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Fish conservation in freshwater and marine realms: status, threats and management

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ABSTRACT

1. Despite the disparities in size and volume of marine and freshwater realms, a strikingly similar number of species is found in each – with 15 150 Actinopterygian fishes in fresh water and 14 740 in the marine realm. Their ecological and societal values are widely recognized yet many marine and freshwater fishes increasingly risk local, regional or global extinction.

2. The prevailing threats in aquatic systems are habitat loss and degradation, invasive species, pollution, over-exploitation and climate change. Unpredictable synergies with climate change greatly complicate the impacts of other stressors that threaten many marine and freshwater fishes.

3. Isolated and fragmented habitats typically present the most challenging environments for small, specialized freshwater and marine fishes, whereas overfishing is by far the greatest threat to larger marine and freshwater species. Species that migrate within or between freshwater and marine realms may face high catchability in predictable migration bottlenecks, and degradation of breeding habitat, feeding habitat or the intervening migration corridors.

4. Conservation reserves are vital to protect species-rich habitats, important radiations, and threatened endemic species. Integration of processes that connect terrestrial, freshwater and marine protected areas promises more effective conservation outcomes than disconnected reserves. Diadromous species in particular require more attention in aquatic restoration and conservation planning across disparate government agencies.

5. Human activities and stressors that increasingly threaten freshwater and marine fishes must be curbed to avoid a wave of extinctions. Freshwater recovery programmes range from plans for individual species to recovery of entire basin faunas. Reducing risks to threatened marine species in coastal habitats also requires conservation actions at multiple scales. Most of the world's larger economically important fisheries are relatively well-monitored and well-managed but there are urgent needs to curb fishing mortality and minimize catch of the most endangered species in both realms.

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INTRODUCTION

Aquatic systems form both a mosaic and a continuum of habitats ranging from the freshwater springs, rivers, lakes and wetlands of continents and islands to estuaries, shallow coastal habitats, reefs and the seas. Their fish inhabitants are numerous - more than 30 000 described species (Nelson et al., 2016) - and remarkably diverse in morphology, physiology, size. habitat requirements, diet and life-history strategy (Helfman et al., 2009). Despite the disparities in the size and volume of marine and freshwater realms, a strikingly similar number of species is found in each, with 15 150 Actinopterygian fishes in fresh water and 14 740 found in the marine realm (Carrete Vega and Wiens, 2012). The greatest species diversity is found along continental shelves, in reefs associated with islands and in freshwater habitats, where isolation by the rise of mountains, creation of island systems, and sea-level fluctuations has created opportunities for speciation (Leidy and Moyle, 1997).

Fish comprise a large fraction of standing biomass of aquatic ecosystems (Jennings *et al.*, 2008). They constitute over half of all vertebrate species and contribute in numerous ways to the diversity and functioning of aquatic ecosystems, and to the health, well-being and economies of societies in every geographic realm (Craig, 2015; Hughes, 2015). Nevertheless, many marine and freshwater fishes are threatened by critical population declines and increasingly risk local or global extinction (Helfman, 2007; Darwall and Freyhof, 2016).

This contribution offers an appraisal of the conservation status and relative extinction risk for freshwater and marine fishes, comparing and contrasting the shared features and peculiarities of threatening processes and patterns of species imperilment in these realms. Conservation and management challenges to pre-empt extinctions and recover threatened freshwater and marine fishes form the concluding section. This fresh perspective could help to guide restoration efforts and promote population recovery of the world's threatened fishes while balancing short-term and long-term sustainable development needs of many of the poorest people and countries in the world.

DIVERSITY AND CONSERVATION STATUS OF FRESHWATER AND MARINE FISHES

Freshwater species are defined as those that live all, or a critical part of their life in either freshwater inland or brackish estuaries. This definition includes: all 'primary' (salt intolerant or stenohaline) freshwater fish (e.g. carps, characins, cichlids), all 'secondary' (salt tolerant or euryhaline) freshwater fish (e.g. salmons, some eels, some rays and sawfish), some estuarine fish (e.g. archer fish and gobies), and soda and salt lake fish (Freshwater Fish Specialist Group (http://www. iucnffsg.org/). By this definition, freshwater species make up 48% of all fishes and 25% of all vertebrates (Eschmeyer and Fong, 2013). Some 13 000 strictly freshwater fish species live in lakes, rivers and wetlands that cover less than 1% of the earth's surface, whereas 14 740 species live in salt water habitats covering 71% of the earth's surface (Dawson, 2012). The freshwater realm is small at 272 605 km^3 and pales in comparison with the ecologically habitable volume of the marine realm (1 367 000 000 km³) which represents 99.83% of the habitable volume of this planet (Dawson, 2012). On a per unit basis Eukaryotic diversity is 14 times greater in fresh water than the marine realm (Dawson, 2012). This startling difference reflects the low number of species living in the oligotrophic pelagic and aphotic deepwater habitats of the major oceans compared with those inhabiting shallow continental shelves and reefs associated with islands (Leidy and Moyle, 1997). The high diversity and levels of endemism in freshwater fishes stem largely from the fact that their habitats are highly fragmented, linear and unidirectional (rivers) or completely isolated (many lakes and springs) with rare opportunities for natural range extension.

The IUCN's Freshwater Biodiversity Unit (www. iucn.org/about/work/programmes/species/our_w ork/about_freshwater/), and the IUCN Freshwater Fish Specialist Group (http://www.iucnffsg.org/), have been working since 2004 towards a comprehensive global assessment of the conservation status of the world's freshwater fishes and major threats to their conservation and sustainability. As of 2013 the group has applied the IUCN Red List Categories and Criteria (Mace *et al.*, 2008) to 7300 (46%) of described freshwater species (Darwall and Freyhof, 2016). Of these, 31% are threatened with extinction (classified as Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) on the IUCN Red List). A further 1571 species are classified as Data Deficient and 69 species are classified as Extinct or Extinct in the Wild (Darwall and Freyhof, 2016).

Comprehensive freshwater IUCN assessments have been completed for Europe, Africa, India, Indo-Burma, the United States, New Zealand, Oceania and the Middle East but are incomplete for South America, large areas of Northern and Eastern Asia and Indonesia (Darwall and Freyhoff, 2016). As more regional assessments become available (e.g. for the Tropical Andes, Darwall, pers comm., 2016) a full global picture will emerge. Across the regions for which published assessments are available, freshwater fish diversity and levels of threatened species (sum of CR, EN and VU) vary significantly.

Following the success of the IUCN Shark Specialist Group SSG (www.iucnssg.org), the Global Marine Species Assessment GMSA (http://sci.odu.edu/gmsa/) formed in 2005 is more than half way to its goal of listing 20 000 marine fishes and invertebrates. It has assessed more than 13 000 species, increasing the representation of marine species on the IUCN Red List from 1% to 13% by 2014 and many taxonomic and regional summaries have now been published. The taxonomic focus has been on the most economically and functionally important lineages, such as tunas and billfishes (Collette et al., 2011), hagfishes (Knapp et al., 2011), parrotfishes and surgeonfishes (Comeros-Raynal et al., 2012). The SSG has completed an assessment of the entire taxonomic class of chondrichthyans and is reassessing all species to develop a Red List Index for chondrichthyans by 2020 (Dulvy et al., 2014). Complete assessments are also available for tropical foundation species, including hard corals (Carpenter et al., 2008), seagrasses (Short et al., 2011), and mangroves (Polidoro et al., 2010). Regional assessments document the status of important taxa in key biogeographic regions, such as for European fishes

(Nieto *et al.*, 2015), as well as major marine taxa in the Eastern Tropical Pacific (Polidoro *et al.*, 2012). However, none of these groups and regions are representative of wider marine biodiversity, and aside from these few thematic studies the systematic and representative analysis of marine threatened fishes is incomplete.

Although IUCN assessments of the world's threatened and extinct fishes are incomplete they do suggest that documented fish extinctions in the wild are relatively rare, and surprisingly similar in the freshwater and marine realms – 69 freshwater species and 65 marine extinctions at local, regional or global scale (Dulvy *et al.*, 2003; Darwall and Freyhof, 2016). The depressing picture is that a great many more species are threatened with extinction or their status is unknown. Nevertheless, IUCN classifications and species lists provide informed sources from which to extract an appreciation of the main threatening processes and how they differ in freshwater and marine habitats.

THREATS TO FRESHWATER FISHES

The concentration of people and cities around freshwater systems and increasing human demands for water have led to high levels of degradation and threats to biodiversity in fresh waters. Recent estimates suggest that the 'human footprint' has significantly influenced more than 83% of the land surface surrounding freshwater systems (Vörösmarty et al., 2010). Effects of human activities are manifest as widespread catchment disturbance, deforestation, riparian loss, water pollution, river corridor engineering, dams and water diversions, extensive wetland drainage, groundwater depletion, aquatic habitat loss and fragmentation, establishment of introduced alien species, and overfishing (Dudgeon et al., 2006). Processes operating at regional scales (nitrogen deposition, acid rain, climate change) may be superimposed on all of these threats and typically intensify impacts on freshwater ecosystems.

Several sources document the principal threats to freshwater fishes, including a global summary by the IUCN (Figure 1) and an equivalent analysis for European threatened freshwater fishes (Freyhof

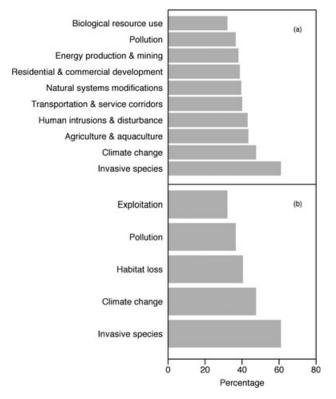


Figure 1. Proportion of global freshwater species threatened within each of (a) all IUCN threat categories, and (b) main categories of threat (redrawn from Darwall and Freyhoff, 2016, with permission from Cambridge University Press). In (b) habitat loss was calculated as the average of six IUCN threat categories: Residential and commercial development, Agriculture and aquaculture, Energy production and mining, Transportation and service corridors, Human intrusions and disturbance, and Natural systems modifications.

and Brooks, 2011). Both follow the IUCN's unified threats classification scheme (Salafsky *et al.*, 2008) comprising 12 major direct threat categories (Figure 1(a)). The following sections discuss the most serious threats (Figure 1(b)), followed by a comparable analysis for marine species.

Habitat loss and degradation

Damaging modifications to freshwater systems are ubiquitous, ranging from complete destruction or fragmentation to degradation of physical structures and vital environmental regimes and resources.

Dams and alteration of river flow patterns form one of the clearest threats by directly blocking, damaging and reducing river and floodplain habitats (Vörösmarty *et al.*, 2010). Artificial lakes are created upstream and the dam wall usually acts as a barrier to upstream and downstream fish and invertebrate migrations, consequently fragmenting meta-populations (Fagan, 2002). Many threatened diadromous species, such as salmonids, eels (Anguilla spp.), striped bass, shads (Alosa spp.), river sharks (Glyphis spp.), largetooth sawfish (Pristis pristis), and sturgeons (Acipenser spp.), are prevented from migrating by the fragmentation of rivers by dams. Facilities designed to allow fish passage are frequently ineffective (Olden, 2016). Within the newly created or enlarged water body itself, subsequent volatility in water levels often has adverse impacts on native fish spawning, nursery or feeding areas (Winfield, 2004). Dam operations often dampen or remove seasonal flow patterns that govern fish life-history strategies, such as flood pulse spawning. Cool hypolimnetic releases can lead to reductions in spring-summer temperatures, causing significant population declines or local extinctions of native fishes, such as in the Colorado River (Olden and Naiman, 2010). Modified riverine habitats, artificial lakes above dams and ponded areas formed along fragmented river channels often harbour invasive non-native fishes (Bunn and Arthington, 2002). The disturbances caused by the barrier effects of dams, floodplain levee banks and flow alterations often propagate downstream, where the consequences may include drying of coastal wetlands, reduced sediment and nutrient inputs, increased estuarine and near shore salinity, fragmented migration corridors, and loss of habitat diversity followed by impacts on fish diversity and fishery stocks.

Riparian loss and degradation also affect the ecological functioning of river systems and aquatic biodiversity. Impacts on fish are associated with alterations to shading and the thermal characteristics of streams, the failure of diminished vegetation to intercept runoff and filter sediments and nutrients, loss of bank stability, degraded aquatic habitats and reduced energy subsidies (Pusey and Arthington, 2003). At the landscape scale, deforestation and associated sediment runoff pose significant threats for freshwater systems. For example, 60% of Madagascar's native fishes are affected by sedimentation of aquatic habitats resulting from deforestation and regular burning of grasses on the pseudo-steppe (Benstead et al., 2003).

Invasive species

Fish have been introduced to freshwater habitats intentionally for aquaculture and recreational fishing (e.g. cichlids, salmonids) and biological control (e.g. mosquitofishes - Gambusia spp.). Unintentional introductions occur through ballast-water discharge from shipping, bait-bucket releases by anglers, and escapes from the ornamental fish trade and fish farms (Canonico et al., 2005). In many developed countries there has been a general decline in fish invasions caused by deliberate releases (e.g. fish stocking), in part due to positive responses from fishing communities to awareness raising (Winfield and Durie, 2004) whereas invasions related to shipping, the aquarium trade and other unintentional releases have increased (Winfield et al., 2011).

Invasive species threaten native taxa by predation, competition, habitat alteration, hybridization and the transfer of parasites and diseases (Strayer, 2010; Sheath *et al.*, 2015). Release of the piscivorous Nile perch (*Lates niloticus*) into Lake Victoria (African Rift Valley) has contributed to the threats to some 81 native fish species (Snoeks, 2000). Several species of *Gambusia* (Poeciliidae) introduced for biocontrol of pest mosquitoes threaten native fish species in numerous freshwater habitats by preying on eggs, competition for food and aggressive behaviour (Pyke, 2008).

Introduced plants also have impacts on river, wetland and lake ecosystems and indirectly, fish. Invasive plants such as the ponded pasture grass (*Urochloa mutica*) and water hyacinth (*Eichhornia* spp.) disrupt the hydrology, habitat structure, native fish communities and ecological processes of streams and wetlands (Perna *et al.*, 2012), including those of fresh waters as large as Lake Victoria (Villamagna and Murphy, 2010). Furthermore, by changing habitat structure in streams and wetlands, non-native plants can facilitate the establishment of non-native fishes.

Water pollution

Pollutants that affect freshwater fishes are derived from direct discharges by industries, mining developments, land-based runoff from agriculture and urban areas, and atmospheric deposition.

Inland water bodies (including even some of the planet's largest lakes) are particularly vulnerable because they typically lack the volume of open marine waters, limiting their capacity to dilute contaminants or mitigate other impacts (Dudgeon et al., 2006). Such contaminants do not have to be directly damaging to fish to have an adverse impact. For example, the widespread problem of eutrophication is commonly driven by an excess of macronutrients such as phosphorus which have been added to catchments to increase agricultural productivity (Winfield, 2015). Although the resulting elevations in phosphorus concentrations do not impinge on fish directly, they can have significant indirect effects by reducing oxygen availability, increasing sedimentation on spawning grounds and altering competitive balances. Massive fish kills have resulted from point source toxic discharges at the reach scale of rivers and, in along large river some cases. distances downstream from the point of discharge, as well as in wetlands and lakes (Kangur et al., 2013). At least eight of the 13 globally extinct species of European freshwater fishes were 'victims of water pollution and lake eutrophication' (Freyhof and Brooks, 2011).

Overfishing

Inland fisheries are diverse, multi-species and geographically diffuse, involving commercial, subsistence. recreational and aquaculture components (Cooke et al., 2016). Fishing pressure is often intense in many capture fisheries where large apex predators face the 'double jeopardy' of high value and long life (Winemiller et al., 2016a). Overfishing for food or to provide ornamental aquarium species often exacerbates the pressures on fish populations depressed by other threats. For example, illegal fishing and overfishing, in combination with obstructed migration routes and pollution, have driven 21 of the world's 27 species of sturgeons and paddlefishes (Acipensiformes) to critically endangered status, and at least one species may already be extinct (Jarić et al., 2009). Intense multi-species fishing can lead to the syndrome of 'fishing down the food web' - the successive removal of large individuals and species of high value and their replacement by smaller fish at lower trophic levels (Castello *et al.*, 2015). In areas with a preference for small species and individuals (e.g. Africa) or the use of small fish in pastes and sauces (e.g. Asia), fishing pressure can deplete the entire assemblage.

Climate change

Shifts in climatic regimes and associated alterations to global precipitation and runoff patterns, evapotranspiration rates and other environmental regimes are already bringing about changes in flow and thermal regimes, longer and more severe drought episodes, and more intense and frequent storm events followed by flooding (IPCC, 2007). Rising temperatures, hydrologic intensification and sea-level rise are all expected to exert impacts on freshwater ecosystems across the spectrum of fish individuals, populations, species and communities (Heino et al., 2016), including those supporting fisheries (Winfield et al., 2016a). Patterns of warm-water cyprinid increases and cold-water salmonid decreases are already apparent in European lakes (Jeppesen et al., 2012), including declines in the salmonid Arctic charr (Salvelinus alpinus) (Figure 2) in areas such as the UK towards the southern limit of its circum-polar distribution (Winfield et al., 2010).

The effects and implications of climate change, itself a complex mix of stressors, are increasingly recognized as a further complication of the 'multiple stressor' problem - the exposure of ecosystems and biota to multiple stressors acting simultaneously or sequentially (Ormerod et al., 2010). Climatic shifts are of growing concern, not least because the consequences of complex synergies with intensified threats may produce unexpected outcomes and 'no analogue' or 'novel' systems (Strayer, 2010; Acreman et al., 2014). For example, Edeline et al. (2016) have shown that a recent water temperature increase has had a significant impact fish predator-prev on interactions within a large temperate lake. Deciding how best to maintain or restore aquatic systems subjected to multiple stressors, including climate change, will challenge managers and planners, as discussed below.

THREATS TO MARINE FISHES

In the marine realm the principal threats are overfishing and habitat loss, based on syntheses of threatened North American marine fishes (excluding salmonids, Musick *et al.*, 2000) and a global analysis of 65 local, regional and global marine extinctions (Dulvy *et al.*, 2003) (Figure 3).

Figure 2. A pair of Arctic charr *Salvelinus alpinus* (male in the foreground) near their spawning ground in the inflowing River Liza of Ennerdale Water, U.K. Photograph © Linda Pitkin/naturepl.com. Published with permission.



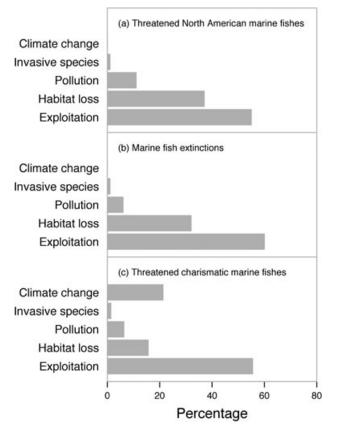


Figure 3. (a) Proportion of marine, estuarine and diadromous fish stocks at risk of extinction in North America in 2000; (b) local, regional and global marine fish extinctions in 2003; (c) threatened charismatic species in 2012.

More than half (55%) of North American marine fishes were threatened from overfishing and 60% of marine fish extinctions were caused primarily by overfishing (Figure 3(a), (b)). The secondary threat was habitat loss and degradation (38% N American fishes threatened; 32% of marine fish extinctions) followed by pollution (11%) N American fishes threatened, 5% of marine fish extinctions). In the early 2000s threat and extinction risk caused by marine invasive species was comparatively minor (<2-3%; Reynolds *et al.*, 2005). Climate change was barely on the radar, yet the first global coral reef bleaching event occurred in 1998-2002 causing mass loss of coral and the temporary disappearance of obligate corallivores and coral dwellers, such as the orange spotted filefish (Oxymonocanthus longirostris) and some newly discovered gobies in Papua New Guinea (Munday, 2004).

Since then there has been one additional thematic summary of the status of some of the most charismatic marine organisms (McClenachan et al., 2012). Choosing which species to include is fraught with difficulties, and a pragmatic solution was to focus on those 1568 species from the 13 families where representative species had 'speaking' parts in the film Finding Nemo. This list is inevitably biased, but in an interesting manner. It focuses on shallow water, mainly coral reef species in the Indo-Pacific coral triangle – undeniably the most megadiverse marine biodiversity hotspot in the world and subject to numerous threatening processes (Carpenter and Springer, 2005; Tittensor et al., 2010). This analysis reveals that one in every six species related to characters in *Finding Nemo* is threatened by extinction (McClenachan et al., 2012). Sixteen percent (12-34%) of those that have been evaluated are threatened, with an average of 9% (7–28%) of bony fishes threatened. The principal threatening process was still overfishing (55%), but following the 1998 ENSO event, climate change (21%) has overtaken habitat loss and degradation (15.6%) as a driver of threat in this region.

As for freshwater systems, the following sections discuss the most serious threats to marine fishes in order of severity.

Overfishing

Fishing is one of the most pervasive yet hidden threatening processes, yet we have little sense of the map of fishing mortality. Instead, these are indirect measures of fishing mortality, imperfectly represented as estimates of numbers of fishers (Teh et al., 2013) and spatial maps of expanding fishing effort, catch, and activity (Anticamara et al., 2011; Pauly and Zeller, 2016). We also have a far better sense of the dose-response relationship between climate change and marine ecosystems and indeed there are sufficient future projections of climate change to drive ecosystem and economic models of future fish and fisheries (Cheung et al., 2010; Merino et al., 2012). Understanding of the biodiversity impact of overfishing is compounded by its long history, the absence of systematic data collection for much of the world's coastal seas and

oceans until recently, and the 'shifting baseline' psychology that means we are blind to changes prior to our human experience (Thurstan *et al.*, 2015). As an example, overfishing is the main cause of decline and near extinction of iconic species including sawfishes (Everett *et al.*, 2015; Dulvy *et al.*, 2016), and the giant yellow croaker (*Bahabia taipingensis*; Sadovy and Cheung, 2003). These taxa depend on, and are highly catchable in, estuarine habitats (Figure 4).

Habitat loss and degradation

The scale of habitat loss and degradation in the marine environment is far lower than that in fresh waters; nevertheless, there are concerning trends particularly in shallow tropical ecosystems. The conversion of mangroves into shrimp farms to supply western seafood demands has led to the loss of more than one-third of the global extent of mangroves in just half a century (Alongi, 2002). The consequences for fish biodiversity and fishery catches (artisanal, recreational, industrial) from mangrove loss are complex (Blaber, 2007), but may well contribute to sawfish declines (Dulvy *et al.*, 2016).

Seagrass coverage is shrinking globally and the principal causes are declining water quality, other species (including invasive species), habitat conversion, and direct damage (Orth *et al.*, 2006).

Almost 30% of the global area of seagrass was lost between 1879 and 2006, with the annual rate of loss accelerating after 1980 (Waycott et al., 2009). Seagrass loss is associated with declines in fish biodiversity and fishery catches (Orth et al., 2006; Blandon and Ermgassen, 2014) and impacts on seagrass-dependent threatened species. An estimated 58 species of fish listed as threatened or vulnerable depend directly on seagrass during at least one stage of their life cycle, including species syngnathids, 21 species 31 of of species actinopterygian fishes, and six of chondrichthyans (Hughes et al., 2009). This is likely to be an under-estimate because of the number of seagrass-associated species whose conservation status has not been assessed and the numbers of species with an indirect association with seagrass.

Caribbean coral reefs have lost 80% of coral cover and complexity in the past half century, owing to a combination of urchin outbreak and die-off, hurricanes, disease and coral bleaching induced by climate change (Gardner *et al.*, 2003; Alvarez-Filip *et al.*, 2009), which has led to annual declines in fish abundance of 2.7-6% (Paddack *et al.*, 2009). As a consequence of widespread coral loss over the 1998 ENSO event, up to a third of reef-building corals have declined in cover to the point where they were categorized in one of the IUCN Red List threatened categories (Carpenter *et al.*, 2008).



Figure 4. Largetooth sawfish Pristis pristis in an aquarium. Photograph by David Wachenfeld. Published with permission.

In addition to direct loss and degradation of habitats, near-shore and reef-associated fish face habitat-degrading threats originating from land, such as coastal residential and commercial development. which predominantly affects seahorses (Syngnathidae; McClenachan et al., 2012). Endemic marine fishes in the Eastern Tropical Pacific (Polidoro et al., 2012), and elsewhere are threatened by habitat loss. For example, the endemic Ascension Island white hawkfish (Amblycirrhitus earnshawi) has an area of occupancy of 22 km² threatened by military and industrial development, emerging fisheries and tourism (Carpenter et al., 2015). However, the greatest effects of habitat loss and degradation are most profound for diadromous fishes, such as sturgeons, shads and alewives, salmon, and eels discussed above and below.

Climate change

A wealth of analysis and modelling has shown that fishes and other marine organisms are extending deeper and polewards tracking climate velocities to match their thermal preferences (Sunday et al., 2012). It is increasingly clear that there will be considerable species turnover, local extinction and invasion (Cheung et al., 2009) and the key challenge will be to track local, regional and global species extinctions through Red List Assessment (Stuart et al., 2010). Here we illustrate progress in assessing risk within three of the marine ecosystems most affected by climate change: the Eastern Tropical Pacific (Polidoro et al., 2012), the Indo-Pacific Biodiversity Triangle (McClenachan et al., 2012), and temperate south-eastern Australia (Last et al., 2011).

In the Eastern Tropical Pacific, climate change (mediated through El Ninõ Southern Oscillation (ENSO) events of unprecedented intensity) is the principal threat for bony fishes with 80% (71 of 92 species) affected. This is especially problematic given that most species in this region are very small ranging, primarily island endemics found in shallow inshore waters within a narrow depth zone (Polidoro *et al.*, 2012). Overfishing, as a result of large coastal populations of subsistence and artisanal fishers, is driving elevated extinction risk, particularly in larger-bodied bony fishes (19%, 207 of 1102) and in sharks and rays owing to target fisheries and bycatch retained for meat and fins.

Climate change was second only to overfishing in the Indo-Pacific Biodiversity Triangle, with climate change driving threat status in 64 of 242 species, mainly the highly coral-associated butterflyfishes (Chaetodontidae, n = 52), damselfishes (Pomacentridae, n = 8), a seahorse (Syngnathidae), and a pufferfish (Tetrodontidae) (McClenachan *et al.*, 2012).

The poster child of climate change is not the polar bear but the Galapagos damselfish (Azurina eupalama). This species was found only in the Galapagos Islands and has not been seen in the 25 years since the 1982/1983 ENSO event, which is the first of the ENSOs categorized as 'Very Strong' (http://ggweather.com/enso/oni.htm). Despite targeted searches in the more accessible parts of this species' range, it has yet to be declared extinct, but has been flagged as Critically Endangered (Possibly Extinct) (Allen et al., 2010). The disappearance of this endemic could presage a much greater role for climate change in driving marine extinctions in the coming decade. Temperate south-eastern Australia is a global hotspot for ocean warming related to climate change (Ridgway, 2007). The impacts of ocean warming on fish communities are exacerbated by a history of habitat modification and fishing pressure, and teasing apart the timing and relative importance of each in driving changes in the fish fauna is challenging (Hobday et al., 2007). About 20% of Tasmanian coastal fish species have experienced a change since the late 1800s: five species of large predatory fishes are now absent or occur at very reduced abundances and the distribution of 52 species (17% of the coastal ichthyofauna) has changed. Of these, the changes in 45 species are believed to be climate-related. At least 16 species disappeared from Tasmanian waters between the late 1800s and the 1980s (Last et al., 2011).

Invasive species

On land invasive species are a key driver of extinction risk, particularly for birds and amphibians, but there have been few vertebrate invasions and relatively few species are at risk owing to invasive species in the oceans (Gurevitch and Padilla, 2004). However, we are seeing the spectre of the introduction and invasion of the Indo-Pacific lionfish (Pterois spp.) into the already heavily degraded Caribbean Sea. It is not clear that lionfishes have caused irreversible damage such as extinctions, but it is clear that they are preving heavily on the smallest sizes classes of coral reef fishes and substantially depleting their number (Albins and Hixon, 2008; Green et al., 2014). A number of gobies, and other small species, are listed as threatened because of the potential detrimental effects of this invasive vertebrate, e.g. the Exuma goby (Elacatinus atronasus) is listed as Endangered as a result both of a small geographic range and its high susceptibility to lionfish predation (Pezold et al., 2015).

In Tasmania, the introduction of the invasive North Pacific seastar (Asterias amurensis) further depleted populations of the spotted (Brachionichthvs handfish hirsutus. family Brachionichthyidae) that had already been reduced by habitat damage from a scallop fishery. The seastar may have further reduced numbers of handfish by predation on its egg masses or predation on its preferred spawning habitat (stalked ascidians). The spotted handfish is listed as Critically Endangered (Bruce et al., 1998; Lynch et al., 2015).

Pollution

Despite being highly visible, and subject to considerable media attention, it is far from clear that pollution is an important driver of extinction risk in marine fishes compared with other threats (Figure 3(a), (b)) and by comparison with its importance in fresh water (Figure 1(a), (b)).

CONSERVATION AND MANAGEMENT OF FRESHWATER AND MARINE FISHES

Aquatic ecosystems present unique and difficult challenges for biodiversity conservation and the maintenance of the goods and services that humans derive from healthy ecosystems (Halpern *et al.*, 2015; Closs *et al.*, 2016). From the array of

actions available to conserve and restore aquatic ecosystems (Geist, 2015) and their fish populations, three main topics dominate the following discussion: understanding the extent, causes and correlates of extinction risk; the role of conservation reserves; and the restoration and management of aquatic habitats, fish populations and fisheries.

Assessment of extinction risk

Conservation of the world's freshwater and marine fishes will require management and restoration strategies focused on species at the greatest risk of extinction. Assessment of extinction risk presents an enormous challenge vigorously addressed over the past decade by the IUCN's Global Marine Species Assessment (GMSA) and the Freshwater Fish Specialist Group (FFSG) and partners. Both groups are about halfway towards assessing extinction risk for all described fish species. several taxonomic and regional Although summaries have been published, they are neither representative of wider freshwater and marine fish diversity nor complete in either realm.

Levels of extinction present the most depressing part of global IUCN and national threat assessments for freshwater and marine fishes. Yet there is always the possibility that remnant populations will be discovered, especially where habitats are difficult to sample and the chances of finding rare species are low. For example, the Eacham rainbowfish (Melanotaenia Lake eachamensis) was recorded as extinct in its only wild habitat (deep volcanic Lake Eacham on the Atherton Tableland, north Queensland) until careful surveys found it in tableland streams nearby (Pusey et al., 1997). A less dramatic example of the apparent local extinction of a lacustrine vendace (Coregonus albula) population being 'reversed' by natural recolonization from a nearby lake is provided by Winfield et al. (2016b). Science has yet to save a marine species, but work is proceeding to secure a future for sawfishes and devil and manta rays through conservation planning (Dulvy et al., 2016; Lawson et al., 2016). Such examples aside, a designation of extinct in the wild usually means no further options for recovery planning or population restoration, whereas an IUCN threat listing offers opportunities for conservation action that may protect the listed species as well as associated habitats. Harrison and Stiassny (1999) advocate a systematic and cautionary approach to declarations of extinction, but this 'evidentiary' approach risks overlooking and acting upon species that are headed to extinction – IUCN instead recommends a precautionary approach to assessment (Collen *et al.*, 2016).

Of more concern for global fish conservation is the 'extinction debt' – the number or proportion of species (or populations) expected to become extinct as the fish assemblage reaches a new equilibrium following environmental disturbance (Kuussaari et al., 2009). Many fish species may already be doomed to become locally, regionally or globally extinct but remain undetected by methods currently available to predict delayed extinctions. Early predictions of species likely to become extinct over time but still remaining extant should encourage systematic conservation planning of reserves and other conservation or restoration actions tailored to mitigate individual and interacting stressors.

Correlates of extinction risk

Risks of extinction are greatest for those species adapted for life in large rivers, small streams, lakes and arid freshwater environments, inland marine habitats, estuaries, reefs and other shallow marine habitats, and among endemic species restricted to very small, isolated habitats such as springs and caves (Leidy and Moyle, 1997). Isolated and fragmented habitats typically present the most challenging environments, especially for small fish species exposed to human disturbances. However, isolated habitats, being spatially confined, are often readily identified (e.g. by remote sensing methods) and practical management activities are likely to be well targeted, largely local and more readily executed and monitored than in large water bodies. Such relatively small water bodies also tend to have relatively simple ownership arrangements, which may greatly simplify and so expedite practical management actions. Recovery of the critically endangered red-finned blue-eye (*Scaturiginichthys vermeilipinnis*) confined to isolated springs of Australia's Great Artesian Basin (Kerezsy and Fensham, 2013) is one example.

Another thread in efforts to assess extinction risk has been the study of characteristics, or traits, that predispose fishes to risk. The most threatened freshwater species generally have small body size, specialized requirements (habitat and/or diet), low fecundity, low population size, low dispersal capability, and are often geographically isolated or live in fragmented habitats. The group of freshwater fishes commonly known as mudminnows (formerly known as the family Umbridae but recently reclassified as Esocidae) are a typical example (Kuehne and Olden, 2014) while desert fishes (e.g. Catostomus and Gila spp.) comprise perhaps the most extreme freshwater example (Fagan et al., 2002). Small coral reef species such as angelfishes (Pomacanthidae), damselfishes (Pomacentridae) and wrasses (Labridae) face the same triple jeopardy of extinction risk as small freshwater species - small geographical ranges, small population sizes, and specialized habitat requirements (Polidoro et al., 2012).

Large species can be very susceptible to local extinction if they have limited tolerances to changing environmental conditions and limited dispersal options. However, by far the greatest threat to larger species of marine and freshwater fishes is overfishing. Their size and high economic value stimulate intense commercial or artisanal fishing pressure in most parts of the world, while the predatory habits of many large species also make them prime targets for sport fisheries. In Asian rivers, seven large, long-lived endangered and/or migratory species are or critically endangered (e.g. giant Mekong catfish - Pangasianodon gigas) by overfishing and habitat fragmentation by dams (Dudgeon et al., 2006).

In marine systems, the most widely understood and best-supported correlate of fish population decline and extinction risk (as a result of overfishing) is maximum body size, usually indexed as total length (Reynolds, 2003; Juan-Jordá *et al.*, 2015). Body size can be measured with little error and is indirectly related to 'speed of life' traits, particularly growth completion rate (k of the von Bertalanffy growth equation) and longevity that best describe a species' extent and rate of decline (Juan-Jorda *et al.*, 2015). Both body size and depth limits reflect accessibility by fisheries and degree of exposure to fishing mortality, and provide accurate estimates of risk for data deficient groupers and chondrichthyans (Dulvy *et al.*, 2014; Luiz *et al.*, 2016). Whole animal value appears to be a strong correlate of extinction risk, particularly for the most valuable megafauna that are traded internationally (Collette *et al.*, 2011; McClenachan *et al.*, 2016).

Many species of fish, which are relatively long-lived and late-maturing, are exposed to 'ontogenetic jeopardy' in which they sequentially encounter a series of environmental threats resulting from ontogenetic movements between very different habitats (e.g. between stream, river and estuary and the return journey) or due to ontogenetic changes in their abilities to cope with such threats. Mobile or diadromous fishes that traverse and use a variety of habitats along their migration pathways face a long and diverse series of environmental threats in an extreme form of ontogenetic jeopardy (McIntyre et al., 2016). Accounting for scenarios of ontogenetic and other jeopardies can focus restoration interventions on habitats and migration pathways that most limit long-term prospects for freshwater, marine and diadromous fishes.

Conservation reserves

Conserving the world's fishes in the long term will require mixtures of management actions. The mix must include conservation reserves that protect species-rich habitats and vital resources, important species radiations, and the greatest number of threatened endemic species. To be most effective, freshwater protected areas should have control over the upstream drainage network, the surrounding land, the riparian zone, and downstream reaches (Dudgeon *et al.*, 2006), and maintain both connectivity pathways and habitat patchiness.

Recent developments in systematic conservation planning for rivers include methods to incorporate

longitudinal, lateral (river to floodplain), vertical (surface-groundwater) and temporal connectivity as well as accounting for threatening processes that may compromise biodiversity protection (Linke et al., 2012) including climate change (Pittock et al., 2008). Planning and legislation for conservation reserves also has to consider the socio-economic landscape and identify opportunities for maximum protection of biodiversity within the constraints of catchment land-use, river infrastructure, human activities and climate change. For example, strategic conservation planning is urgently needed in species-rich basins threatened by numerous new hydropower dams, such as the Mekong, Congo and Amazon basins (Frederico et al., 2016; Winemiller et al., 2016b).

Conservation plans are usually developed for regions that encompass only one environmental realm (terrestrial, freshwater or marine) because of logistical, institutional and political constraints (Beger et al., 2010). However, the persistence of many species and ecosystem functions involves connectivity between realms, such as riparian influences on streams, migrations of diadromous fishes across the freshwater-marine interface, and the dependence of floodplains and estuaries on freshwater flows (Arthington, 2012; Kingsford, 2015). The integration of processes that connect terrestrial, freshwater and marine realms in appropriate configurations promises more effective conservation outcomes for fish. For example, estuaries should not be managed as isolated systems but as part of comprehensive plans for catchments, rivers and coastal habitats. In the Salmon River estuary, Oregon, removal of levees expanded rearing habitats for juvenile salmonids and restored pathways connecting freshwater to saltmarsh habitat, enhancing population resilience at the catchment scale (Flitcroft et al., 2016).

Despite the challenges of integrating management across realms, the aim is achievable. In Australia, Reef Plan (2013) aims to reduce damage from land-based agricultural practices on the Great Barrier Reef (GBR), essentially managing land use in catchments to reduce the input of sediment and nutrients into waters of the GBR. The Reef Plan involves considerable public funding and cooperation from farmers and the first two years of the programme reduced anthropogenic suspended sediment load by 6% (Brodie, 2014). The Plan involves cooperation among the Commonwealth marine reserve (the Great Barrier Reef Marine Park), Queensland State Government agencies, and the farming sector.

Marine reserves can also produce increases in species richness, abundance, biomass, length, and fecundity of groups of species that are fished elsewhere (McCook et al., 2010; Edgar et al., 2014;); recovery of habitats (Babcock et al., 1999); resistance to ecological disturbances (McCook et al., 2010); and spillover of adults or export of larvae (Russ and Alcala, 2011; Harrison et al., 2012). The existence and magnitude of these responses depends upon a reserve's area, age, extent of fishing exclusion, degree of isolation from surrounding habitats, and compliance with management regulations (Ballantine, 2014; Edgar et al., 2014). Despite these benefits, the implementation of marine reserves has been contentious with some stakeholder groups (Agardy et al., 2003; Voyer et al., 2012; Gladstone, 2014) or criticised for not adequately protecting biodiversity (Edgar, 2011; Devillers et al., 2015). Progress in the appropriate use, site selection and design of marine reserves needs to address questions relating to the ability of reserves to meet both biodiversity and socio-economic objectives, the impacts of climate change, efficacy of surrogates for biodiversity and socio-economics, opportunity costs, and their place in ecosystem-based management (Devillers et al., 2015; Fulton et al., 2015; Ruiz-Frau et al., 2015).

Restoration and management

Human activities and stressors that threaten freshwater and marine fishes are likely to become more widespread, intense and damaging unless they are curbed through prevention, improved management (e.g. fisheries) and restoration or adaptation programmes.

In the freshwater realm, decades of research and practical experience provide ample guidance on methods for integrated catchment management (Collares-Pereira and Cowx, 2004), restoration of aquatic habitats (Roni *et al.*, 2008), dam

management and removal (Olden, 2016), provision of environmental flows (Arthington, 2012) and restoration of riparian and floodplain processes (Naiman *et al.*, 2010; Kingsford, 2015). Fished populations can be rehabilitated by applying appropriate regulations (e.g. catch-and-release), no-take zones in critical areas for breeding and recruitment, and even managed relocation and reintroductions (Cooke and Schramm, 2007).

Recovery programmes range from individual species to the fauna of entire river basins. Numerous studies integrate basic knowledge of fish biology and focused threat assessment into individual species' recovery plans. Conservation of the vendace and whitefish (*Coregonus lavaretus*), the UK's rarest freshwater fishes, has involved protection and improvement of their habitats and the establishment of refuge populations (Winfield *et al.*, 2012, 2013). A remarkable effort at basin scale is the rehabilitation of fish communities throughout Australia's Murray–Darling Basin, where native fishes are subject to severe impacts by many stressors (Koehn and Lintermans, 2012).

The exposure of freshwater systems and their fishes to many different coincident or sequential stressors intensifies ecological impacts and vastly complicates restoration and conservation planning, especially where spatially diffuse stressor multiple jurisdictions syndromes span and legislation, management agencies, or nationalities (Closs et al., 2016). The management of freshwater fishes under scenarios of climate change may be the greatest conservation challenge in regions where aquatic ecosystems are already exposed to multiple interacting stressors. The underlying science builds on two spheres of research – conservation physiology and conservation biogeography (Olden et al., 2010; Heino et al., 2016). Even without data-intensive research, simple and easily coded vulnerability analyses can be used to determine conservation priorities (Moyle et al., 2015).

In the marine realm overfishing, compounded by under-assessment, under-management, and international trade for valuable meat, fins and live animals for the aquarium trade, is the overwhelming threat and warrants particular attention. The bulk of the world's larger economically important industrial fisheries are relatively well-monitored and well managed; for example, most of the world's market tuna catch is assessed and managed within safe biological limits. However. there are serious sustainability challenges facing the internationally traded and valuable bluefin tunas (Collette et al., 2011). Of the 51 Scombridae species there are 32 data-poor species subject to target fisheries of which 10 species are in either a threatened or a Data Deficient IUCN category. This is a not uncommon and highly risky prospect, especially for those poorest people in tropical coastal nations who often relv on Spanish mackerels (Scomberomorus spp.) and other mackerels (Rastrelliger spp.) to support their livelihoods and well-being (Juan-Jordá et al., 2013). Furthermore, there is serious under-management of the shark and turtle bycatch of these sustainable tuna fisheries, resulting in serious population declines (Clarke et al., 2013). Progress is being made in the development of the Ecosystem Approach to Fisheries Management at the main tuna Regional Fisheries Management Organisations, but implementation of the most basic scientific assessment, catch limits, and prohibitions of bycatch, particularly of pelagic sharks, is limited (Dulvy et al., 2014).

While limited progress is being made on assessing the bulk of the world's fisheries catch (Pauly and Zeller, 2016), many of the world's fisheries remain unassessed and unmanaged. For example, in the tropics it is estimated that the coral reef fisheries of more than half (55%) of the 49 island countries are unsustainable. Overall, coral reef fisheries are currently taking catches that are 64% higher than can be sustained (Newton et al., 2007). This will only be exacerbated with the continuing growth of human populations and climate change induced coral bleaching that is curbing recovery and fisheries productivity (MacNeil et al., 2015). There are urgent needs to curb fishing mortality and minimize catch of the most endangered species; clearly this will take considerable societal reorganization and attendant development aid in the tropics.

Reducing or eliminating risks to species requires conservation actions at scales from individual examples of habitats to entire ecosystems (including associated catchments) and restoration, as in the freshwater realm. In addition to protection (in conservation reserves or via legislation for habitat protection), efforts to restore mangrove forest and seagrass beds by seed planting or transplants have had mixed outcomes (Golden et al., 2010; Orth et al., 2012). Seagrass restoration has the lowest success rate, with a median survival of 38% compared with 64.5% for coral reefs (Bayraktarov et al., 2016). New approaches, involving the use of artificial substratum facilitate seedling to seagrass establishment, have led to recovery (Tanner, 2014) and their associated biodiversity (McSkimming et al., 2016). Seagrass damage at smaller scales is reduced or eliminated through modifications to the designs of docks (eliminating the shading impacts of traditional docks) (Gladstone and Courtenay, 2014) and by replacing traditional boat moorings with seagrass-friendly moorings (Demers et al., 2013). Habitat enhancement, involving the addition of complexity to artificial structures or the addition of biotic habitat elements to shoreline protection measures, has increased the abundance of seahorses and their prey (Hellyer et al., 2011), established fish assemblages that still differed from natural undisturbed habitats (Peters et al., 2015), and provided food for fish (Ng et al., 2015). Transplanting coral fragments to degraded coral reefs to facilitate juvenile recruitment or adult immigration is feasible but the response times vary from months to years and do not deal with the underlying causes of coral reef loss (Yap, 2009; Merolla et al., 2013).

Even with the sophisticated risk most assessments. conservation planning, fisheries management and restoration tools, improvements in fish conservation present scientists, managers and citizens with significant challenges and trade-offs, especially under novel scenarios of threat and climatic change. Human pressures on marine and freshwater fish and fisheries must be limited to the maximum degree possible, within constraints of food security, to restore resilience and allow human-assisted adaptations to take effect in novel and managed environments. Implementation, monitoring and review of fish conservation and management regimes must feed

new information back and forth between researchers, managers and citizens to achieve consensus on what is worth doing, and achievable, in the uncharted waters of the future.

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