FRESHWATER ECOLOGICAL PRINCIPLES

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Key messages

Five high level ecological principles common to all freshwater ecosystems are presented

Although they have different ramifications for each ecosystem type these principles are fundamental to the design and management of all freshwater Protected Areas (PAs) and the conservation of aquatic biodiversity.

1. A universal guiding principle for PA management is that the entire catchment with its land, water, biogeochemical resources and processes is the ideal unit to be protected and managed. Where full protection is not possible, the catchment needs to be managed in a sustainable way that minimises threats and impacts from non-reserved lands. Protected area management that fails to recognise and address the threats and pressures arising in the catchment risks loss of environmental quality, species diversity and ecological resilience.

2. The flow of water is one of five dynamic environmental regimes that regulate much of the structure and functioning of every running water ecosystem and many aspects of lentic and groundwater systems. The naturally dynamic flow regime plays a critical role in sustaining native biodiversity and ecosystem integrity in streams and rivers. Likewise the characteristics and variability of lentic (lakes and estuaries) and subsurface water regimes are critical to their dynamics, management and conservation.

3. *The spatial and temporal connectivity patterns and processes of aquatic ecosystems in their natural state are important elements for consideration in PA design and management. Connectivity in rivers is defined in three spatial dimensions: longitudinal (upstream–downstream), lateral (interactions between channel and riparian/floodplain systems), and vertical (connections between the surface and groundwater systems), with temporal dynamics influencing all spatial dimensions of connectivity. Thus minimising the impacts of dams and levee banks as barriers, and changes to water flows, is crucial for conservation. The hydrological connectivity between lakes, streams, estuaries and subsurface environments also requires special attention in PA design and management, and forms a central pillar of Integrated Lake Basin Management (ILBM).*

4. *A primary goal of biodiversity conservation is to delineate PAs that conserve species-rich habitats and vital resources, important species radiations and the greatest number of threatened endemic species. Significant interbasin differences in biodiversity and levels of endemism mean a lack of “substitutability” among freshwater habitat units, adding to the complexity of freshwater biodiversity conservation. The tools of systematic conservation planning lend themselves to identification of the most beneficial options for biodiversity protection.*

5. *Freshwater species have long histories of exposure and adaptation to variable environmental conditions and extremes (e.g. drought and flood cycles), conferring resistance and resilience at the individual, community and ecosystems levels. Maintaining catchment integrity, natural flow and standing water regimes, the spatial and temporal dimensions of connectivity, and native biodiversity hotspots will help to maintain the ecological resilience*

of aquatic systems in protected areas, and support societal adaptations to shifting environmental and climatic regimes.

Characteristics of freshwater ecosystems

Freshwater ecosystems, also often referred to as freshwater wetlands, encompass many different types, geomorphic forms and sizes and have been defined and classified in different ways, although not all efforts are systematic or readily comparable (see overviews in Milton and Finlayson, 2017, Gerbeaux et al., 2017). They develop where water that is fresh is the primary factor controlling plant and animal life and the wider environment, where the water table is at or near the land surface, or where water covers the land. While there is uncertainty about the areal extent of surface freshwater wetlands, global estimates suggest that they contain only a small portion of the world's water and surface area, with Gleick's (1996) estimates being about 0.01% and 0.8%, respectively.

Wetlands arise from the atmospheric and precipitation component of the global water cycle that percolates into soils and superficial groundwater, or runs off the land into rivers and other aquatic systems. Flowing or 'lotic' surface waters – streams and rivers – are prominent directional features of most landscapes, even deserts. They exert a significant influence on landscape form and function through erosion, transport and deposition of materials from the mountains to valleys, to inland wetlands and lakes, and to estuaries and the oceans. Lakes, as well as ponds, swamps and estuaries, are 'lentic' water systems that pool or store freshwater. These ecosystems are often linked hydrologically to upstream rivers or tributaries flowing into them, to downstream water systems into which they discharge, and often to sub-surface groundwater. Peatlands are areas of land with a naturally accumulated layer of peat formed under a wide range of vegetation types including lowland or upland fens, reed beds, wet

woodland, bogs, and mangroves. Rivers and springs, lakes, wetlands, peatlands and estuaries may be partly or fully dependent on the surface expression of groundwater, for example as river baseflow and the water in window lakes and desert springs. The hydrologic linkages between these lentic and lotic ecosystems regulate physical, biogeochemical and ecological connectivity, and have important implications for the design and management of PAs.

Five high level ecological principles relevant to all freshwater ecosystems are proposed and presented here. In brief, they relate to i) the intimate links between freshwater ecosystems and the surrounding catchment (basin or watershed); ii) the importance of the water regime (standing, flowing or sub-surface); iii) the hydrological, biogeochemical and ecological connectivity within and between freshwater (and estuarine) ecosystems; iv) protecting evolved patterns and ‘hot spots’ of native aquatic biodiversity and endemism; and v) the importance of these principles to the maintenance of ecological resilience in the aquatic ecosystems of the present and the future. Although these principles have different ramifications for each ecosystem type, they are fundamental to the design and management of all freshwater PAs and the conservation of aquatic biodiversity.

Ecological principles for freshwater ecosystems

Catchment characteristics and processes

Freshwater ecosystems are deeply influenced by the characteristics of the catchment (basin or watershed) in which they are situated and from which most receive their water. “In every respect, the valley rules the stream” (Hynes, 1975). Their low position in landscape valleys means that rivers, lakes, groundwater dependent ecosystems and estuaries are the recipients of water, sediments, nutrients and organic matter generated from their catchments, as well as wastes and pollutants carried in runoff (Baron et al., 2002). Climate, geology,

geomorphology and vegetation significantly influence these natural delivery processes. However, the natural environmental regimes of catchments are vulnerable to disturbance arising from human activities, such as deforestation and logging, livestock grazing, cropping, salinization, industrial developments, transport infrastructure and urbanization (Allan, 2004; Pittock et al., 2017a,b). Furthermore, the disturbances wrought by catchment landuse, regulated river flows and degraded water quality often propagate downstream into estuaries, deltas and coastal habitats, affecting sediment and nutrient dynamics, estuarine and near shore salinity, habitat diversity, biodiversity and fishery stocks (Adams, 2013).

A universal guiding principle for PA management is that the entire catchment with its land, water, biogeochemical resources and processes is the ideal unit to be protected and managed (Finlayson et al., 2017). Management plans targeting the catchment scale can offer opportunities for protected-area managers to favourably influence stakeholders and neighbouring land use, as well as promoting resilient ecosystems and ecosystem services (Flitcroft et al., 2017). Although catchment scale management is widely advocated and clearly beneficial, gaining management control over relatively large areas of land in order to protect relatively small waterbodies, or the entire length of connected waterways (including standing waters, groundwater and estuaries), is complex and challenging in practice (Dudgeon et al, 2006). Alternative principles for freshwater protected area design and catchment management have been proposed, including identification of multiple-use zones, use of vegetated buffer strips, attention to ecological flow requirements, eradication of alien species (Saunders et al, 2002), the concepts of freshwater focal area, critical management zone and catchment management zone (Abell et al, 2007), and maintaining intact tributaries to achieve river conservation targets since tributaries are generally less regulated than main rivers (Nel et al., 2007).

Although difficult, catchment scale management can be achieved, such as for Kakadu National Park in northern Australia, and even for large downstream protected areas such as coastal waters and reefs. In Australia, Reef Plan (2013) aims to reduce damage from land-based agricultural practices on the Great Barrier Reef by managing land use in upland catchments to reduce the input of sediment and nutrients into freshwater wetlands, rivers and the far distant waters of the reef ecosystem (Brodie, 2014; Pearson et al. 2013). Other examples of successful catchment-scale planning have been documented in the USA (Flitcroft et al., 2009; Margerum, 2012) and Europe (Warner et al., 2012).

An ideal solution is management that integrates protection of catchment and freshwater environments (including estuaries) and connects PAs in these ecological realms, generating benefits over and above those achieved by individual terrestrial and freshwater PAs (Beger et al, 2010). This approach would have the advantage of protecting important parts of the catchment, the riparian zone and the floodplain as well as the biodiversity and habitats within river channels and the processes that link these systems (Dudgeon et al., 2006; Pusey and Arthington, 2003). Further downstream, estuaries should be managed as part of comprehensive plans for catchments, rivers and coastal habitats, rather than as isolated systems (van Niekerk and Turpie, 2012). As an example, removal of levees in the Salmon River estuary, Oregon, 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).

Protected area management that fails to recognise and address the threats and pressures arising in the catchment risks loss of environmental quality, biodiversity and ecological resilience, as has been highlighted with freshwater PAs along the Murray-Darling River in

south-eastern Australia (Pittock and Finlayson, 2011) and in Kruger National Park, South Africa, where upper tributaries of the park's rivers flow through developed catchments (Roux et al, 2008).

Water regimes and eco-hydrological principles

The flow of water is one of five dynamic environmental regimes that regulate much of the structure and functioning of every stream and river ecosystem and many aspects of lakes, estuaries and groundwater systems - water, sediments, chemicals and nutrients, organic matter, light and temperature (Baron et al, 2002). A river's flow regime defines the rates and pathways by which precipitation enters and circulates within river channels, wetlands, floodplains and connected groundwater systems, and the residence time of water in the surface and groundwater compartments of the fluvial hydrosphere. Ecologists recognise five ecologically relevant characteristics of natural stream and river flow regimes – the magnitude, frequency, timing, duration, rate of change of hydrological conditions, and the predictability of these flow patterns (Richter et al, 1996; Poff et al, 1997). Taken together, the five facets of a river's flow regime provide a summary of the hydrological character of the system, as well as details of individual flow events and temporal patterns of profound ecological significance: for example, seasonal patterns of discharge (e.g. summer or winter floods, timing of dry spells), whether the flow is ephemeral (flowing briefly only after storm events), intermittent (flowing after storm events and during wet seasons when fed by groundwater) or perennial (with year round flows), the seasonal (or intermittent) timing, extent and duration of floods and dry periods, and the overall variability and predictability of flows over days, months and years (Arthington, 2012).

Flow has been called the “master variable” or the “maestro ... that orchestrates pattern and process in rivers” (Walker et al, 1995). The naturally dynamic flow regime plays a critical

role in sustaining native biodiversity and ecosystem integrity in streams and rivers, and this “natural flows paradigm” underpins universal principles of river conservation, restoration and environmental flow management (Poff et al, 1997; Bunn and Arthington, 2002). These issues have been widely explored for the Amazon River and its tributaries where natural pulse flows are seen as critical for sustaining the high biodiversity and productivity of the floodplains (Junk, 2000). Likewise the characteristics and variability of lakes and subsurface water regimes are critical to their dynamics, management and conservation (Arthington et al, 2017).

Bunn and Arthington (2002) proposed four guiding eco-hydrological principles driving freshwater biodiversity in unaltered rivers and their floodplains, and illustrated how altered flow regimes can affect aquatic biodiversity (Figure 4):

- Flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition. Modified flow regimes alter habitat at varying spatial scales and influence the distribution and abundance of species and the composition and diversity of aquatic communities. Bunn and Arthington (2002) record numerous examples of biotic responses to altered flow regimes in relation to flow induced changes in habitat. Dams managed to generate hydroelectricity can be particularly damaging by severely altering downstream flows to the extent of dewatering entire river reaches and aquatic habitats, or by imposing daily water level fluctuations that strand aquatic species or disrupt fish spawning and larval emergence (Renofalt et al, 2010).
- Aquatic species have evolved life history strategies primarily in direct response to the natural flow or water regime. Flow pattern and water temperature have a major influence on shaping the life history strategies of aquatic species and alteration of

flow regimes can lead to recruitment failure, such as for salmon in North American streams (Lenhardt et al, 2006) and sturgeon in Europe and Russia (Safford and Norman, 2011). Cold-water releases from the deep hypolimnion of impoundments can lead to reductions in spring–summer temperatures downstream and cause significant population declines or local extinctions of native fishes, such as those of the Colorado River, USA (Olden and Naiman, 2010). The management of environmental flow releases from stratified impoundments must give consideration to downstream water temperatures in tandem with flow patterns (Rolls et al., 2013).

- Maintenance of natural patterns of longitudinal and lateral connectivity is essential to the vitality of populations of many riverine species. Loss of longitudinal and lateral connectivity through construction of barriers can lead to isolation of populations, failed recruitment and local extinction of fish and other aquatic biota. Many threatened diadromous species, such as salmonids, eels (*Anguilla* spp.), striped bass, shads (*Alosa* spp.), river sharks (*Glyphis* spp.), largemouth sawfish (*Pristis pristis*), and sturgeons (*Acipenser* spp.), are prevented from migrating by the longitudinal fragmentation of rivers by dams (Arthington et al., 2016). Large hydroelectric dams proposed or planned for the Andean tributaries of the Amazon River would cause the first major break in connectivity between protected Andean headwaters and the lowland Amazon (Finer and Jenkins, 2012). In the lateral dimension, the regular flood pulses of tropical rivers create hydrological connections with backwater habitats and the floodplain, generating food-rich habitats used for rearing of young fish and adult growth. Numerous studies highlight how loss of these connections can cause declines in fish diversity along rivers and reduced floodplain fisheries production (Junk, 2000; Welcomme et al, 2006).

- The invasion and success of alien and translocated species in rivers is facilitated by the alteration of flow regimes and IBTs. Flow regulation and the creation of large human-made lakes can affect the establishment, spread and persistence of introduced species. Examples include the establishment of large mats of the floating fern, *Salvinia molesta*, in human-made lakes, such as Lake Kariba in southern Africa (Mitchell and Tur, 1975). Introduced species of *Gambusia* (Poeciliidae) have established in many regulated rivers and wetlands (often in association with alien vegetation) where their competitive predatory behaviour can seriously depress native fish and invertebrate populations (Pyke, 2008). Inter-basin transfers of water (IBTs) and artificial connectivity can act as a major mechanism for the transfer of alien and pest species between catchments. The movement of species through the Volga-Baltic Waterway connecting the Caspian basin with the Baltic region, is one example that has enabled translocation of many aquatic species, as well as the Main-Danube Canal that has allowed many Ponto-Caspian invertebrate species to reach the Rhine basin and from there to disperse further (Finlayson and D'Cruz, 1995). Lake trout (*Salvelinus namaycush*) declined in the upper Great Lakes after the establishment of the parasitic sea lamprey (*Petromyzon marinus*) introduced originally via the Welland Canal between the Welland and Niagara rivers. The zebra mussel (*Dreissena polymorpha*), a prohibited invasive species native to Eastern Europe and Western Russia, was transported to the Great Lakes in the ballast water of ships: their filter-feeding behaviour causes “a withering of the pelagic food web and a flourishing of the littoral food web” (Strayer, 2010). By forming large colonies attached to native American unionid clams this tiny mussel has caused their near

extinction in Lake St. Clair and the western basin of Lake Erie (Schloesser and Thomas, 1994).

The four eco-hydrological principles outlined above with examples of their implications for river management have provided the foundations for holistic environmental flow assessment methods designed to achieve river conservation or restoration through provision of water allocations and other restoration techniques (Arthington, 2012).

Connectivity of freshwater ecosystems

Connectivity in rivers is defined in three spatial dimensions: longitudinal (upstream–downstream), lateral (interactions between channel and riparian/floodplain systems), and vertical (connections between the surface and groundwater systems), with temporal dynamics influencing all spatial dimensions of connectivity (Ward and Stanford, 1989). Population viability of many aquatic species depends on their ability to move freely through the stream network to access habitat, food resources, mates and spawning grounds (Bunn and Arthington, 2002). Aquatic species from shrimps to fish and river dolphins use different habitats at different life history stages, and longitudinal migrations may be an obligatory component of life histories, particularly when migration is associated with breeding (Welcomme et al, 2006). Dudgeon (2010) provides a summary of the impact of dams, along with pollution, on the migration of sturgeon and paddlefish in the Yangtze River with a pessimistic view for the future of many species in this large river. For example, dam construction, reduced access to large tributary lakes, boat collisions and overfishing have been implicated in the decline of the Yangtze River dolphin or baiji, *Lipotes vexillifer*, now declared extinct (Turvey et al., 2007). Diadromous fishes migrate across the freshwater–marine interface, thus connectivity pathways between these aquatic realms must be

recognised and protected from fragmentation by floodplain levees, degraded habitat and upstream dams (Arthington et al, 2016; Flitcroft et al., 2016).

In the lateral dimension, the regular flood pulses of tropical rivers create hydrological connections with backwater habitats and the floodplain, generating food-rich habitats used for rearing of young fish and adult growth (Junk, 2000). Lateral exchanges with the river continue when flood levels fall and water, nutrients, sediments and aquatic species are returned to the channel and its aquatic habitats (Welcomme et al., 2006). Closer to rivers, the riparian zone performs a suite of vital physical and ecological functions, including food and habitat for many species, the regulation of the light environment of flowing and standing water, water temperature, nutrient transfer and sedimentary processes such as bank erosion and deposition (Naiman et al., 2005; Davies, 2010; Capon et al., 2013). Riparian and littoral vegetation stands and root systems contribute physical structure to stream banks and beds, constrain bank erosion and shape channels and wetland aquatic habitat. Logs and other plant fragments contribute to habitat complexity and influence water flows and channel formation. In forested headwater catchments, riparian inputs (leaves, flowers, fruits) provide energy to aquatic food webs through biological processing and decay (Vannote et al, 1980). Large woody debris (LWD) derived from riparian trees and shrubs provides submerged logs and leaf packs where invertebrates and fish find refuge from thermal extremes, protection from predators and safe spawning sites (Pusey and Arthington, 2003). Fish and aquatic invertebrates often decline after riparian clearing and removal of LWD and increase locally in response to LWD additions (Lyon et al, 2009). Salmon enhancement programs over much of the western United States and Canada are replacing wood by direct reintroduction or by leaving large trees growing alongside streams for future supply of timber to waterways.

Many terrestrial and semi-aquatic animals and birds feed and breed on floodplains and in the riparian zone, and depend on access to water during dry periods (Dudgeon et al, 2006). In recognition of the seasonal habitat use and activities of terrestrial, riparian and amphibiotic fauna (frogs, water dragons and snakes, platypus, otters, and many water birds) their water needs are often included in holistic environmental flow assessments (e.g., King et al., 2003).

Surface-groundwater connectivity is the invisible dimension linking aquatic ecosystems.

Lakes, rivers, riparian zones, alluvial floodplains and estuaries have various dependencies on groundwater and on water derived from the unsaturated zone and surface runoff from land (Arthington et al, 2017). The longitudinal, lateral and vertical dimensions of groundwater systems associated with rivers and other GDEs are critical to their functionality. Connectivity with groundwater influences water chemistry, thermal properties, biological composition of subsurface (hyporheic) and surface water communities, and ecological processes therein (Boulton and Hancock, 2006). Hyporheic and stygofauna communities are often surprisingly diverse. Human activities contributing to water-table decline include groundwater abstraction for irrigation, domestic water use and mining, whereas groundwater recharge can be altered by land use (deforestation, afforestation, cropping, urbanisation). Dam construction, water impoundment, river flow regulation, channelisation and the construction of drainage ditches can also interfere with groundwater tables and impact GDEs. Eamus and Froend (2006) stress that “there is no level of groundwater extraction that will not, in the long run, result in declines of natural discharges, with consequent environmental impacts”.

The spatial and temporal connectivity patterns and processes of aquatic ecosystems in their natural state are vital elements for consideration in PA design and management, as discussed above in relation to hydrological connectivity. Large connected areas are especially important for biodiversity conservation because they allow gene flow and opportunities for adaptation

to disturbances (e.g. by migration to more favourable habitats). Paradoxically, artificial connectivity, for example through inter-basin transfers (IBTs) of water, can be detrimental to biodiversity conservation. IBTs can alter the physical and chemical features of the giving and receiving waterbody, and enable species and propagules (seeds, insect eggs, fish larvae) to become established beyond their natural distributional boundaries (Ghassemi and White, 2007). Water transfers within a river system (intra-basin transfers) can also disrupt natural patterns and processes along the river continuum from headwaters to the middle and lower reaches of rivers. The consequences of “unwitting experiments in genetics” (Davies and Day, 1998), when species previously separated in different catchments or tributaries are brought together, are perhaps the most difficult to predict and manage. Biodiversity decline and the loss of future evolutionary potential are likely outcomes in many instances.

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 (Hermoso et al, 2012; Linke et al, 2012), including climate change (Pittock et al, 2008). The hydrological connectivity between lentic and lotic environments also requires special attention in PA design and management, and forms a central pillar of the Integrated Lake Basin Management (ILBM) Platform Process (Arthington et al., 2017).

The principle of connectivity can be broadened further to consider networks of rivers, wetlands and lakes that are never connected hydrologically but form landscape mosaics of aquatic habitat used by mobile water dependent taxa such as insects, turtles and waterbirds (Hermoso et al, 2012) with the latter in particular providing an example where the links can occur within (Bellio et al, 2016) and between continental landscapes (e.g. Boere and Stroud, 2006). Protecting these forms of connectivity, such as migratory bird flyways and the

waterbodies needed for resting and feeding along migration routes, is an important dimension of freshwater biodiversity conservation (Finlayson et al, 2017).

Aquatic biodiversity, endemism and conservation

Freshwater ecosystems support extraordinary biological diversity given that they contain a small amount only of the world's water and cover a very small area of the Earth's surface. At least 15,150 Actinopterygian fishes live in fresh water, and they constitute over 50% of global fish diversity (Carrete Vega and Wiens, 2012) and 25% of global vertebrate diversity (Dudgeon et al, 2006). Freshwater biodiversity in surface ecosystems represents about 2.4% of total global biodiversity, compared to 15% for marine ecosystems, but taking into account the smaller area involved they contain a disproportionately higher number of species (Millennium Ecosystem Assessment, 2005), even relative to more recent analyses that estimate that marine ecosystems contain 25% of all species (Mora et al., 2011). Estimates for global freshwater biodiversity are likely to increase as more species are described from poorly studied habitats such as groundwater and wetlands in remote regions (Finlayson et al., 2017).

The global distribution of freshwater biodiversity and the biotic communities of freshwater ecosystems reflect a long evolutionary history of adaptations to dynamic, heterogeneous environments and the biological processes of colonization, succession and extinction, competition and predation, played out at multiple spatial and temporal scales. The totality of species (biodiversity) in any river or lake at a particular location can be envisaged as a function of the number of species in the regional species 'pool' and the effects of various historical and contemporary processes that selectively remove species from the pool (Smith and Powell, 1971, Jackson and Harvey, 1989, Tonn, 1990). Climate, landscape features and biotic processes act like a series of 'filters' through which species in the regional pool must

pass to have a good chance of persisting at a particular locality (Poff, 1997). Species can only pass through each filter if they possess certain ecological characteristics or ‘traits’ like thermal or velocity tolerances, or their habitat and reproductive needs are met (Poff and Allan, 1995; Poff et al., 2006). The filter model was originally applied to lake fish assemblages (Tonn, 1990). Lake faunas are shaped by past and recent climatic regimes, barriers to dispersal (e.g. catchment divides, saltwater barriers), geomorphology, lake size and habitat diversity, water sources, thermal and chemical regimes, optical characteristics and biotic processes. The isolation of lakes by catchment divides and salt-water barriers limits gene flow and promotes local adaptations, radiations and high levels of endemism. Lake Malawi in the western African Rift Valley has “outstanding fish diversity including 400–800 cichlid species (99% endemic), a radiation of 17 deep-water clariid catfishes (*Bathyclarias* spp.) and many other endemic species” (Dudgeon et al, 2006, based on data from Thieme et al, 2005).

A primary goal of biodiversity conservation is to delineate PAs that conserve species-rich habitats and vital resources, important species radiations and the greatest number of threatened endemic species. Significant interbasin differences in biodiversity and levels of endemism may mean a lack of “substitutability” among freshwater habitat units, adding to the complexity of freshwater biodiversity conservation (Dudgeon et al, 2006), especially in regions with many isolated species-rich aquatic habitats and ancient lineages. Protection of a few such waterbodies may rarely protect all freshwater biodiversity within a region, or even a small proportion of endemic or endangered species.

The tools of systematic conservation planning lend themselves to identification of the most beneficial options for biodiversity protection, especially in that they can simultaneously

address threatening processes that may compromise success (Linke et al, 2012) such as the effects of new dams and flow regulation. For example, Winemiller et al. (2016) call for strategic planning of new hydropower dams to prevent species extinctions and basin-wide declines in fisheries and other ecosystem services in mega-diverse tropical rivers of the Mekong, Congo and Amazon basins.

Ecological resilience

Freshwater ecosystems are exposed to numerous threats and pressures for which the general parameters of ecological outcomes from individual pressures (such as water pollution, flow regulation, habitat loss and alien species) are well established (Ormerod et al, 2010; Pittock et al., 2017a). Although there are many scientific challenges, understanding of the interactions among individual forms of pressure is increasing steadily; for example, altered flow patterns and lowered water temperature below dams can inhibit fish spawning (Rolls et al, 2013). However, new pressures are emerging, such as nanoparticles and different categories of chemicals (endocrines, etc), producing novel combinations of pressures and unforeseen interactions among pressures. Adding to the complexity of disentangling the ecological impacts of interactions is that shifting environmental regimes, such as those associated with climate change (water availability and temperature) and alien species invasions, create new contexts for the impacts of individual and interacting pressures, and are generally expected to exacerbate ecological impacts (Kopf et al. 2015; Capon et al. 2015).

Freshwater species have long histories of exposure and adaptation to variable environmental conditions and extremes (e.g. drought and flood cycles), conferring resistance and resilience at the individual, community and ecosystems levels. Maintaining catchment integrity, natural

surface flows and standing water regimes, and the spatial and temporal dimensions of connectivity, will help to enhance the ecological resilience of aquatic systems in protected areas. Nevertheless there are limits to ecosystem capacity to return to former more natural states, and this may be particularly so where the envelope of environmental conditions is shifting in response to human demands, novel pollutants, invasive alien species and/or climate change (Strayer, 2010; Acreman et al., 2014). How to envisage, plan, configure and manage PAs under climate change is discussed in greater detail by Finlayson and Pittock (2017).

Recommendations to apply ecological principles in PAs

While recognizing that conserving whole river systems in PAs has seldom been a practical management option (Nel et al., 2007) there are ways in which the representation of freshwater ecosystems within PAs could be improved. These include four steps proposed by Nel et al. (2007) and listed here: i) giving explicit consideration to representing freshwater ecosystems in protected areas; ii) understanding the relative contribution different land makes to freshwater conservation in consolidating land around existing protected areas; iii) avoiding the use of rivers to delineate boundaries of protected areas; and iv) using alternative design and management strategies, in combination with existing PAs areas, to protect rivers before they enter the PA. In effect, a mix of strategies will need to be considered, including those that ensure the protection of key, biodiverse freshwater ecosystems and their catchments, programs to avoid or eliminate invasive alien species, and plans that focus on particular species or habitats while reconciling biodiversity conservation with human uses of water (Dudgeon et al, 2006).

There have been many calls for scientists to more effectively communicate with decision makers at all levels of governmental and society to make certain that the values of freshwater ecosystems are recognised and effective cases are made for their conservation. These messages were central to the outcomes of the Millennium Ecosystem Assessment (2005) and given the continuing decline and loss of freshwater ecosystems (Davidson, 2014; Dixon et al., 2015) they are as important now as they were then, possibly more so. The five high level principles proposed and developed here provide a basis for assessing the values of freshwater ecosystems, and also, possibly even more importantly, provide a basis for further communication, including the development of more sophisticated messages and motivations for conservation.

The principles we have proposed speak to the relationships between people and water and the biodiversity components that support our livelihoods and cultures by providing settings for human developments, health and well-being (*sensu* Horwitz and Finlayson, 2011). There are challenges in fostering these relationships but by following the proposed principles we have the basis for a way forward from the ineffective policies of the past. While focussed on ways to conserve freshwater ecosystems and their native species within and beyond PAs, the principles also provide guidance for ensuring beneficial relationships between people, as individuals and societies, and freshwater ecosystems in all landscapes.

In brief, the principles relate to the:

- intimate links between freshwater ecosystems and the surrounding catchment (basin or watershed);
- ecological roles of the water regime (standing, flowing or sub-surface);

- hydrological, biogeochemical and ecological connectivity within and between freshwater (and estuarine) ecosystems;
- protection of evolved patterns and ‘hot spots’ of native aquatic biodiversity and endemism; and
- maintenance of ecological resilience in the aquatic ecosystems of the present and the future.

Although these principles have different ramifications for different freshwater ecosystems, they are fundamental to the design and management of all freshwater PAs and the conservation of aquatic biodiversity, and vital to the maintenance and strengthening of the important relations that occur worldwide between people, fresh water, and ecosystems.

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