific conservation-oriented actions (e.g. dam removal, habitat protection policies, managed relocation of species) that have been met with varying levels of success. Moving forward, we advocate hybrid approaches that manage fresh waters as crucial ecosystems for human life support as well as essential hotspots of biodiversity and ecological function. Efforts to reverse global trends in freshwater degradation now depend on bridging an immense gap between the aspirations of conservation biologists and the accelerating rate of species endangerment.

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I. INTRODUCTION

It has been over a decade since Dudgeon *et al.* (2006) published their seminal review of ecological stressors responsible for global freshwater biodiversity decline. This authoritative paper has been cited over 1800 times, placing it among the top-cited 1% of papers in the field of Biology and Biochemistry (Web of Science®). Dudgeon *et al.* (2006) identified 'overexploitation', 'water pollution', 'flow modification', 'destruction or degradation of habitat' and 'invasion by exotic species' as five leading causes of population declines and range reductions of freshwater organisms worldwide. However, over the last decade, and as we advance into the epoch now being referred to as 'The Anthropocene' (Crutzen, 2006), these threats have escalated and/or evolved, and new or previously unrecognised threats have become more apparent. The current scale of biodiversity loss in fresh waters is now so rapid that we consider it an invisible tragedy – hidden beneath the water surface (Richter *et al.*, 1997) – that attracts little public, political or scientific interest (Cooke *et al.*, 2016). It is timely, therefore, to revisit the questions: which emerging threats pose the greatest challenge to freshwater biodiversity conservation, and where do opportunities for intervention exist?

This overview identifies these emerging threats and updates our knowledge of continuing challenges to freshwater conservation, paying special attention to issues that may have global, undesirable effects. The scope includes: (*i*) threats identified by expert opinion and supported by primary literature; (*ii*) threats that vary in magnitude, geographic extent and/or frequency around the world; and (*iii*) threats that are entirely novel since 2006 (see Section V.7), or previously known issues with trajectories that require renewed consideration (see Section V.9). We begin by describing the status of global freshwater biodiversity and changes identified since Dudgeon *et al.* (2006). Twelve emerging threats are discussed and exemplified using diverse taxonomic groups with examples of mitigation provided where possible. We close with a discussion of the risks and benefits of various conservation tools, finally describing areas of conservation optimism that could contribute to a 'good' Anthropocene (Bennett *et al.*, 2016) for freshwater biodiversity.

II. FRESHWATER BIODIVERSITY: A DEEPENING CRISIS

Fresh waters comprise only 0.01% of the water on Earth, with lakes, reservoirs and rivers covering approximately 2.3% (and freshwater wetlands encompassing an estimated 5.4–6.8%) of the global land surface area, excluding large ice sheets (Lehner & Döll, 2004). An initial global inventory – the Freshwater Animal Biodiversity Assessment (FABA) (Balian *et al.*, 2008) – revealed that these ecosystems host almost 9.5% of the Earth's described animal species, including one-third of vertebrates; wetland ecosystems which are highly biodiverse were not included in FABA. Despite the much greater area and total production of marine environments, the species richness of marine and freshwater fishes (Actinopterygii) is similar (14736 and 15149 species, respectively), with all saltwater species derived from a freshwater ancestor (Carrete Vega & Wiens, 2012).

Alarmingly, indicators are revealing rapid population declines and a large extinction risk in freshwater organisms. The World Wide Fund for Nature (WWF) Living Planet Index (LPI) (Collen *et al.*, 2009) disclosed that the index for populations of freshwater species fell more steeply from 1970 to 2012 than either the index for marine or terrestrial populations (see Fig. 1) (WWF, 2016). The LPI for freshwater vertebrates has declined by 81% (range 68–89%) relative to index declines of 38 and 36% for land and sea, respectively; by 2014, this value for freshwater ecosystems had risen to 83% (WWF, 2018). This represents an annualised index decline of 3.9% for monitored freshwater populations, which is close to four times greater than that of terrestrial populations (1.1%). In this analysis, all 881 freshwater species (and 3324 populations) used to calculate the LPI are vertebrates, with detectable taxonomic and biogeographic biases across the data sets available. How the reported LPI trends relate to that of broader biodiversity remains largely unknown (Collen *et al.*, 2009). Nonetheless, other data, such as the International Union for Conservation of Nature (IUCN) Red List, confirm the high proportion of threatened species among freshwater-associated vertebrates (Ricciardi & Rasmussen, 1999; Collen *et al.*, 2014). For example, almost 40% of European and North American freshwater fishes are at risk (Kottelat & Freyhof, 2007; Jelks *et al.*, 2008). Although less comprehensively recorded than vertebrates, freshwater invertebrates are also faring worse than their terrestrial counterparts (Taylor *et al.*, 2007; Clausnitzer *et al.*, 2009; Cumberlidge *et al.*, 2009).

Despite the downward trajectory of many freshwater taxa, the conservation literature is persistently biased towards terrestrial organisms, with fewer than 20% of recent papers dealing with aquatic species (Di Marco *et al.*, 2017). This is problematic for at least three reasons. First, terrestrial biodiversity indicators are a poor surrogate for fresh waters (Darwall *et al.*, 2011). Second, while some primary solutions to freshwater conservation problems depend on management at the terrestrial–freshwater interface (e.g. reduced agricultural runoff), many land-based conservation efforts for freshwater
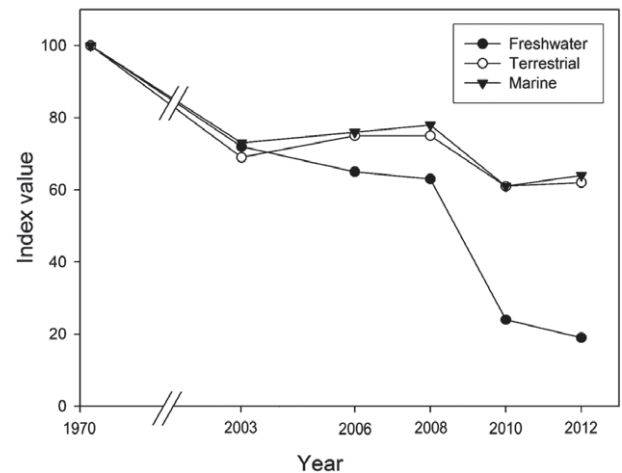

Fig. 1. The 2016 World Wide Fund for Nature (WWF) Living Planet Index (LPI) shows population trend data for a collective 'basket' of vertebrates in the freshwater (black circles), terrestrial (white circles) and marine (black triangles) realms, revealing remarkable index decreases among freshwater species. These index declines are relative to a benchmark value of 100 in 1970. Dates given here refer to years in which estimates of abundance were made, as LPI reports typically refer to data from four years earlier (e.g. the 2016 LPI is based on 2012 data). The 2012 index value of 19 for freshwater populations has confidence limits ranging from 11 to 32; the value of 62 for terrestrial populations has limits from 49 to 79; and the value of 64 for marine populations has limits from 52 to 80 (WWF, 2016).

biodiversity require implementation over large spatial extents at channel, riparian or catchment scales (Darwall *et al.*, 2011). For example, 84% of threatened freshwater megafauna ranges fall outside of existing protected areas (Carrizo *et al.*, 2017). Finally, freshwater ecosystems represent hotspots of endangerment as a result of the convergence between biological richness and the many forms of human freshwater exploitation that are not only generated by land-based actions. Projecting these issues forward suggests that freshwater extinction risks will remain high over the next few decades, regardless of actions taken now, due to an incurred 'debt' arising from low-viability populations that are in the process of dwindling to extinction (Strayer & Dudgeon, 2010). Nor will anthropogenic pressures on freshwater ecosystems ease soon, in view of the threats reviewed herein, particularly the ambitious plans for water infrastructure development globally (see Section V.5) as well as through expanding population pressure and the growing needs for domestic water use and food production (Mekonnen & Hoekstra, 2016).

III. PERSISTENT THREATS TO FRESHWATER BIODIVERSITY

Habitat degradation is a leading and persistent cause of population declines in freshwater systems (Dudgeon *et al.*, 2006; WWF, 2018). While this threat is ubiquitous as a risk

to biodiversity in nearly all biomes and freshwater ecosystem types on Earth, it is likely to be augmented or exacerbated as new threats emerge (see Section V.12). For example, while water pollution is well established in the degradation of freshwater ecosystems (Cope, 1966), the pollutants and processes involved are changing rapidly (see Section V.6). The Earth's surface under land management with high pollution risk (e.g. urban zones, cropland) is increasing as the global human population expands (Martinuzzi *et al.*, 2014).

Habitat degradation through flow modification is another persistent threat to global freshwater biodiversity (see Section V.5) (Dudgeon *et al.*, 2006). Thousands of dams are planned or under construction worldwide (Zarfl *et al.*, 2015), with little or no consideration of their ecological consequences (Winemiller *et al.*, 2016). Freshwater ecosystems are at risk of incurring one or more of the well-studied effects of dam-induced flow modification (e.g. reduced discharge, impaired fish migration, decreased river–floodplain connectivity) (Juracek, 2015). In addition, by decreasing fish abundance and biodiversity, dams pose threats to fish-based economies and the food security of individuals who rely on fishes (Orr *et al.*, 2012). They can also create or exacerbate infectious disease threats by enhancing transmission opportunities for water-related parasites (e.g. Steinmann *et al.*, 2006). Moreover, climate change is expected to alter hydroclimates and increase sea levels (see Section V.1), with potentially harmful socioeconomic and ecological effects on humans and ecosystems in coastal areas (see Section V.10).

Overexploitation of organisms for consumption (primarily fishes, certain aquatic invertebrates) is another major driver of freshwater biodiversity loss (Dudgeon *et al.*, 2006; WWF, 2018; He *et al.*, 2017), which has long been recognised (Allan *et al.*, 2005; Pikitch *et al.*, 2005) and in some areas curtailed (Buszkiewicz *et al.*, 2016). Overexploitation includes both targeted harvest and mortalities through bycatch. Although once thought to be primarily a problem of marine fisheries (Alverson *et al.*, 1994), bycatch also affects a wide range of freshwater taxa (Raby *et al.*, 2011). While the magnitude and extent of exploitation are greater in marine systems than in fresh waters (Arthington *et al.*, 2016), there are several key examples where overexploitation of freshwater fishes continues as a persistent freshwater threat (see Dudgeon *et al.*, 2006).

Other significant drivers of freshwater biodiversity decline are invasive species and disease (Dudgeon *et al.*, 2006; WWF, 2018). In a global meta-analysis of 151 publications and 733 separate cases of invasive species incursions in aquatic ecosystems from 1994 to 2014, Gallardo *et al.* (2016) documented strong negative effects on the abundances of macrophytes, zooplankton and fish. In a globalised world where people, materials and information move constantly (see Section V.2), invasive species are particularly threatening in freshwater ecosystems. They, like islands, are historically isolated but increasingly connected through human actions that facilitate invasive species dispersal and transport (Gherardi, 2007). Increasing connectivity also facilitates the

transmission of novel pathogens and disease (see Section V.3), with implications for both human well-being and wildlife conservation.

IV. FORESEEING THE FORESEEABLE

Although challenging, predicting the effects of threats to fresh waters aids the identification of gaps in knowledge and policy (Sutherland *et al.*, 2007), while fostering informed decision-making. By 'foreseeing the foreseeable', practitioners can prioritise research, plan strategically and manage risk to enable improved management and conservation of fresh waters. While there are 'emerging threats' reviews for terrestrial (e.g. Estrada *et al.*, 2017) and marine (e.g. Harvell *et al.*, 1999) systems, they are often habitat- or issue-specific (e.g. Calmon *et al.*, 2011), and we know of no such recent publication for freshwater biodiversity. This synthesis of global freshwater stressors is therefore intended to help identify emerging threats and inform prediction, management decision-making, mitigation and conservation action.

V. EMERGING THREATS

Although not exhaustive, 12 pressing and emerging threats to freshwater biodiversity have been identified by expert opinion and supporting primary literature. These threats vary in their geographic extent, severity of effects and degree of understanding (see Table 1).

(1) Changing climates

Although examples of species extinction or impairment linked clearly to climate change are still scarce (Durance & Ormerod, 2007, 2010), climate change potentially threatens ∼50% of global freshwater fish species (Darwall & Freyhof, 2015). Ecological responses to an average warming of only ∼1°C are already apparent. Of 31 ecological processes that underpin freshwater ecosystem functioning from genes to populations, 23 have been affected by climate change, including reductions in body size, shifts in distribution, changes in phenology, algal blooms and desynchronisation of interspecific interactions (Scheffers *et al.*, 2016).

Persistent freshwater threats from climate change include increasing water temperatures, altered discharge and interactions between these and other stressors (see Section V.12) (Ficke, Myrick & Hansen, 2007; Heino, Virkkala & Toivonen, 2009; IPCC, 2014). Rising freshwater temperatures can alter species distribution (Parmesan, 2006), disease outbreaks (Hermoso, 2017), phenology (Krabbenhoft, Platania & Turner, 2014) and survival (Bassar *et al.*, 2016). Changing flow regimes are geographically variable, but variations in annual precipitation, storm events, floods and droughts are predicted to intensify in northern

Table 1. Characteristics of emerging threats to freshwater biodiversity: their geographical extent (and focal regions); the severity of their effects; examples of attendant ecological changes; our degree of understanding; and potential options for mitigating threat effects. For threat severity, categories are severe (red), moderate (yellow) or unclear (grey) and are based on links to freshwater species extinctions demonstrated in the literature. Degrees of understanding include poor (red), fair (yellow) or good (green) and are based on identified knowledge gaps and existing research challenges or unknowns. Relevant references are presented in the corresponding threat sections (see Section V.).

Emerging Threat	Geographic extent	Severity of effects	Ecological changes	Degree of understanding	Mitigation options
(1) Changing climates	Global	Already causing extinctions; likely to cause more.	Alters species size, range, phenology and survival.	Moderately well understood but high unpredictability.	Global commitments; expand protected areas; restore thermal refugia.
(2) E-commerce & invasions	Global *(primarily developed markets)*	Significant role in trade of non-native plants and animals.	Creates novel modes of long-distance dispersal.	Largely unregulated activities that are poorly understood.	Online consumer accountability tools; awareness campaigns.
(3) Infectious diseases	Global *(especially tropical systems)*	Already causing extinctions; likely to cause more.	Alters species survival, with clear ecosystem effects.	Increasingly well understood but high unpredictability.	Improve surveillance; management to favour ecosystem controls.
(4) Harmful algal blooms	Global *(warm, nutrient-rich areas)*	Linked to species losses; likely to cause more.	Reduces species growth, survival and reproduction.	Increasingly well understood, some unpredictability.	Improve surveillance; management to favour ecosystem controls.
(5) Expanding hydropower	Global *(primarily emerging markets)*	Already causing extinctions; likely to cause more.	Fragments river systems, inhibiting species movement.	Well understood, but interactive stressor effects unclear.	Ameliorate passage infrastructure; assess all project impacts.
(6) Emerging contaminants	Global *(primarily developed markets)*	Unclear how biodiversity will be changed.	Alters some species health, abundance and reproduction.	Largely understudied and thus poorly understood.	Improve medication disposal; advance wastewater treatment.
(7) Engineered nanomaterials	Global *(primarily developed markets)*	Unclear how biodiversity will be changed.	Causes minimal acute toxicity in some species.	Considerable uncertainty around long-term effects.	Improve detection and characterization; create targeted formulations.
(8) Microplastic pollution	Global *(primarily developed markets)*	Unclear how biodiversity will be changed.	Potentially detrimental effects on species health.	Considerable uncertainty around long-term effects.	Reduce plastic usage; enact legislation to curb use of specific products.
(9) Light & noise	Global *(primarily developed markets)*	Linked to species disturbance; likely to continue.	Alters behaviour and physiology of some species.	Well understood, but ecosystem-level effects unclear.	Identify less harmful types; reduce usage; educate users.
(10) Freshwater salinisation	Coastal lowlands	Linked to species losses; likely to cause more.	Reduces species growth, survival and reproduction.	Increasingly well studied and understood.	Control point sources; strategic release of freshening flow.
(11) Declining calcium	Softwater lakes	Linked to species declines; likely affecting foodwebs.	Causes shifts in lake invertebrate assemblages.	Increasingly well understood, but solutions unevaluated.	Further reduce acidic precipitation; replenish calcium in watersheds.
(12) Cumulative stressors	Global	Contributing to extinctions; likely to cause more.	Can magnify impacts and create ecological surprises.	Poorly understood with high levels of unpredictability.	Identify multi-purpose solutions that protect biodiversity hotspots.

Europe, endangering molluscs and other species (Hastie *et al.*, 2003), while in more arid regions such as Australia, rainfall and river flows are anticipated to decrease, threatening waterbirds and other species (Pittock, Hansen & Abell, 2008).

Extreme events are anticipated to become more prevalent (IPCC, 2014), with rates of change and unpredictability exceeding what can be accommodated by species' evolution (Brook, Sodhi & Bradshaw, 2008; Loarie *et al.*, 2009). As well as warming, rapid decreases in water temperature (termed 'cold shock') might also occur in some locations. For example, a 2010 cold shock event in Bolivia caused mass mortality of fishes in the Amazon (Szekeres *et al.*, 2016). Already, over half of the world's rivers are characterised by periodic drying events, but increased frequency and intensity of droughts (Milly *et al.*, 2002) will see many perennial rivers transition to intermittent rivers (Datry, Fritz & Leigh, 2016). Physical and chemical properties of fresh water are also changing, for example the timing of ice formation and break-up are shifting on a global scale (Magnuson *et al.*, 2000). Changes in lake stratification are likely to magnify hypolimnetic hypoxia and affect lake productivity (Kraemer *et al.*, 2015), restricting pelagic habitat availability for many species (Ficke *et al.*, 2007). Increasing water temperatures and CO_2 concentrations are expected to favour cyanobacteria over eukaryotic algae, making it imperative to limit nutrient inputs to mitigate harmful blooms (Visser *et al.*, 2016) (see Section V.4).

Climate change is further anticipated to amplify many of the emerging concerns identified herein [e.g. invasive species (Rahel & Olden, 2008), pathogens (Marcogliese, 2008), eutrophication (Elliott, 2012), hydropower (Knouft & Ficklin, 2017), salinity (Henman & Poulter, 2008), although in some cases it could function to mitigate certain threats]. In anticipation of shifting precipitation and temperature, humans are further altering flow regimes by constructing dams and 'hard' engineering projects to protect against floods, increase water storage and enhance irrigation capacity (Palmer *et al.*, 2008). Global government commitments to reduce greenhouse gas (GHG) emissions (that would build on the 2015 Paris agreement), expand freshwater protected areas (Pittock *et al.*, 2008) and restore habitats to provide refugia for thermal adaptation (Heino *et al.*, 2009) are critical to mitigate the effects of climate change on freshwater biodiversity.

(2) E-commerce and invasions

Invasive species are a primary threat to freshwater biodiversity, and modes of species introductions may develop further in the future (Rahel & Olden, 2008). Global trade and the associated movement of live organisms are long-standing primary pathways for biological invasions (Levine & D'Antonio, 2003; Perrings *et al.*, 2005), but developing vectors (transportation mechanisms) and trade routes (geographic paths between source and recipient regions) pose an emerging conservation challenge. Specifically, the recent surge in global electronic commerce (e-commerce) linked to Internet sales of novel invasive species (e.g. Walters *et al.*,

2006; Humair *et al.*, 2015) may be expanding potential links among established and emerging trade partners, concomitant with changes in societal attitudes towards unusual pets (Prokop & Randler, 2018) and non-native species (Humair, Kueffer & Siegrist, 2014). Large and small 'brick and mortar' stores traditionally played a significant role in the pet, aquarium and horticulture trade (Reichard & White, 2001; Padilla & Williams, 2004), often culminating in pet owners releasing unwanted organisms into natural waterbodies (Gertzen, Familiar & Leung, 2008). Interestingly, some of the most popular fish sold are also the most likely to become established in the wild (Duggan, Rixon & MacIsaac, 2006). Individual hobbyists, collectors and breeders can now easily participate in an Internet species market (Tissot *et al.*, 2010). These largely unregulated activities challenge current management, policy and educational strategies aiming to address live-trade pathways (Strecker, Campbell & Olden, 2011).

Recent evaluations have highlighted the significant role of e-commence in the trade of non-native plants and animals. Aquatic weeds are sold internationally through the Internet in several regions (Kay & Hoyle, 2001; Walters *et al.*, 2006; Martin & Coetzee, 2011), and more invasive than non-invasive plant species are available on major online auction websites (Humair *et al.*, 2015). Broad overviews identify e-commerce as a significant contributor to national-level biosecurity risk (e.g. Parrott & Roy, 2009; Derraik & Phillips, 2010). In large Brazilian cities such as São Paulo and Rio de Janeiro, non-native fishes from the Amazon, Australia, Southeast Asia and Africa are sold without apparent restrictions (Magalhães, 2015). Global environmental change may also intensify and shift the geographic routes of e-commerce trade. Bradley *et al.* (2012) demonstrated how climate change and water restrictions may increase demand for horticultural species adapted to warm and dry environments. The net result is the creation of novel modes of long-distance dispersal (Lenda *et al.*, 2014).

Managing e-commerce risks is challenging. The array of mechanisms for making transactions is diverse, including standard retail websites, auction sites, local businesses, wanted ads, online portals and chat fora (NISC, 2012). Social media is further complicating the landscape, particularly through informal retail (Magalhães *et al.*, 2017). Web crawlers have been used to monitor the Internet for the sale of illegal animals and plants (Sonricker Hansen *et al.*, 2012); similarly, enforcement authorities could use Internet tools such as machine-learning algorithms to identify sellers of prohibited invasive species (Di Minin *et al.*, 2018). Other tools focusing on accountability may seek to educate buyers, for example with online warning labels or pop-ups when an invasive species is about to be purchased. Increasing outreach and education to enhance buyer and seller awareness of invasive species remains paramount.

(3) Infectious diseases

Fresh waters are often transmission foci for human and wildlife pathogens (Johnson & Paull, 2011; Okamura & Feist, 2011). Because of the importance of water to the

survival of most life forms, freshwater ecosystems often function as reliable yet concentrated hotspots of multi-species interactions. The aquatic medium also facilitates the survival of many parasitic infectious stages (by preventing desiccation) as well as their likelihood of contact with potential hosts, either directly or indirectly *via* ingestion. The biphasic life cycles of some freshwater taxa (e.g. aquatic insects, amphibians) also link infections across ecotones. As a result, many microparasites (e.g. viruses, fungi, protozoans, bacteria) and macroparasites (e.g. flukes, roundworms, tapeworms, arthropods) depend on freshwater hosts for transmission (Marcogliese, 2008; Johnson & Paull, 2011). Many new infectious diseases are themselves invasive species, and some are transmitted by non-native taxa.

In some cases, infections can dramatically affect freshwater biodiversity. Introduced diseases (e.g. crayfish plague and salmonid whirling disease), for instance, have devastated native taxa (e.g. European crayfish and North American salmonids, respectively) (Hoffman, 1990; Holdich & Reeve, 1991). The global spread of chytridiomycosis caused by the fungal pathogen *Batrachochytrium dendrobatidis* (Bd) has been linked to the extirpation or extinction of 200 species of frogs and toads (Rödder *et al.*, 2009). A second, recently discovered invasive chytrid (*B. salamandrivorans*) is expected to be similarly problematic for salamander species in Europe and North America (Feldmeier *et al.*, 2016). Collectively, these epizootics have significant community- and ecosystem-level effects. As examples, crayfish plague indirectly enhanced macrophyte and mollusc populations (Alderman *et al.*, 1984), whirling disease caused diet shifts in bears and birds (Koel *et al.*, 2005), and Bd altered algal growth and nutrient cycling in tropical streams (Whiles *et al.*, 2013).

The relative importance of infectious diseases in threatening freshwater biodiversity, however, remains incompletely understood (Daszak, Cunningham & Hyatt, 2000). Johnson & Paull (2011) presented evidence of increased incidence of water-related disease in amphibians, freshwater fishes and crayfishes over the preceding 40 years (1970–2009). For amphibians, there was a more than fourfold increase in disease-related research and reports on Bd, ranavirus and infection by flukes, with ranaviral infections also linked to turtle die-offs (Johnson *et al.*, 2008). Fishes had the highest volume of research and broadest pathogen diversity; viral infections such as viral haemorrhagic septicemia and infectious salmon anemia have spread from marine environments and aquaculture, respectively (Murray, Smith & Stagg, 2002). Emerging diseases, such as proliferative kidney disease (PKD), reflect warmer temperatures (Okamura *et al.*, 2011), and in 2016, PKD caused a die-off of 10000 fish in the Yellowstone River following an unusual warming event. For crayfishes, white spot syndrome and porcelain disease have caused population-level declines, often in association with aquaculture, alongside the ongoing effects of crayfish plague (Edgerton *et al.*, 2004).

Disease monitoring often requires information on more than just parasite presence or abundance. Many reports of emerging freshwater infections are linked to at least one of invasive species, aquaculture intensification, nutrient and pollutant runoff or changing food-web structure (Daszak *et al.*, 2000; Johnson & Paull, 2011). Policy changes and improved surveillance have been advocated to decrease the likelihood of pathogen introduction and maximise opportunities for control – with considerable potential to inform human disease management (e.g. malaria, schistosomiasis, giardiasis, West Nile fever) (Steinmann *et al.*, 2006). Where infections involve both wildlife and human hosts, or have parallels in transmission control, freshwater management to limit eutrophication, maintain higher trophic levels (e.g. predators) and prevent invasive species could help regulate infections across a range of host taxa.

(4) Harmful algal blooms

Freshwater algae occupy a pivotal trophic position, providing energy and nutrients to connected aquatic food webs. Periodically, and arguably more frequently, algal species are selected by environmental (bottom-up) or ecological (top-down) forces allowing for the accumulation of biomass. These conditions of accumulated biomass of algal species are termed harmful algal blooms (HABs). Often viewed as physiologically simple organisms, investigation into the formation of HABs (D'Alelio *et al.*, 2016) reveals that these organisms can occupy a plethora of niches, and these niches are open to native species that are in low concentrations in natural waters as well as to invasive species, with both contributing to HABs.

Global changes have increased opportunities for algal species to become ecologically prevalent, contributing to the recent upsurge in HABs, and include climate warming (Elliott, 2012; Huisman *et al.*, 2018), hydrological intensification (where dry areas become drier and wet areas become wetter, with increased frequency of intense precipitation events even in areas where precipitation decreases) (Huntington, 2006; Trenberth, 2011), eutrophication (Downing, 2014) and brownification (Kritzberg & Ekström, 2012). These physical changes in surface waters (e.g. elevated and constant temperatures) enhance the growth of potentially harmful algae (Paerl & Huisman, 2009), and provide the water column stratification required for photosynthetic prokaryotes to dominate and express toxicity (Burford *et al.*, 2016). Furthermore, chemical changes in surface waters can select for species able to exploit the altered inorganic–organic matrices of iron and phosphorus (Kritzberg & Ekström, 2012), significantly affecting the speciation of dominant algae, the distribution of primary producer dominance (pelagic *versus* benthic) and overall water quality through the production and release of select toxins (e.g. microcystins) (Ekvall *et al.*, 2013). The cumulative effects of these global changes result in greater complexity and uncertainty in our ability to predict the magnitude, frequency and duration of HAB events.

Once established, HABs threaten freshwater biodiversity. Some result in fish kills – either indirectly by reducing dissolved oxygen availability, or directly through toxin

production. The bloom species create adverse physiological conditions for their competitors, altering energy or nutrient fluxes through food webs as they produce allelopathic or toxic compounds that reduce growth, survival and reproduction in other organisms or contaminate food webs. For example, the trophic transfer of cyanotoxins, the best studied group of freshwater toxins, into secondary and tertiary consumers leads to physiological and behavioural impairments (Ferrão-Filho & Kozlowsky-Suzuki, 2011). Humans can also be exposed to cyanotoxins through inhalation of aerosolised toxins, ingestion of lake water or consumption of fish (Caller et al., 2009). One environmental toxin that has gained considerable attention is the amino acid β-N-methylamino-L-alanine (BMAA) (Brand et al., 2010; Merel et al., 2013). BMAA is a neurotoxin that has been identified as an emerging compound of concern because of its putative role in neurodegenerative illnesses (e.g. amyotrophic lateral sclerosis and Alzheimer's disease) (Banack et al., 2015). BMAA biosynthesis is thought to be a ubiquitous trait shared among most genera of cyanobacteria (Cox et al., 2005) and can accumulate in aquatic food webs plagued by cyanoHABs (Brand et al., 2010; Jiao et al., 2014). Despite these findings, the lack of a universal protocol for quantifying BMAA and ambiguity surrounding the production of BMAA by cyanobacteria creates great uncertainty surrounding this topic (Faassen, 2014).

Surveillance is needed to monitor the incidence of HAB-associated illnesses (Backer et al., 2015). Coordinated national and international research agendas must develop effective HAB policies and management systems (Creed et al., 2016). Preventative measures include one or more of the following: reducing or removing external nutrient loads (Paerl, Hall & Calandrino, 2011); aerating lake sediments (Prepas et al., 1997); or chemically treating lake sediments to suppress internal nutrient recycling (Molot et al., 2014). Mitigation measures include chemical controls (e.g. algicides or flocculants), physical controls (e.g. increasing flows to reduce water residence time and remove cyanobacteria) and biological controls (e.g. introducing organisms that consume HAB species) (Rastogi, Madamwar & Incharoensakdi, 2015). Ultimately, managing HAB risks requires comprehensive analyses of the effectiveness and compliance of the entire management system, including hard controls that prevent pressures and impacts, as well as soft controls that enable, facilitate or track the effectiveness of hard controls.

(5) Expanding hydropower

Almost half (48%) of global river volume is altered by flow regulation and/or fragmentation (Grill et al., 2015). There are currently 3700 major hydropower dams either planned or under construction, mostly in countries with emerging economies (Zarfl et al., 2015; Winemiller et al., 2016). Completion would cause 93% of all river volume to be affected by flow regulation and/or fragmentation (Grill et al., 2015), adding to the accumulating effects of existing dams on discharge, temperature, solutes, sediment transport and fish migration (Reidy Liermann et al., 2012; Pelicice,

Pompeu & Agostinho, 2015). Hydropower dam construction endangers freshwater biodiversity as dams modify natural flow and thermal regimes and decrease river–floodplain connectivity, aquatic productivity and fish access to spawning and nursery habitats (Freeman, Pringle & Jackson, 2007; Juracek, 2015). Even when hydropower projects involve fish passage structures to promote movement through dams, such structures may be ineffective (Pompeu, Agostinho & Pelicice, 2012) or even function as ecological traps (Pelicice & Agostinho, 2008). Despite evolving viewpoints regarding the sustainability of large hydropower plants (LHPs), there has been a major increase in support for the widespread development of small hydropower plants (SHPs). Tens-of-thousands of SHPs are operating or are under construction (11 SHPs for every LHP) and this number is estimated to triple if all potential generation capacity were to be developed (Couto & Olden, 2018). Fuelled by considerable political and economic incentives in recent decades, the growth of SHPs has greatly outpaced available ecological science.

A major related concern is reservoir aging. Sediment imbalances associated with dam operation and tributary inputs cause reservoirs to 'age' through sedimentation, shoreline erosion, and channel degradation after time periods (e.g. 50 years) that vary regionally (Juracek, 2015). Sedimentation fragments aquatic habitats, impairs fish health and survival, decreases fish production, lowers primary production and reduces storage capacity. Altered waterfront access impairs the ability of reservoirs to support other human needs (e.g. flood control, water supply, navigation) (Chapman et al., 2014; Juracek, 2015). Many large-river impoundments are reaching 50+ years of age as they were built in the mid-twentieth century when political and economic conditions favoured dam construction (Avakyan & Iakovleva, 1998).

Fish harvest and food security of river-dependent peoples may also be impaired by hydropower, including proposed projects in large river systems such as the Amazon (Winemiller et al., 2016) and Mekong (Orr et al., 2012; Ziv et al., 2012) – basins with high fish biodiversity that historically had limited hydropower. In the Amazon, where there are now 154 large hydropower dams, completion of all 277 proposed dams would leave only three free-flowing tributaries and thereby threaten fish biodiversity, fish-based economies and food security (Pelicice et al., 2015). The lower Mekong, the world's largest inland capture fishery, is likewise jeopardised by dam construction along the river's mainstem (Ziv et al., 2012; Winemiller et al., 2016). In addition, flooding lands to create reservoirs increases the methylation of mercury and its transfer to fish, also affecting food security for communities (Bodaly et al., 2007). Reservoirs, particularly in the tropics and subtropics, are major sources of GHG emissions (Deemer et al., 2016) – hydropower offers a renewable but not climate-neutral energy source.

Shifting the food security of rural inhabitants from aquatic protein to land-based, livestock-derived protein presents considerable socioeconomic challenges, including

the need for additional land and water for livestock operations (Orr *et al.*, 2012). Potential interactions between hydropower development and other freshwater stressors (e.g. climatic changes, land cover alterations) (Hermoso, 2017), and associated effects on ecosystems and human populations, remain unclear. At present, hydropower projects are generally assessed on a site-specific basis that does not account for such interactions or potential environmental–socioeconomic tradeoffs (Orr *et al.*, 2012; Winemiller *et al.*, 2016). There is thus a need for comprehensive hydropower assessments that synthesise multiple potential impacts.

(6) Emerging contaminants

Surface waters receive pollution from point-source discharges such as mining, agriculture and aquaculture, pulp and paper production, oil and gas production, and urban runoff. Each of these can impair freshwater biodiversity indirectly through impacts on habitat or through direct toxicity. However, because of environmental treaties such as the Stockholm Convention (2001), the global production and use of chemicals have shifted from persistent, bioaccumulative and toxic compounds, such as the insecticide dichlorodiphenyltrichloroethane (DDT), to pesticides and industrial chemicals with shorter environmental residence times and lower toxicities. In addition, with improved wastewater treatment across sectors (e.g. municipal effluents) (Holeton, Chambers & Grace, 2011), the focus in developed countries is less on addressing acute toxicity (e.g. ammonia) and more on assessing and mitigating longer-term effects from both older legacy and emerging contaminants. The latter is a broad, all-encompassing term that covers both newer substances or known contaminants for which there are newer concerns and includes, but is not limited to, active pharmaceutical ingredients, illicit drugs, personal-care-product additives, newer pesticides, endocrine disrupters, nanomaterials (see Section V.7) and microplastics (see Section V.8); all have garnered widespread attention because of their unexpected or unknown biological activity and/or stability (or pseudo-persistence) in aquatic environments. As an example, surveys of wastewater-impacted rivers show the global presence of pharmaceuticals such as antibiotics, antivirals and antidepressants, with antibiotics being the most frequently detected (Hughes, Kay & Brown, 2013). Yet, the effects of these individual compounds and their mixtures on aquatic populations and communities, as well as ecosystem function, remain understudied.

The endocrine-disrupting chemicals and, more specifically, the oestrogen mimics are relatively well understood with respect to their impacts on some aquatic species (Sumpter & Jobling, 2013). Across taxa, fishes are most susceptible to the natural and synthetic hormones present in municipal effluents, with effects ranging from the production of vitellogenin and development of intersex in males (Jobling *et al.*, 2002) to reduced abundances (Kidd *et al.*, 2007). More recently, individual-level effects – specifically intersex – have been linked to transgenerational effects in offspring (Schwindt *et al.*, 2014), reduced fitness (Harris *et al.*, 2011) and potential declines in genetic diversity (Hamilton *et al.*, 2016). Although these chemicals are of low risk for lower-trophic-level taxa, there is the potential for food-web-mediated effects on primary consumers through reduced predation pressure following declines in fish abundance (Kidd *et al.*, 2014). The attendant risks to ecosystems are not yet clear.

Antimicrobial compounds, including antibiotics and personal-care-product additives, are found in municipal wastewaters and agricultural runoff. It is not surprising that chemicals designed to kill microorganisms in humans would also affect natural microbial communities (Barra Caracciolo, Topp & Grenni, 2015). It was unexpected, however, that these contaminants (e.g. triclosan) could affect algal diversity and periphyton, as well as some primary consumers (Nietch *et al.*, 2013). More recent studies reveal effects of other emerging contaminants (e.g. anti-inflammatories, antidepressants) on algal communities (Bácsi *et al.*, 2016; Richmond *et al.*, 2016). In addition to affecting species abundance and composition, antimicrobial compounds could also affect aquatic ecosystem function (Nietch *et al.*, 2013), but downstream biodiversity implications are speculative.

Potential mitigation of emerging contaminants includes advanced treatment of municipal wastewaters and source reductions. Although outfall concentrations are sometimes reduced (e.g. acetaminophen, oestrogens) by more advanced treatment processes – and with subsequent benefits downstream (Hicks *et al.*, 2017) – some emerging contaminants (carbazepine, triclosan and diclofenac) are more recalcitrant and require the development of novel interventions (e.g. Bean *et al.*, 2016). Source reductions are effective and necessary for some emerging contaminants given the lack of treatment options, and gains are being made (e.g. reducing use of antibiotics in livestock production and microbeads in cosmetics in some jurisdictions). Reductions in human pharmaceutical usage are unlikely, but downstream gains and better protection of biodiversity could occur through both improved disposal of unused medications and advanced wastewater treatment.

(7) Engineered nanomaterials

Engineered nanomaterials (ENMs) are manufactured materials (size range 1–100 nm) used in a multitude of industrial, clinical and consumer applications (Stone *et al.*, 2010). ENMs have exceptionally high surface area to volume ratios and often exhibit unique physical and chemical properties compared to conventional materials. While these characteristics make them desirable in a multitude of applications (Lee, Mahendra & Alvarez, 2010; Tong *et al.*, 2014), they can also make ENM bioactivity difficult to predict. Large quantities are finding their way into fresh waters, but analytical limitations (von der Kammer *et al.*, 2012) mean that current burden estimates are based primarily on models (Gottschalk, Sun & Nowack, 2013;

Sun *et al.*, 2014; Dale *et al.*, 2015). In rivers, predicted concentrations for common ENMs are in the ng/l range (or lower), with some formulations possibly reaching μg/l (Gottschalk *et al.*, 2013). Many formulations are prone to aggregation and precipitation in natural waters, meaning that epifaunal and infaunal organisms will be exposed to ENM concentrations orders of magnitude higher than pelagic species in the same system (Selck *et al.*, 2016). Specific estimates of freshwater sediment concentrations are unavailable, but for surface waters in general they are likely in the μg/kg range and will increase with continued growth of the nanotechnology industry (Gottschalk *et al.*, 2013).

Predicted environmental burdens are generally well below toxicity thresholds for common ENMs (Coll *et al.*, 2016), but data on pelagic species are over-represented, so the overall risk may be considerably higher (Selck *et al.*, 2016). It is not uncommon to observe minimal acute toxicity of pristine (i.e. as manufactured) ENMs in freshwater fish and crustaceans at realistic exposure concentrations, but sensitivity can vary by orders of magnitude across species and life stages (Callaghan & MacCormack, 2017). With size as the primary classifier, ENMs can be composed of a variety of organic, inorganic or composite materials, so generalisations about their global safety for freshwater organisms is difficult (Coll *et al.*, 2016).

Core materials are often 'functionalised' with surface coatings to suit specific applications, and changing this coating can increase ENM bioavailability and/or bioactivity by orders of magnitude (Osborne *et al.*, 2013). Many emerging nanotechnology industries are exploiting this 'tunability' to create next-generation products with the potential for significant effects on fresh waters. Nano-pharmaceuticals are an area of intense growth, and the introduction of ENM-enabled drugs or drug-delivery systems into fresh waters warrants careful consideration (Berkner, Schwirn & Voelker, 2016). Agricultural applications, including fertilisers, herbicides and pesticides (Wang *et al.*, 2016), are also a concern. While improvements in targeting and efficacy over conventional chemicals could greatly reduce the total mass of product applied, the increased potency and unique ENM-related properties of these products may introduce new problems once they eventually reach fresh waters. For example, formulations specifically designed to carry bioactive agents may enhance the availability and toxicity of existing environmental contaminants by acting as a 'Trojan horse' (Boncel *et al.*, 2015).

A major barrier to understanding the risks of emerging ENMs is the lack of sufficient detection and characterisation technologies (von der Kammer *et al.*, 2012; Coll *et al.*, 2016). Current models require more detailed inputs to estimate ENM burdens accurately and to predict risks to freshwater ecosystems. Variations in ENM structure (e.g. similar core materials with different coatings) and key parameters like water chemistry, ENM weathering, dissolution and aggregation kinetics can greatly impact particle fate and bioactivity (Peijnenburg *et al.*, 2015) and are not accounted for in current models. Most available bioactivity data again derive from acute studies on pelagic species, and there is still considerable uncertainty about long-term risks from even the most common ENMs (e.g. titanium dioxide, zinc oxide, silver). The additional variability in reported sensitivity ranges and the absence of trends in toxicity mechanisms across taxa (Gottschalk *et al.*, 2013) underscores the need for caution when developing strategies for managing the use and disposal of novel ENMs.

(8) Microplastic pollution

Globally, annual plastic production has reached over 400 million tons (Geyer, Jambeck & Law, 2017) for products designed to be inexpensive and disposable. Rather than biodegrading, plastics are broken down by mechanical forces and ultraviolet (UV) radiation into smaller fragments (Barnes *et al.*, 2009) called 'microplastics' (plastic particles <5 mm). Microplastics include microbeads (particles added to cosmetics), nurdles (small pellets used to produce other plastics), fragments (portions of larger pieces) and microfibres (from synthetic clothing) (Browne *et al.*, 2011). In marine environments, microplastics have negative environmental impacts, such as concentrating contaminants (Rios, Moore & Jones, 2007) and ingestion by animals, which reduces fitness and increases mortality (Sigler, 2014; Provencher, Bond & Mallory, 2015). Although data on freshwater microplastic concentrations are limited, microplastic pollution in freshwater ecosystems is now being reported (reviewed in Eerkes-Medrano, Thompson & Aldridge, 2015), including the Laurentian Great Lakes (Eriksen *et al.*, 2013), the St. Lawrence (Castañeda *et al.*, 2014), the Danube (Lechner *et al.*, 2014) and other river systems that form a plastic conduit between land and sea. In some years, microplastic concentrations in the Danube River can outnumber planktonic larval fish concentrations (Lechner *et al.*, 2014). Microplastic pollutants vary among freshwater systems, but microfibres often comprise >75% of the plastic debris (Ballent *et al.*, 2016; Vermaire *et al.*, 2017). Derived from washing synthetic clothing (Browne *et al.*, 2011), the release of these microfibres is difficult to control in existing municipal wastewater treatment but filters on washing machines may be an option. Microplastics are also deposited in aquatic sediments and benthic habitats (Castañeda *et al.*, 2014; Ballent *et al.*, 2016; Vermaire *et al.*, 2017), exposing benthic organisms.

Microplastics are ingested by freshwater organisms including birds (Holland, Mallory & Shutler, 2016), fishes (Campbell, Williamson & Hall, 2017) and invertebrates (Windsor *et al.*, 2019) and extrapolation from marine findings would suggest emerging risks to freshwater organisms (Sigler, 2014; Provencher *et al.*, 2015). Better management of microplastic pollution in fresh waters requires a clearer understanding of: (*i*) sources, sinks and fluxes; (*ii*) factors controlling spatio-temporal variations in microplastic concentrations; (*iii*) data on co-transported contaminants; and (*iv*) routes of uptake and effects on freshwater organisms (Wagner *et al.*, 2014). Legislation to control microbeads has been implemented in several countries (United States: Microbead-Free Waters Act, 2015; Canada: Microbeads in

Toiletries Regulations, 2016), but these typically represent only a small fraction of the total plastic pollution (Ballent *et al.*, 2016; Vermaire *et al.*, 2017). As plastic production and consumption increase without better control, plastic concentrations in fresh waters are likely to rise. Improved understanding of their fate and impact is therefore a priority. In sum, the science supporting mitigation of emerging contaminants such as microplastics and ENMs lags behind that of the pharmaceuticals and personal-care products. Further research is required on what impacts, if any, these materials are having on freshwater ecosystems.

(9) Light and noise

Contemporary civilisation relies on electricity and combustion engines – often sources of light (Longcore & Rich, 2004) and noise (Kight & Swaddle, 2011). Although well documented in terrestrial systems, most aquatic research has been marine-focused with relatively little effort in fresh waters even though lit road networks, urban development and industrial infrastructure are frequently co-located along rivers and lakes (Gaston *et al.*, 2014).

Light pollution is increasingly regarded as an insidious stressor for freshwater biodiversity (Hölker *et al.*, 2010). Early studies revealed that artificial light alters the diel vertical migration of the zooplankter *Daphnia* (Moore *et al.*, 2000), potentially altering their interactions with fish. Recently, Hölker *et al.* (2015) revealed that even microbial communities can be affected by artificial light at night (ALAN), potentially transforming freshwater systems into nocturnal carbon sinks. Light also alters the behaviour of organisms often closely attuned to circadian cycles and, for example, ALAN can mediate interactions between invasive signal crayfish (*Pacifastacus leniusculus*) and native species (J. Thomas *et al.*, 2016a). For fish, Foster *et al.* (2016) revealed how light pollution increased energy expenditure of nesting smallmouth bass (*Micropterus dolomieu*) during the parental-care period. Street lighting also delays dispersal in juvenile Atlantic salmon (*Salmo salar*), and this effect increased with lighting intensity (Riley *et al.*, 2013, 2015). While most research has focused on individuals, the potential for system-level changes is clear given the importance of light as a cue to processes such as invertebrate drift and feeding by drift-feeding fishes.

The effects of noise in fresh water were first revealed for waterbirds disturbed by aircraft and boats (Ortega, 2012), but Zhang *et al.* (2013) subsequently showed that noise from trucks disturbed endangered black-faced spoonbills (*Platalea minor*) in the Pearl River wetlands of China. Motorboat noise can reduce the extent of basking among freshwater turtles (Jain-Schlaepfer *et al.*, 2017), lowering body temperature and influencing energy assimilation. Traffic and aircraft noise have also affected anurans (Tennessen, Parks & Langkilde, 2014), for example, impeding the ability of frogs to communicate (e.g. changing the spectral frequency used and frequency of calling) during breeding (Kruger & Du Preez, 2016). Interestingly, Bleach *et al.* (2015) revealed that noise generated by invasive cane toads (*Rhinella marina*) impeded

the calling behaviour of native Australian frogs. Recent research revealed that boat noise elevates the stress hormone cortisol (Wysocki, Dittami & Ladich, 2006) and increases metabolic expenditure (Graham & Cooke, 2008) while reducing foraging performance (Purser & Radford, 2011) and antipredator behaviours (Simpson, Purser & Radford, 2015) in freshwater fish. How these disturbances scale up to ecosystem-level effects is unknown, although noise can alter how sediment-dwelling invertebrates affect ecosystem properties (Solan *et al.*, 2016).

For future management, we suggest that there may be opportunities to identify specific light types, lighting regimes or spectra that are less deleterious to aquatic biodiversity. The education of communities and regional governments as typical stewards of lighting regimes (e.g. on roads, docks, bridges) will also be fruitful. Noise-pollution mitigation has perhaps been best developed for boats and has taken the form of motor restrictions (e.g. no combustion motor zones or speed zones) as well as innovations in motor design that reduce noise outputs. But there is still much to do to abate other forms of noise.

(10) Freshwater salinisation

Regional studies suggest that freshwater salinisation is occurring at an unprecedented rate and scale (Herbert *et al.*, 2015), but there remains no global synthesis of this problem. The threat posed by salinisation is far from new, but it is predicted to intensify with climate change. Estimates suggest that 1.5×10^8 ha of forest and wetlands are salt-affected worldwide (Wicke *et al.*, 2011), and 1.5×10^7 ha of freshwater peatlands are vulnerable to sea-level rise (Henman & Poulter, 2008). Vegetation clearance allows for greater accessions of rainfall to groundwater *via* recharge zones. This imbalance increases hydrostatic pressure in lowland aquifers, increasing discharge from saline water tables driving dryland salinisation. The semi-arid zones that are vulnerable to salinisation may experience less rainfall under warming scenarios, mitigating the rise in water tables, yet reduced runoff may lead to increased concentration of salts in surface waters (Mills *et al.*, 2013). Irrigation salinisation arises from the direct application of waters to agricultural lands. These are usually more saline than rainfall, and the salts evapoconcentrate even from the application of very dilute waters, leading to salinised surface soils. In warmer, drier climates, evaporation rates may increase with climate change, and greater volumes of water are likely to be applied to avoid crop desiccation (Vörösmarty *et al.*, 2010). While technologies emerging under precision agriculture may make water application more efficient, increased developing-world populations will likely adopt low-technology-irrigation agriculture, expanding the extent of fresh water at risk.

The proliferation of large impoundments on major rivers (Zarfl *et al.*, 2015), as well as many thousands of smaller dams and the dense matrix of artificial waterpoints in agricultural landscapes, combine to limit the flow of freshwater runoff to coastal zones. Reduced flow also limits

the dilution and flushing of tidal waters, raising their salinity. Many salinising coastal zones are under threat from rising sea levels which are likely to inundate lowland systems (Henman & Poulter, 2008). This will be compounded by the increasing exploitation of fresh groundwater resources and the increasing frequency of hurricanes and storm surges (e.g. Schuerch *et al.*, 2013). Other anthropogenic drivers of freshwater salinisation include: disposal or accidental spillage of saline waste water from the production of coal seam gas and shale oil (Vengosh *et al.*, 2014); strip mining of oil sands which exposes marine sediments and shallow saline aquifers (Gibson *et al.*, 2013); and the expanding use of salt to de-ice impervious surfaces (Findlay & Kelly, 2011; Kaushal *et al.*, 2018).

Biological effects of salinisation include the continued replacement of salt-intolerant taxa with those that can withstand elevated concentrations (Radke *et al.*, 2003). Increased salinity kills freshwater species owing to toxic levels of sodium and chloride ions in their cells and reduced capacity to take in essential ions and water. These effects can reduce species diversity and significantly alter trophic systems by reducing food sources for consumers (Finlayson *et al.*, 2013). While freshwater plants can withstand short intervals of increased salinity, sustained periods can lead to reduced productivity and threaten the viability of rhizomes and stored seeds. Salinisation can induce density stratification rendering surface sediments anoxic, leading to regime shifts in freshwater plant communities (Davis, Sim & Chambers, 2010). The growth, fecundity and diversity of freshwater invertebrates is also known to decline with rising salinity (Pinder *et al.*, 2005). Many vertebrates are also impacted, often *via* indirect effects such as habitat and food-web changes, however anurans are particularly sensitive, especially juvenile stages (Smith *et al.*, 2007). Mitigation of salinisation may include controlling the release of salts from point sources or pumping aquifers to lower water tables, but these tend to be local in scale. The strategic release of freshening flow can be effective at a more regional scale but can come at a considerable cost, including the cost of not using that water for environmental or consumptive purposes (Herbert *et al.*, 2015).

(11) Declining calcium

Most aquatic environmental threats are related to the excess of a limiting nutrient (i.e. eutrophication) or a chemical contaminant that exceeds safe concentrations. By contrast, relatively few anthropogenic stressors are related to diminishing supplies of limiting nutrients. One example of a recently identified threat is the slow but widespread decline in calcium (Ca) concentrations in low-carbonate systems across eastern North America (Likens *et al.*, 1998; Keller, Dixit & Heneberry, 2001; Molot & Dillon, 2008), Europe (Stoddard *et al.*, 1999; Skjelkvåle *et al.*, 2005; Hessen *et al.*, 2017), and likely elsewhere. Ca is an essential nutrient for all forms of life, but the ecological ramifications of this new threat are still not fully understood.

Although Ca-rich dust may play a role (Hedin *et al.*, 1994), the principal source of Ca to freshwaters is the slow weathering of parent bedrock that supplies the Ca pool within catchment soils, which is then potentially available for export to lakes and rivers. Growing evidence shows that human activities have disrupted the Ca cycle of many softwater lakes, reducing the supply of Ca and lowering aqueous Ca concentrations below the demands of some aquatic organisms through two major processes (Jeziorski & Smol, 2017). First, acid rain accelerated the leaching of Ca into lakes, and so, for a period of time lake-water Ca concentrations were likely elevated. In areas with geology characterised by high Ca concentrations (e.g. limestone bedrock), Ca continued to be easily leached into waterways. However, in many low-Ca regions, such as those underlain by Precambrian granitic bedrock, Ca supplies were eventually depleted, as the maintenance of suitable concentrations is mainly dependent on slow weathering processes. Second, as large amounts of Ca are bound up in timber, forestry practices can act as a net export of some of the catchment's Ca reserves, exacerbating watershed Ca loss (Allen, Clinton & Davis, 1997; Watmough, Aherne & Dillon, 2003).

Identifying the ecological effects of long-term Ca declines has, thus far, primarily focused on the Cladocera, often a dominant and keystone group of lake invertebrates. Early analyses revealed that some large-bodied cladocerans (e.g. some *Daphnia* spp.) have relatively high Ca requirements (Jeziorski & Yan, 2006; Ashforth & Yan, 2008), with some populations unable to persist should, for example, ambient Ca concentrations fall below 1.5 mg/l. Given that monitoring programs were already recording lower Ca concentrations in many softwater lake regions, concerns were raised that this environmental threat may be affecting lake food webs. A common thread is that Ca declines have been slow and gradual, requiring either palaeolimnological (Jeziorski *et al.*, 2008) or long-term monitoring data on the order of decades to identify the problem (Molot & Dillon, 2008). For these reasons, Jeziorski *et al.* (2008) used analyses of fossil Cladocera to show that, indeed, major shifts in invertebrate assemblages could be linked to declining Ca levels. They found that many softwater lakes were already showing signs of Ca depletion with concomitant changes in cladoceran assemblages. Furthermore, the palaeolimnological data indicated that the recent declines in Ca concentrations recorded in the lake-monitoring programs were not simply a trend of Ca levels rebounding to pre-acidification levels (as one would have expected higher concentrations of Ca in lakes during the early periods of lake acidification), but that current Ca levels were now lower than pre-acidification concentrations. Palaeolimnologists reached this conclusion because Ca-sensitive *Daphnia* taxa were often common in the pre-acidification fossil record, indicating that Ca levels were sufficiently high prior to acidification. Subsequent studies confirmed this overall trend in a spectrum of softwater lake ecosystems, which may also impact other groups of freshwater biota that have high Ca requirements (reviewed in Jeziorski & Smol, 2017), such as crayfish (Hadley *et al.*, 2015).

Although the study of declining Ca was initially focused on taxa impacted by reduced Ca availability (e.g. large-bodied

Daphnia), subsequent research has begun to centre on organisms that may benefit from this new threat. For example, given that large *Daphnia* are efficient filter feeders, their demise may be linked to recent algal blooms, due to reduced top-down effects (Korosi *et al.*, 2012). In addition, Jeziorski *et al.* (2015) documented the widespread replacement of *Daphnia* with *Holopedium glacialis*, a jelly-clad competitor with low Ca requirements. Although both are filter-feeding planktivores, *Holopedium* have lower nutrient content than *Daphnia* and high concentrations of the jelly-clad *Holopedium* can disrupt water filtration equipment. The ensuing 'jellification of lakes' is a new problem which potentially can cascade through the food web.

The solution to the threat of Ca declines is not a simple one given the large number of affected lakes and their typically remote locations. Further reductions in acidic precipitation is potentially a long-term solution, although one with significant economic repercussions. On a smaller scale, some local attempts have been initiated to replenish Ca in watersheds by, for example, 'fertilising' them with Ca-rich wood ash (e.g. Haliburton, Ontario, Canada). The efficacy of these pilot projects has not yet been evaluated.

(12) Cumulative stressors

Although there is long-standing recognition that environmental stressors can interact to affect freshwater ecosystems, the last decade has seen considerable growth in interest in potential 'multiple stressor' problems (Ormerod *et al.*, 2010; Vörösmarty *et al.*, 2010; Craig *et al.*, 2017). The first of three key reasons is the increasing appropriation of freshwater resources for human use coupled with growing downstream impacts from human activities (Strayer & Dudgeon, 2010). Second, human effects on fresh waters often occur in combination, either because different activities coincide (e.g. urbanisation with industry; agriculture with abstraction; biomass exploitation with invasive species release) or because they affect freshwater ecosystems through multiple pathways. Third, climate change is expected to have widespread direct and indirect effects on fresh waters (see Section V.1). In this growing area of interest, there are three linked and prominent challenges.

First is the need to resolve whether multiple freshwater stressors simply co-occur, or whether they have interacting effects. Early experimental evidence suggested that some stressor combinations could be synergistic (e.g. high temperature × toxic stress), but in most cases stressor combinations were less than additive (Folt *et al.*, 1999). These patterns have been largely borne out by recent meta-analysis, where the net effects of dual stressors on biological diversity and ecosystem function appeared to be dominantly additive and antagonistic, respectively (Jackson *et al.*, 2016*a*). Data from 88 papers and almost 300 stressor combinations revealed interactions were most commonly antagonistic (41%), rather than synergistic (28%), additive (16%) or reversing (15%). This variation among outcomes suggests a need to understand the exact contextual factors that influence stressor interactions. Ecosystems or organisms

of high conservation importance are often characterised by specific requirements that might be disproportionately sensitive to some stressor combinations. Furthermore, biodiversity erosion might increase multiple stressor impacts as ecosystem functions are impaired or sensitivities change. For example, Vinebrooke *et al.* (2004) illustrated how lake community composition could reduce or increase combined stressor response depending on the extent to which species shared stress tolerance. In some cases, multiple stressor effects on fresh waters have led to unexpected 'ecological surprises' through non-linear or delayed interactions in systems that were otherwise well understood (Hecky *et al.*, 2010).

A second challenge is to develop methods for diagnosing the relative importance of stressors with combinatorial effects. A possible explanation for the dominance of antagonistic interactions is that those with a large impact might mask or override the effects of lessor stressors (Jackson *et al.*, 2016*a*). Under these circumstances, removing a dominant stressor might simply reveal the effects of other stressors without a net biodiversity gain. By contrast, identifying any hierarchical effects of co-occurring stressors could help target sequential approaches to management and lead to tangible biodiversity gains (Kelly *et al.*, 2017). Thus far, reliable evidence and case studies from which to develop generalisable best practices are limited, and often based on data-analytical approaches to prevailing stressor combinations that might not represent the effects of sequential stressor management (Gieswein, Hering & Feld, 2017).

Against this uncertain background, a third challenge is to identify pragmatic approaches to managing multiple stressor impacts. The largest benefits would be likely where multi-purpose solutions tackle multiple problems simultaneously – most straightforwardly by prioritising resource protection over exploitation in catchments or water bodies identified for biodiversity importance (e.g. EU Habitats Directive 92/43/EEC; see Section VII). Riparian solutions offer a smaller-scale alternative, for example, where 'buffer zones' simultaneously influence water quality, protect thermal regimes, provide habitat structure and maintain energetic subsidies, although they are not equally effective for all pollutants (Lowrance *et al.*, 1997). Overall, however, there is a pressing need to understand and address multiple-stressor problems, particularly their impacts on freshwater biodiversity.

VI. CONSERVATION AND MANAGEMENT TOOLS

Despite the overall grim prognosis for freshwater biodiversity, there are opportunities for conservation action and effective management. Emerging tools and technologies (see Sections VI.2 and VI.2) will be essential in mitigating some emerging threats (see Jackson *et al.*, 2016*b*). Some existing approaches (see Sections VI.3–5) could also help support biodiversity conservation while meeting human needs; these, however, have been met with varying levels of success, yet offer insight

into the effectiveness of different freshwater conservation strategies. In this section, we present a shortlist of tools and techniques that have relevance to freshwater conservation either in their previously established or potential future uses, and that reflect the expertise of the author group.

(1) Environmental DNA

Deoxyribose nucleic acid (DNA) from lake, wetland and river organisms is present in the water column as secretions, cells, tissues, faeces or gametes, and is transported through drainage networks. Fragments of this environmental DNA (eDNA) can be isolated from organic matter in water samples, sequenced and assigned to known species using metabarcoding (Elbrecht & Leese, 2017). The potential conservation applications of eDNA techniques are substantial in detecting rare and endangered freshwater species whose presence cannot be confirmed easily by more conventional means (Jerde et al., 2013; Laramie, Pilliod & Goldberg, 2015; Bellemain et al., 2016), and for monitoring the colonisation of new habitat by potentially invasive species or pathogens (Rees et al., 2014). This targeted or 'active' surveillance directed towards detection of eDNA for a single species of interest can be contrasted with 'passive' surveillance, using high-throughput sequencing, whereby sampled eDNA is used to assess community composition and opportunistically reveals the presence of a species of interest (Simmons et al., 2016). The latter approach also has potential applications for bioassessment, since the eDNA signal of a community of macroinvertebrates could be used to estimate diversity with less investment of time and effort than the benthic sampling methods that are widely used currently (Rees et al., 2014; Elbrecht & Leese, 2017). Wider application of eDNA techniques will certainly not be a panacea that can replace the requirement for taxonomic expertise about freshwater biota, nor are such approaches (yet) able to provide reliable quantitative information about population sizes of species of interest. Nonetheless, when combined with next-generation sequencing methods, collection of eDNA transported in river networks offers a spatially integrated way to assess the species richness (both aquatic and terrestrial) of entire drainage basins, and could well transform biodiversity data acquisition in the future (Deiner et al., 2016).

(2) Environmental flows

One approach to mitigating the effect of flow regulation on fresh waters is the practice of water allocations (environmental flows, or e-flows) to protect or restore ecosystems. The scientific consensus is that e-flows should provide water levels or discharges that mimic natural hydrologic variability and incorporate a range of flows essential to support functioning ecosystems (Arthington et al., 2018). By accounting for the variability of hydrographs, e-flows permit connectedness longitudinally along rivers and laterally within floodplains; this is vital in allowing adaptive responses by the riverine biota to the challenges of living in a warmer world, permitting movement among potential refugia as conditions change.

e-flows have stimulated much research into the question 'how much water does a river (or stream, or wetland) need'? A one-size-fits-all water allocation for river basins is theoretically possible globally (for example, 37% of mean annual flow) (Pastor et al., 2014), but such 'rules of thumb' are unlikely to capture all ecologically important aspects of flow variability. Instead, the success of river protection and restoration will depend upon accurately modelling relationships between hydrological patterns and ecological responses, followed by implementation of water allocations within a range set by the resilience of these ecosystems (Poff & Zimmerman, 2010). The accumulation of long-term hydrological data is needed to evaluate hydroclimatic trends, to quantify flow regime alteration and associated flow-ecology relationships, and to design and implement e-flows prescriptions; current trends in streamgauging data coverage across the world are not encouraging (Ruhi, Messager & Olden, 2018).

Broad consensus has emerged among e-flow practitioners about how this can be achieved through the Ecological Limits of Hydrologic Alteration (ELOHA) approach to determine regionally relevant hydro-ecological models and water allocations (Poff et al., 2010). In the many parts of the world where data explicitly linking hydrological changes to ecological responses are scarce, e-flow allocations will have to be based on whatever limited data can be deployed for the ELOHA approach, supplemented by best professional judgment and risk assessment. Under such circumstances, an e-flow allocation can be treated as an hypothesis-driven experiment in ecological restoration, with the outcomes monitored, evaluated and refined. Outcome analysis should be essential in any management intervention: a meta-analysis by Palmer, Menninger & Bernhardt (2010) revealed shortcomings in the widely used 'if you build it, they will come' approach of restoring physical habitat and flows in rivers if other stressors continue to limit ecological recovery. Such failures are frequent given that many freshwater habitats are subject to multiple interacting stressors (Craig et al., 2017).

(3) Aliens and aquaculture

Invasive species have inflicted profoundly damaging effects on recipient freshwater ecosystems (Gallardo et al., 2016). However, it must not be ignored that some non-native species can now play important ecological roles in human-altered environments, such as supporting lake food webs (Twardochleb & Olden, 2016) and riverine ecosystem functions (Moore & Olden, 2017). Species have been repeatedly and deliberately introduced outside their native ranges with the aim to support food security, recreation opportunities and ecosystem rehabilitation. Where the preservation of near-pristine freshwater environments is no longer a realistic option, the prospect of enhancing ecosystem services through introduced alien species may become an option – and has clear parallels in terrestrial agriculture. Human livelihoods are a paramount consideration in parts of

Asia, Africa and South America, irrespective of conservation concerns, whereas the need to protect native biodiversity has a stronger bearing on decisions in North America and Europe, where dependence on freshwater artisanal fisheries is generally lower. Some have argued that alien species could, under certain circumstances (e.g. Gozlan, 2008), contribute to conservation goals by providing habitat or performing desirable ecosystem functions (Schlaepfer, Sax & Olden, 2011). Even notorious invaders such as dreissenid mussels may provide lake-management benefits through filtering activity and control of algal blooms (McLaughlan & Aldridge, 2013). However, others strongly disagree (Vitule *et al.*, 2012), arguing that the risks of alien introductions outweigh any beneficial roles they might play in enhancing ecosystem services. For instance, the ecological and economic damage caused by dreissenid mussels (Nakano & Strayer, 2014) is not offset by the filtering service benefit provisioned by these biofouling animals.

Global declines in freshwater capture fisheries (Youn *et al.*, 2014) will boost the case for expanding aquaculture – based often on introduced or potentially invasive species – to meet the shortfall in wild yields to support an ever-increasing human population. Decreasing natural production of freshwater fishes (relative to aquaculture) is a matter of great concern given that it provides the equivalent of all dietary animal protein for 158 million people, with poor and malnourished populations particularly reliant on these fisheries compared with marine or aquaculture sources (McIntyre, Reidy Liermann & Revenga, 2016). Freshwater fishery yields consistently have been underestimated (FAO, 2016; Fluet-Chouinard, Funge-Smith & McIntyre, 2018), and their global importance underappreciated (Lynch *et al.*, 2017; Reid *et al.*, 2017). At least 21 million people engage regularly in freshwater fisheries (over a third of the global total for capture fisheries) and most are small-scale operators concentrated in Asia and, secondarily, Africa (FAO, 2016). Many more, particularly women, engage in subsistence fishing informally with the catch contributing to family welfare. Such practices could not easily be replaced by aquaculture.

Aquaculture can lead to the proliferation of parasites, diseases and species introductions, as well as contaminating receiving waters with wastes and pharmaceuticals associated with intensive fish farming (FAO, 2016). Putting these disadvantages aside, cultured fishes may not be an adequate substitute for capture fisheries. Wild fishes are more nutritious (higher protein and micronutrient content) than farmed individuals, even within species (Youn *et al.*, 2014); thus, a switch to consumption of such fish as wild catches decline (assuming that were practicable) would result in poorer diets. Furthermore, a spatial coincidence between productive freshwater fisheries and low food security (McIntyre *et al.*, 2016), as well as between *per capita* inland catch and extreme poverty (Lynch *et al.*, 2017), highlights the crucial role of rivers and lakes in providing locally sourced, low-cost protein and micronutrients. While further development of aquaculture might substitute for some food needs, it would be far better to secure provisioning of this ecosystem service by protecting these fisheries and the habitats that sustain them, in their own right (Dudgeon, 2014), but also given the apparent correlation between biodiversity and stable, high-yielding fisheries (Brooks *et al.*, 2016). The need to ensure that freshwater capture fisheries are fully considered in decisions about water-resource management will require that their contribution to food security is reliably assessed, valued and communicated to decision-makers and the public.

(4) Fishways and dam removal

Research on devices that enable fish to traverse dams (in both directions) is needed urgently, as many dams are lacking such facilities or they have installed structures that fail adequately to pass focal species – typically salmonids – or the broader fish community (Pelicice *et al.*, 2015). Indeed, some well-respected fish ecologists regard fishways as a failed technology that does not provide adequate passage – even for focal species – despite decades of use (Brown *et al.*, 2013). Assessments of the effectiveness of different fishway designs and types to facilitate passage for representative species of migratory fish is urgently needed, especially in the tropics (Silva *et al.*, 2018). Such targeted research might pay conservation dividends as the results could be applied readily. A range of stream types needs to be assessed to identify the most effective design for multispecies fishways (e.g. Steffensen *et al.*, 2013; Yoon *et al.*, 2015), but one obvious generalisation is that, irrespective of design details and ecological context, fishway effectiveness is inversely proportional to dam height. Some success in re-establishing fish migration has been reported for brown trout (*Salmo trutta*) (Calles & Greenberg, 2009), Atlantic salmon (Nyqvist *et al.*, 2017) and Macquarie perch (*Macquaria australasica*) (Broadhurst *et al.*, 2013) – yet results have been mixed for other species despite targeted research to inform fishway design and operation (Baumgartner *et al.*, 2014).

Even for those species that respond well to fishways, such structures are no more than a partial solution to the obstacles presented by dams, as the associated reservoirs are also a barrier to migration – especially in a downstream direction (Pelicice *et al.*, 2015). Furthermore, they do little or nothing to alleviate the effects of dams and reservoirs on non-fishes, such as migratory shrimp (Holmquist, Schmidt-Gengenbach & Yoshioka, 1998). The only known technical solution is to open or completely remove dams. More than 1200 dams have been removed in the USA in the last 40 years, and the decadal rate of removal is increasing exponentially (Bellmore *et al.*, 2016). Such events are often spurred by the hazards posed by aging infrastructure, but can result in conservation gains where migration routes are re-established. Larger dams are becoming subject to attention, with the largest being the 2014 removal of the Glines Canyon Dam (64 m tall) from the Elwah River. Rivers respond quickly to dam removal, eroding and redistributing sediment and returning to pre-impoundment conditions within years, rather than decades (O'Connor, Duda & Grant, 2015). Ecological recovery is slower but nonetheless fairly rapid, and salmonids and

other migratory fishes readily colonise newly available habitat upstream (Grant & Lewis, 2015). While rates of dam construction – especially large ones – far outpace the number of removals (Bellmore *et al.*, 2016), the practice has momentum: in 2016, the governments of California and Oregon announced plans to remove four hydropower dams on the Klamath River as part of an effort to restore salmon fisheries.

(5) Climate change and managed relocation of species

The rapidity of climate change is predicted to exceed the ability of many freshwater species to adapt or to disperse to more climatically favourable surroundings (Brook *et al.*, 2008; Loarie *et al.*, 2009). Conservation of these species may require managed relocation (also called assisted migration or assisted colonisation) of individuals to locations where the probability of their future persistence is likely to be high, but where the species is not known to have occurred previously (Olden *et al.*, 2011). Yet, there is good reason to question whether managed relocation is a viable conservation strategy. For example, managed relocation promotes the distributional expansion of species and thus may have undesirable effects on other species or ecological processes (Ricciardi & Simberloff, 2009). Decisions regarding the managed relocation of freshwater species are clearly complicated. Quite simply, the effects of introducing a freshwater species to a new location are uncertain (and potentially disastrous), therefore the need for managed relocation must be balanced against the probability of species loss associated with doing nothing [see Olden *et al.*, 2011 for discussion].

VII. IS THERE HOPE FOR CONSERVING FRESHWATER ECOSYSTEMS?

Current rates of extinction, habitat degradation and emerging challenges show that freshwater ecosystems already face pressures larger than any other ecosystem, and threats will intensify in future as the exploitation of freshwater resources grows to meet human demand. Conservation scientists working in freshwater ecosystems, therefore, have potentially important roles in providing evidence for actions to arrest decline, and to protect or restore the world's lakes, reservoirs, rivers, streams and wetlands. Here we highlight positive actions that illustrate potential options across scales, from local to global. The mechanisms vary, but they include legal regulation, fiscal incentives, market opportunities and voluntary action by learned or civil society, or ideally some combination of these drivers.

In Europe, regulatory instruments range from aiming to achieve good qualitative and quantitative status of all water bodies (e.g. The Water Framework Directive 2000/60/EC) through to protecting specific freshwater ecosystems to support target taxa (e.g. The Habitats Directive 92/43/EEC), for which there is evidence of opportunity. For example, the European Union Urban Waste Water

Treatment Directive (91/271/EEC) led to extensive and long-term ecosystem recovery in urban rivers that were once among the world's most grossly polluted (Vaughan & Ormerod, 2012). Continental-scale regulation has also contributed to the recovery of formerly acidified lakes and rivers ranging from local (e.g. Sudbury, Ontario, Canada) to more extensive areas of Europe and North America – although in these cases biological responses have yet to match chemical trends fully (Kowalik *et al.*, 2007; Ormerod & Durance, 2009; Labaj *et al.*, 2015).

Fiscal incentives are sometimes used by governments to protect water courses in otherwise intensifying agricultural systems using agri-environment schemes (AESs). Examples include: riparian buffer zones to reduce nutrient flux; conservation easements in the USA; and various forms of catchment-sensitive farming with reduced agro-chemical use or livestock density. Although promising for some pollutants (Zhang *et al.*, 2010), comprehensive data are needed to illustrate wider success in tackling multiple stressors sufficiently to engender whole-ecosystem recovery, including that of biodiversity.

Beyond government support, market mechanisms are increasingly considered as a means of managing freshwater catchments – specifically through natural capital accounting and markets for ecosystem services (Ormerod, 2014). The basic concept is to protect catchments as a 'first line of defence' or as units of production for natural services from which financial gains can then flow. Investments are typically made to protect soil carbon, maintain runoff, regulate water quality or provide natural flood management, thus providing a financial return, for example, in tradeable water supply, reduced water treatment costs or reduced need for traditional engineered infrastructure. Biodiversity is protected either collaterally, or because organisms have a key role in ecosystem-service delivery (Durance *et al.*, 2016). Although this utilitarian view of natural systems is sometimes criticised, recognition of the role of freshwater ecosystems in human life support – as in the planetary health movement – may be an essential step towards their long-term protection. Key needs are to motivate investors, to move beyond small-scale demonstration projects and to ensure that conservation gains can be guaranteed to outweigh the risks of some resource exploitation implied in some forms of this paradigm.

Members of society and, in particular, non-governmental organisations (NGOs) act as important sources of lobbying, hope and demonstration in freshwater conservation. At a global scale, for example, the 2007 Brisbane Declaration at the Environmental Flows Conference, revised at the 2017 International River Symposium (see Arthington *et al.*, 2018), emphasised the ecosystem-service role of fresh waters and called on governments, development banks, donors, river basin organisations, NGOs, community-based organisations, research institutions and the global private sector to take a range of actions to restore and maintain e-flows (Olden *et al.*, 2014). The effectiveness of this call to action, however, remains to be assessed. Indeed, e-flow requirements have yet to be adequately assessed for most aquatic ecosystems

and have been implemented in even fewer. There is still no comprehensive global record of e-flow implementations, nor a good understanding of why some projects have succeeded, while other initiatives have failed to materialise. Major obstacles to e-flow implementation lie largely outside the realm of ecology. They include a lack of political will and public support; constraints on resources, knowledge and local capacity; and institutional barriers and conflicts of interest (Arthington *et al.*, 2018). These are matters of particular concern as a global boom in construction of hydropower dams is underway (Zarfl *et al.*, 2015; Winemiller *et al.*, 2016; Couto & Olden, 2018), and demands for water continue to grow, especially in arid regions, or those experiencing shortages as a result of climate change.

Civil society action has also been instrumental in dam removal – particularly in North America – to restore river systems through improved longitudinal connectivity. Over 1200 dams have now been removed, but evaluations of effects are still scarce or short-term, and there is thus a need for further post-intervention appraisal (Bellmore *et al.*, 2016). In the UK, the NGO sector has been involved both in lobbying for improved river protection, but also in demonstrating practical steps in river conservation. One example is the concept of 'Keeping Rivers Cool' by restoring riparian woodlands. In the wake of climate change, the thermal benefits of improved riparian shading under summer conditions are clear, but advantages for native fish conservation, stream energetics and the reduction of sediment loads also appear likely (Lawrence *et al.*, 2014; Wohl *et al.*, 2015; S. Thomas, Griffiths & Ormerod, 2016*b*).

Potentially the biggest gains for freshwater conservation would arise when different sectors combine efforts. For instance, the new global initiative, the *Alliance for Freshwater Life* (Darwall *et al.*, 2018), seeks to unite freshwater specialists, from individuals to organisations to governments, who engage in freshwater research, data synthesis, conservation, education and outreach as well as policymaking. Indeed, the global significance of freshwater ecosystems means that all stakeholders – ecosystem managers, policymakers, resource users, NGOs and citizens – should collaborate to make informed decisions that affect freshwater ecosystem viability and productivity. When the voices of inland fisheries professionals and citizens are heard in concert, fisheries success stories often ensue, as evidenced by 'good news fisheries' from walleye (*Sander vitreus*) in Red Lake, Minnesota, USA, to brown trout in Swedish rivers, among many others (Taylor *et al.*, 2016). Moreover, attempts to engage the public through various forms of science communication and education (e.g. citizen science, participation in decision-making) have great potential to alter individual behaviour (e.g. how they vote, how they relate to water) and generate the political will necessary to protect and restore freshwater ecosystems (Cooke *et al.*, 2013).

This short overview of potential actions indicates that there can be hope for the world's freshwater ecosystems and their biota – but only if these examples inspire action at local, national and global scales in the face of overwhelming pressure. A potential roadmap for the future was outlined in the Rome Declaration (Taylor *et al.*, 2016), which consists of 10 steps – ranging from biological and nutritional to social, economic and political – for responsible inland fisheries that, if followed, will address many emerging threats. However, beyond the sustainability of inland capture fisheries, there remains a lack of specific goals to achieve the conservation of freshwater biodiversity at large. For example, the 2015 United Nations (UN) Sustainable Development Goals (SDGs; see https://sustainabledevelopment.un.org/sdgs) include a goal dedicated to 'life below water' (SDG 14) that is concerned exclusively with the oceans, and the constituent targets say nothing about inland waters (Reid *et al.*, 2017). We are in need of numerical targets that forcefully put the case for protecting freshwater ecosystems (e.g. Griggs *et al.*, 2013). Such targets must: (*i*) treat the causes, not the symptoms, of freshwater biodiversity degradation; (*ii*) delineate how they are to be delivered, limiting their openness to interpretation; and (*iii*) include clear and feasible timelines, with short-, medium- and long-term objectives so they may be periodically reviewed and revised (e.g. 1983 management strategy for Lake Balaton, Hungary) (UNEP, 2017). We urge freshwater scientists to engage with the next phases of development of the UN Convention on Biological Diversity, and in particular the post-2020 follow-up to the Aichi Targets, to ensure that these most critically endangered ecosystems are given due prominence. On those actions, the future integrity of fresh waters and their denizens may well depend.

VIII. CONCLUSIONS

(1) In the 12 years since the major pressures responsible for global freshwater biodiversity loss were reviewed in Dudgeon *et al.* (2006), the prognosis for freshwater biodiversity has worsened, with freshwater species exhibiting steeper population declines (declining by 83% between 1970–2014) than their marine or land-based counterparts.

(2) Freshwater biodiversity continues to be under-represented in the conservation literature (Strayer & Dudgeon, 2010) despite estimates that fresh waters are hotspots of endangerment due to the convergence of disproportionately high biological richness and multiple anthropogenic pressures. Habitat degradation, overexploitation and invasive species – stressors all identified by Dudgeon *et al.* (2006) – continue to be persistent and ubiquitous threats to freshwater biodiversity with potentially harmful socio-economic effects on human welfare and wellbeing.

(3) Twelve emerging threats to freshwater biodiversity, that are either entirely new since 2006 or have since evolved and require renewed consideration, have been identified herein: (*i*) changing climates; (*ii*) e-commerce and invasions; (*iii*) infectious diseases; (*iv*) harmful algal blooms; (*v*) expanding hydropower; (*vi*) emerging contaminants; (*vii*) engineered nanomaterials; (*viii*) microplastic pollution; (*ix*) light and noise; (*x*) freshwater salinisation; (*xi*) declining calcium; and (*xii*) cumulative stressors. The Anthropocene has ushered

in innumerable direct and indirect anthropogenic effects on diverse freshwater taxa, including amphibians, fishes, invertebrates, microbes, plants, turtles and waterbirds, and there exists strong potential for ecosystem-level changes through bottom-up and top-down responses.

(4) As topographically low and hydrologically connected ecosystems, freshwater lakes, reservoirs, rivers, streams and wetlands incur particular risk because chemical, physical, climatic and biological stressor effects can propagate and accumulate from the atmospheric, terrestrial and riparian environments in which fresh waters are embedded. Multiple-stressor problems are therefore a growth area for research. Projected future trajectories of human population growth, accelerating urbanisation, increasing irrigation, rising global temperatures and climatic unpredictability are likely to exacerbate human demands for fresh water while also impairing water quality to compromise ecosystems and threaten biodiversity further. There are clear signs that climate change has already directly impacted freshwater ecosystems and ecological processes, and ambitious water infrastructure projects, coupled with the uncertainties generated by climate change, will further alter fresh waters, posing challenges for human water and food security.

(5) To cope with the increasing pressures on water quantity and quality, decision-makers are primarily considering engineering solutions such as the implementation of environmental flows, as well the construction of fishways and the removal of dams. These solutions have been met with relative success, but are highly context dependent and require cautionary and targeted research approaches. Conversely, alien introductions, aquaculture and the managed relocation of species are techniques unlikely to support human wellbeing while maintaining healthy freshwater ecosystems due to the multiple implicit ecological risks.

(6) A desirable alternative is the effective protection of freshwater capture fisheries and the habitats that sustain them. This provides locally sourced, low-cost and nutritious protein in often impoverished areas while also promoting ecological integrity. Freshwater fisheries' contribution to human food security must be reliably assessed, valued and communicated if it is to be included in resource-management decisions. At the same time, aquaculture is the fastest growing sector of the food-production industry, with potentially major consequences for freshwater biodiversity.

(7) Environmental DNA as a biomonitoring and bioassessment tool could augment biodiversity data acquisition in the future. It offers a promising potential remedy to the insufficient surveillance technologies and baseline-data deficiencies presented as common obstacles to emerging threat-mitigation efforts. Owing to the fact that fresh waters are subject to multiple pressures, however, any conservation tool or mitigation strategy that mitigates individual stressors will only be effective if co-occurring stressors are also alleviated.

(8) Positive conservation action has brought real and sustained benefits across scales, from local to global, *via* a variety of mechanisms including: regulatory instruments (e.g. The Water Framework Directive); fiscal incentives (e.g. agri-environment schemes); market opportunities (e.g. investments in ecosystem services with financial returns); and/or societal actions (e.g. dam removal, participation in restoration activities, considering freshwater ecosystems when voting in elections).

(9) We are merely at the beginning of the 'great acceleration' of the Anthropocene. Indeed, we may not even be able to imagine which environmental challenges we will face in the coming decades. In order to protect biodiversity and to support human well-being, we need to manage fresh waters collectively across sectors and as hybrid systems – managing freshwater ecosystems as both a pivotal resource for humans as well as highly valuable ecosystems.

(10) A global effort, such as that outlined by the *Alliance for Freshwater Life*, the 10 steps for responsible inland fisheries in the Rome Declaration and the post-2020 follow-up to the Aichi Targets, is needed to address and reverse global trends in the degradation of freshwater ecosystems, which is to the detriment of both humans and nature. However, how the gap is closed between these lofty goals and the current state of freshwater ecosystems and human use of their services presents an immense but necessary challenge.

IX. ACKNOWLEDGEMENTS

X. REFERENCES

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