

Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries

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Abstract: Freshwater ecosystems and the fisheries they support are increasingly threatened by human activities. To aid in their management and protection, we outline nine key principles for supporting healthy and productive ecosystems based on the best available science, including laws of physics and chemistry apply to ecology; population dynamics are regulated by reproduction, mortality, and growth; habitat quantity and quality are prerequisites of fish productivity; connectivity among habitats is essential for movements of fishes and their resources; freshwater species and their habitats are tightly linked to surrounding watersheds; biodiversity can enhance ecosystem resiliency and productivity; global processes affect local populations; anthropogenic stressors have cumulative effects; and evolutionary processes can be important. Based on these principles, we provide general recommendations for managing and protecting freshwater ecosystems and the fisheries they support, with examples of successful implementation for each strategy. Key management strategies include engage and consult with stakeholders; ensure that agencies have sufficient capacity, legislation, and authority to implement policies and management plans; define metrics by which fisheries resources and management success or failure will be measured; identify and account for threats to ecosystem productivity; adopt the precautionary approach to management; embrace adaptive management; implement ecosystem-based management; account for all ecosystem services provided by aquatic ecosystems; protect and restore habitat as the foundation for fisheries; and protect biodiversity. Ecosystems are complex with many intertwined components and ignoring linkages and processes significantly reduces the probability of management success. These principles must be considered when identifying management options and developing policies aiming to protect productive freshwater ecosystems and sustainable fisheries.

Key words: biodiversity, connectivity, cumulative effects, global processes, habitat, watershed.

Résumé : Les écosystèmes d'eau douce et les pêcheries qu'ils supportent sont de plus en plus menacés par les activités humaines. Afin d'aider leur aménagement et leur protection, les auteurs établissent neuf principes de base pour supporter des écosystèmes productifs et en santé, basés sur les meilleures connaissances disponibles, incluant les lois de la physique et de la chimie appliquées à l'écologie; la dynamique des populations est régie par la reproduction, la mortalité et la croissance; la quantité et la qualité des habitats constituent des préalables pour la productivité du poisson; la connectivité entre les habitats est essentielle pour les mouvements des poissons et de leurs ressources; les espèces d'eau douce et leurs habitats sont étroitement reliés aux bassins versants environnants; la biodiversité peut augmenter la résilience et la productivité des écosystèmes; les processus globaux affectent les populations locales; les agents stressants anthropogènes exercent des effets cumulatifs; et, les processus évolutifs peuvent être importants. Basés sur ces principes, les auteurs proposent des recommandations générales pour l'aménagement et la protection des écosystèmes d'eau douce et des pêcheries qu'ils supportent, avec des exemples de mises en place réussies de plans d'aménagement pour chaque stratégie. Les stratégies déterminantes incluent : l'engagement et la consultation avec les parties prenantes; l'assurance que les agences ont la capacité, la législation et l'autorité suffisantes pour mettre en oeuvre les politiques et les plans d'aménagement; la définition métrique par laquelle seront mesurés les succès ou les

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échecs des ressources et de l'aménagement des pêcheries; l'identification et la prise en compte des menaces à la productivité des écosystèmes; l'adoption de l'approche par précaution dans l'aménagement; viser l'aménagement adaptatif, mettre en place l'aménagement basé sur l'écosystème; tenir compte de tous les services écosystémiques fournis par les écosystèmes aquatiques; protéger et restaurer l'habitat en tant que base des pêcheries; et protéger la biodiversité. Avec plusieurs composantes inter reliées, les écosystèmes sont complexes et l'ignorance des liens et des processus réduit significativement la probabilité du succès de l'aménagement. Ces principes doivent être considérés lorsque l'on identifie des options d'aménagement et définit des politiques visant à protéger les écosystèmes d'eau douce productifs pour des pêcheries durables. [Traduit par la Rédaction]

Mots-clés : biodiversité, connectivité, effets cumulatifs, processus globaux, habitat, bassin versant.

Introduction

Freshwater ecosystems are among the most imperiled on Earth (Richter et al. 1997; Strayer and Dudgeon 2010), with extinction rates of freshwater fauna higher than for many other ecosystems and vastly exceeding historic background rates (Leidy and Moyle 1997; Harrison and Stiassny 1999; Ricciardi and Rasmussen 1999). Freshwater is vital to humans, and clean water is rapidly becoming a limiting resource for many societies (Vörösmarty et al. 2010). The greatest threat to freshwater ecosystems is the loss or alteration of freshwater habitats through human development (e.g., Dudgeon et al. 2006), yet our societies and economy depend directly on the services provided by healthy freshwater ecosystems (Postel and Carpenter 1997). These services include provisioning of clean water and food, regulation of climate, flow regimes, and pollution, support for nutrient cycling, and cultural services such as recreation, tourism, and spiritual benefits (Vörösmarty et al. 2005). Fishes in particular provide many services including food, linkage of ecosystems through migrations and food-web contributions, acting as indicators of ecosystem stress, and providing social value through recreation and aesthetic values (Holmlund and Hammer 1999). Most ecosystem services of fishes are supported by a diverse fauna, not by merely the few species directly favoured by humans. Humans live side-by-side with fishes and other aquatic organisms in watersheds, and we derive our quality of life from the health of these ecosystems (Limburg et al. 2011).

Freshwater fisheries are undervalued for their vital contributions to food security and biodiversity (Welcomme et al. 2010; Beard et al. 2011; Welcomme 2011). Inland fisheries are part of an integrated community, dependent on biodiversity for their resiliency to natural variation and anthropogenic disturbance. The concept of ecosystem health is comprehensive, including biotic and abiotic components along with chemical and nutrient cycles, as well as the services provided to humans (Rapport et al. 1998, 1999). A healthy and productive aquatic ecosystem may, therefore, be defined as one that is resilient to disturbance and maintains attributes of ecosystem structure and function such as habitat, species composition, genetic diversity, and production at levels similar to those observed in the absence of modern human activities. Conversely, perturbed ecosystems have one or more of these attributes compromised. Productive fisheries depend on healthy ecosystems, and the protection of fisheries requires the ongoing maintenance of ecosystem health.

In seeking to outline the requirements for healthy and productive freshwater ecosystems, we draw upon our collective experience in Canada and beyond. Recent changes to Canadian fisheries policies have motivated responses by the public and the scientific community (Reynolds et al. 2012; Cooke and Imhof 2012; de Kerchove et al. 2013, Hutchings and Post 2013), yet a broad contemporary scientific assessment of what is required to manage freshwater fisheries resources is lacking. A template of the core ecological concepts underlying sound fisheries policies, based on the best available science (Sullivan et al. 2006), will support policy and management decisions and the design of monitoring programs to evaluate the success of these actions.

Here we review the best available science to describe nine key ecological principles governing the functioning of freshwater ecosystems and the fisheries they support. To develop each of these principles,

existing literature was broadly reviewed, and a mix of classic papers, more recent reviews, and empirical studies related to each principle was cited. These principles must be accounted for to protect sustainable and productive fisheries and healthy aquatic ecosystems. Adherence to these principles is essential to the success of national and regional fisheries management plans, aquatic biodiversity protection plans, and associated policies, laws, and governance structures, along with monitoring programs. These principles are founded on our understanding of fish ecology, fisheries science, aquatic ecology, limnology, landscape ecology, evolutionary biology, conservation science, and watershed hydrology. Additionally, we discuss key components of successful fisheries management plans based on the history (including successes and failures) of freshwater fisheries management in Canada and beyond. The principles outlined here are generalized, though they are particularly relevant to both north temperate regions and those that are vast and diverse in terms of peoples, physiography, and ecology.

Key ecological principles

i. Laws of physics and chemistry apply to ecology

Though living resources are renewable, there are limits to their ability to compensate for fishing and other stressors. Limits, such as those imposed by surface area to mass relationships, govern exchange of matter and energy by organisms with their immediate environment, leading to the well-known scaling and power laws (Marquet et al. 2005; Schuster 2010) that ultimately bound biological- and ecological-rate processes. The broad consequences of these laws are realized at individual organism, population, and ecosystem levels, with mass-balance relations such as the bioenergetics principle (Kitchell et al. 1974) relating an individual's ingestion rates to the energetic costs imposed by its need for homeostasis. At the population level, persistence requires that reproduction offsets mortality (including fisheries) and immigration balances emigration (Cohen 1968). Turchin (2001) emphasized the fundamental importance of (1) the geometric growth potential that all populations possess, (2) the self-limitation capacities (density-dependence) that make birth and death rates a function of space and food resources (Pulliam 1988; Seidl and Tisdell 1999), and (3) the inherent oscillatory property fundamental to consumer-resource dynamics. Both the finite carrying capacities of the ecosystem for given populations and finite capacities of populations to compensate for mortality imposed by fishing and other stressors ultimately derive from these underlying principles.

At the ecosystem level, populations are linked through food webs and ultimately to the physical environment, and subject to the same mass-balance limitations (cf Walters et al. 1997). Aquatic predators are usually much larger than their prey, and both biomass and productivity decline with trophic level due to the increasing energy dissipations associated with ingestion, assimilation, anabolism and catabolism. Consumers are generally more mobile than their prey and integrate their activities over larger spatial scales, leading to important scale-dependent regulatory processes (McCann et al. 2005). Ultimately, solar input sets limits on all biomass and production in ecosystems, which may be partially offset by inputs from adjacent ecosystems, including terrestrial litter falling into streams and lakes or river inputs of

nutrients and organic matter into coastal oceans (Richardson et al. 2010a). As with populations, ecosystems have a finite carrying capacity (Monte-Luna et al. 2004); hence, there are limits to the aggregate exploitation of ecosystem goods and services.

The laws of thermodynamics and the associated mass–balance principles define the “outer limits” to the ability of living resources and ecosystem services to compensate for human activities such as fishing. They by themselves can neither specify where sensitive thresholds exist, nor when fishing or other extractions may put populations at risk of extinction or irreversible alteration, nor can they precisely predict the degree to which the system can return to its initial condition.

ii. Population dynamics are regulated by reproduction, mortality, and growth

Establishing simple cause and effect relationships for assessing the impacts on fish populations of any single stressor, natural or anthropogenic, is difficult because fishes in their natural environment are subject to the collective action of all stressors. These include favourable and unfavourable variations in habitat physicochemical factors, variations in community structure, predator-prey cycles, intra- and inter-specific competition, parasites, disease, food availability, and random catastrophic perturbations. Alone, or in combination, stressors invariably trigger the reallocation of energy away from growth and reproductive functions and reduce the capacity of individuals to tolerate additional stress (Adams et al. 1993). When aggregated across a collective of like individuals inhabiting an identifiable area (a population), stress responses operating through individual energy or trophic pathways can induce effects that have relevance for the group as a whole (Barton 1997) because of the ways in which the distribution of individual growth, survival, and reproduction attributes may be altered. A full understanding of population responses to environmental perturbations induced by economic-driven development will require knowledge of both the ways in which individuals respond to the stressor and the feedback effects of collective individual responses on the processes that govern fish-population dynamics (Shuter 1990; Power 2002; Grossman et al. 2012).

Possible responses to stressors (e.g., survival, growth, and reproduction) are moderated by density-independent and density-dependent adjustments that compensate for abnormally low or high levels of abundance. Ecologists have recognized for some time that populations persist only if some form of compensatory response exists to offset the effects of natural environmental fluctuations (e.g., Nicholson 1933) and there is general agreement that population abundance fluctuations result from both density-dependent and density-independent processes (Clark et al. 1967; Hassell 1986; Begon et al. 1990; Elliott 1994). Density-dependent processes operating on populations via feedbacks include competition for resources (e.g., food, habitat) that lead to adjustments in growth (Vincenzi et al. 2012), shifts in the sex ratio, variation in fecundity, predation, cannibalism, spawning-habitat congestion, agonistic behaviour, variations in dispersal rates, and disease events (Goodyear 1980; Hassell 1986; Calow and Sibly 1990; Barton 1997; Lobon-Cervia 2012). Compensation mechanisms need not act in isolation and the role of each mechanism can vary among different populations of the same species, or within populations among years (Goodyear 1980; Evans et al. 1990).

In fisheries ecology, density-dependent factors are viewed as the critical regulators of abundance (Grossman et al. 2012). Knowledge of the underlying density-dependent model regulating survival (e.g., Ricker 1954; Beverton and Holt 1957), together with a predictive understanding of critical compensatory mechanisms, is required for reliable predictions of abundance and sustainable fisheries limits (Frank and Leggett 1994). Determining the relative importance of compensatory mechanisms for a population is thus essential to understanding probable responses to stressors and the assessment of “harm” simply because populations with little

or no compensatory capacity will be particularly vulnerable to stressors (Fogarty et al. 1991).

Density-independent factors are also widely believed to be important (e.g., Grossman et al. 2010) in both marine and freshwater environments. In marine fishes, density-independent factors operate largely, though not exclusively, through effects on juvenile survival resulting from a match or mismatch between spawning times and variability in temperature and (or) food (Frank and Leggett 1994; Dingsor et al. 2007). In freshwater fishes, density-independence operates mainly through broad random fluctuation in the critical environmental variables that control growth, survival, and reproduction throughout the life cycle. In both environments, density-independent factors may also operate indirectly through density-dependent processes to attenuate or amplify the effective action of concurrently operating density-dependent processes (Evans et al. 1990; Power 1997). For example, low rainfall may reduce usable habitat, leading to density-dependent reductions in survival.

The effects of any stressor may only be interpretable if the detailed ecology of given fish species is known (Amundsen et al. 2011). While some of the required understanding may be derived from laboratory studies, detailed field studies are required to elucidate the causal links between stressors and population responses. A list of common measures useful for assessing effects of natural and anthropogenic stressors on fish-population status (e.g., Power 2002, 2007) is provided in Table 1. The metrics listed within each category are not necessarily independent of those in other categories. For example, changes in growth affect fecundity and may change survival through density-dependent compensation in subsequent generations.

iii. Habitat quantity and quality are prerequisites of fish productivity

Habitat degradation and loss is the major threat to the survival of freshwater fish populations (Richter et al. 1997; Reed and Czech 2005; Magurran 2009; Vörösmarty et al. 2010). But what is “fish habitat”? The definition is critical for effective policies and management. Aquatic ecosystems may be perceived as two- (e.g., shallow rivers) or three-dimensional (e.g., lakes) mosaics of different types of spatially distinct units (Wiens 1976; Pringle et al. 1988; Wu and Loucks 1995; Boisclair 2001; Dunham et al. 2002). We can call these “ecosystem patches”, and they may be defined according to similar physical, chemical, and biological attributes across their complete surface area or volume (e.g., light intensity, water temperature, oxygen concentration, nutrient concentration, substrate composition, depth, flow velocity, turbulence, turbidity, macrophyte cover; Brind’Amour and Boisclair 2006). Ecosystem patches provide habitat for fish only if they are suitable for successfully conducting at least one ecological function that is directly linked to their demographic success (i.e., survival in refuges, growth on feeding grounds, and reproduction at spawning sites). Patches may play similar ecological roles (habitat supplementation; Dunning et al. 1992), or different roles (habitat complementation; Kocik and Ferreri 1998), but must be connected to each other to ensure the long-term maintenance of a fish population (see next section on connectivity). The demographic performance of fish populations has repeatedly been shown to depend on the spatial arrangement, within an ecosystem, of fish-habitat patches (Thompson et al. 2001; Wall et al. 2004; Labonne and Gaudin 2006).

The productivity of a fishery is determined in part by the spatial extent of suitable habitat for its component species. Total fish abundance and biomass (rather than kg or ha) are positively related to the area of suitable habitat in lakes and streams, including lake depth and surface area (Cote et al. 2011), stream width (Binns and Eiserman 1979), and the area or proportion of pool habitats in a stream reach (Bowlby and Roff 1986; Warren et al. 2010). The extent of accessible floodplain habitat is also an

Table 1. Metrics of individual responses to the processes that govern fish survival, growth, and reproduction and thus govern fish population dynamics.

Survival	Growth	Reproduction
Age-specific survival rates	Mean mass-at-age	Age-at-maturity
Density or abundance	Mean length-at-age	Fecundity
Year-class strength	Allometric relationships	Reproductive life span
Mean age	Specific growth rates	Sex ratio
Population age structure	Population size (length) structure	Gonad somatic index
Maximum age	Liver somatic index	Egg size
Catch per unit effort	Condition factor	Incidence of atresia
Recruitment indices	Incidence of parasites	Spawning frequency
	Proximate body composition	

important determinant of fish productivity in large river systems (Junk et al. 1989). Fish populations ultimately decrease when the amount of habitat is reduced, for example through flow reduction (Zorn et al. 2012), or infilling of aquatic habitats. The area of useable habitat varies temporally as water levels change; shoreline and littoral habitats expand and contract as water levels change, creating seasonally available habitats that are important to many species. Along with habitat quantity, the physical, chemical, and biological properties of a given habitat patch help to determine its quality and, therefore, potential productive capacity (Minns 1997; Minns et al. 2011), though what is considered ideal for one species may not be suitable for others. Both loss of habitat area and changes to habitat quality can affect the ongoing productivity of a fishery (Randall et al. 2012). The abundance and biomass of a variety of species have been linked to numerous habitat properties beyond areal measures, including overhead and in-stream cover, flow velocity and variability, turbidity, invertebrate biomass, and aquatic vegetation (Binns and Eiserman 1979; Bowlby and Roff 1986; Hubert and Rahel 1989; Stoneman and Jones 2000; Inoue and Nakano 2001). Temperature and pH are often the most important limiting factors to the productivity of a given species, particularly over broad geographic ranges (Jowett 1992; Kwak and Waters 1997; Warren et al. 2010). Indeed, the volume of habitat with optimal thermal conditions for a given species is strongly linked to its productivity (Christie and Regier 1988).

As such, management for healthy and productive aquatic ecosystem for fishes must preserve fish habitats, including: (1) the number and the size of habitat patches; (2) the physical, chemical, and biological attributes of these patches; (3) the spatial arrangement and the longitudinal and lateral connectivity of these patches (see next principle); and (4) the temporal dynamics of the ecosystem such that the mosaic of habitat patches will allow all fish species and life stages originally found in an ecosystem to survive, grow, and reproduce successfully.

iv. Connectivity among habitats is essential for movements of fishes and their resources

Connectivity is a multilayered concept linking ecosystem elements in space and time. Changes in connectivity can fragment fish populations, reduce overall productivity, increase extinction risk for population fragments, and alter paths of energy and nutrient flow among ecosystem elements (Moilanen and Hanski 2001; Moilanen and Nieminen 2002). Ecologists have found it useful to distinguish between ecological and landscape connectivity (Fischer and Lindenmayer 2007). Ecological connectivity refers to the connectedness of ecological (e.g., energy flow) and evolutionary (e.g., gene flow) processes at multiple spatial scales (Soulé et al. 2004). Landscape connectivity refers to the degree to which the landscape facilitates movement of organisms among resource patches (Taylor et al. 1993). It is commonly divided into structural connectivity and functional connectivity. Structural connectivity refers to the quantity and spatial arrangement of landscape features serving as habitat patches and potential movement routes (corridors) between habitat patches (Tischendorf and Fahrig 2000) (see previous principle). It is often a

human-based perspective of connectedness derived from maps of landscape features believed to be important to a species' movement and survival (Fischer and Lindenmayer 2007). Functional connectivity includes the behavioural responses of animals to these features (Tischendorf and Fahrig 2000) and the outcome of those responses in terms of survival and reproduction. For fishes in lotic systems, landscape connectivity is influenced by the interplay between the habitat preferences, swimming and jumping abilities, and perception of risks for individual fish species and the landscape features the fish encounter, such as abrupt changes in elevation (Adams et al. 2000), water velocity (Castro-Santos 2005), water temperature (Agostinho and Zalewski 1995), and water depth (Lonzarich et al. 1998).

Fishes are important to ecological connectivity because they move among habitat patches through migration corridors (Lucas and Baras 2001). Fishes move because watersheds are characterized by longitudinal, altitudinal, and latitudinal changes in geomorphological and ecological processes, creating functional zones or patches differing in hydrodynamic, thermal, and lighting characteristics, as well as availability of food, shelter, and reproductive habitat. Longitudinal and lateral inputs of water, sediments, and nutrients are also important in creating spatial and temporal variation in habitat (Frissell et al. 1986; Junk et al. 1989; Poole 2002; Fausch et al. 2002). The most obvious movements are longitudinal, such as migration between rivers and lakes or oceans (MacKeown 1984; Northcote 1997); however, lateral movements between the floodplain and main channel are also common among fishes (Junk et al. 1989).

Movements of fishes are important to the transfer of energy, nutrients, genes, and even other taxa (e.g., mussels; Watters 1996; Newton et al. 2008) between lentic and lotic, downstream and upstream, or main- and off-channel habitats (Lucas and Baras 2001; Flecker et al. 2010). Fish movements are also part of the exchanges of energy and nutrients between aquatic and terrestrial environments (see next principle). Even infrequent, long-distance movements made by few individuals over inhospitable habitat can be important to the persistence of fish populations. The spatial arrangements of functional zones are often complex and poorly understood for freshwater fishes (Ward et al. 2002) because they have rarely been studied at the appropriate spatio-temporal scales (Fausch et al. 2002). Further, the magnitude and timing of infrequent disturbances of magnitudes significantly beyond what could be sustained by fishes or their habitats over extended periods of time (e.g., floods, flushing flows) can play a major role in shaping landscape and ecological connectivity (Poff et al. 1997) and maintaining the long-term integrity of aquatic ecosystems (Kondolf and Wilcock 1996).

Humans have disrupted landscape and ecological connectivity of riverscapes around the world through installation of dams for hydropower, irrigation, flood control, and drinking water abstraction (Nilsson et al. 2005; Dudgeon et al. 2006). These alterations have societal costs as well as benefits. Costs arise from the negative consequences of river alterations, including the obstruction of fish movements, most notably for migratory fishes, and the

longitudinal fragmentation of rivers. These alterations can block migratory species from reaching critical habitats, such as potential spawning habitat upstream for salmon, or outlets to spawning habitats downstream for eels, leading to the losses of species along with the ecosystem services they provide. Even small dams can block fish movement and alter the numbers and kinds of fishes found in streams and rivers (Porto et al. 1999; Dodd et al. 2003). Stream crossings associated with roads and railway lines are even more common than dams (Januchowski-Hartley et al. 2013). The culverts found on smaller rivers and streams can create obstacles for fish movement if water velocities within the culvert are high relative to fish swimming ability, or if the culvert outflow is perched above the water, creating a height barrier to movement. Such barriers can be pervasive across landscapes, considerably restricting the amount of upstream habitat available to fish populations (e.g., Chestnut 2002). Fishways can mitigate changes in landscape connectivity created by dams, yet only a small fraction of dams in most countries, including Canada, have a fishway, and effectiveness is rarely evaluated adequately (Hatry et al. 2013). In addition, fishways may only partially mitigate changes in landscape connectivity created by dams. These structures vary greatly in their ability to attract and pass fishes, and most fishways fail to maintain natural levels of landscape, and likely ecological, connectivity (Roscoe and Hinch 2010; Bunt et al. 2012). Dam removal provides an alternative option for restoring connectivity (e.g., Winter and Crain 2008). While use of this restoration tool is increasing, success rates remain poorly quantified and dam removal can require trade-offs between gains in aquatic ecosystem services and losses of societal benefits provided by dams. Fishway installation and dam removal can also lead to unwanted effects, such as the spread of invasive species (McLaughlin et al. 2012) or the creation of an “ecological trap” because of poor-quality reservoir habitats upstream and mortality associated with downstream passage (Coutant and Whitney 2000; Pelicice and Agostinho 2008).

Ecological, management, and conservation objectives pertaining to connectivity can only be defined if one understands the full suite of habitat needs for all life stages and species (beyond those that are affected by barriers) as well as needs for population mixing and genetic exchange among metapopulations (e.g., Gotelli and Taylor 1999; Fausch et al. 2002; Neville et al. 2006). Given that connectivity is a scale- and target-dependent phenomenon, conservation and management applications depend on knowledge of the taxa and processes of interest, and the spatial and temporal scales at which they occur (Crooks and Sanjayan 2006). Multiscale (spatial and temporal) analyses identifying dominant patterns of connectivity to inform fish-management activities remain a pressing research need (Fullerton et al. 2010).

v. Freshwater species and their habitats are tightly linked to surrounding watersheds

Freshwater systems bear the imprint of the surrounding landscape in many ways, from the physical and chemical system to the support of ecosystem productivity. Because water and materials travel over and through the catchment to receiving waters (streams, wetlands, lakes), the characteristics and dynamics of the watershed are reflected in freshwater ecosystems, making the catchment the unifying scale. Many decades of research have shown the overwhelming influence of the catchment on freshwater ecosystems, from habitat creation and maintenance (Frissell et al. 1986; Imhof et al. 1996), nutrient inputs (e.g., Dillon and Rigler 1974) to inputs of organic carbon supplies that are critical to the productivity of most freshwaters (Carpenter et al. 2005; Richardson et al. 2010a).

There have been long-lasting legacies of changes to the landscape and riverscape that are exceedingly well documented. Catchment-scale activities such as agriculture, urbanization, forestry, mining, and other land uses influence catchment hydrology through the amount, quality, and timing of water and sediment

discharges. One of the most pervasive alterations to freshwater is flow regulation, which affects the quantity, timing, and quality of water and sediments available to ecosystems, usually at great cost to the species living there (e.g., Arthington et al. 2010; Poff and Zimmerman 2010). Forest harvesting increases the rate at which water runs off into streams, resulting in larger peak flows and more erosive energy, which can both reduce the long-term storage and base-flow amounts of water (e.g., Moore and Wondzell 2005). It can also affect the channel's structure and reduce potential habitat volume (Northcote and Hartman 2004; Sweeney et al. 2004). Agriculture and urbanization also affect patterns of flow and sediment discharges, especially through impervious surfaces that lead to high instantaneous peak flows (e.g., Chadwick et al. 2006). At the other extreme, natural low flows, exacerbated by high demands of humans for water for irrigation and domestic uses, can result in stranding of fishes with increased rates of mortality (Harvey et al. 2006; Grantham et al. 2012). This is also evident, for example, in stranding of fishes by dam operations that reduce flows too quickly for fishes to respond (Bradford et al. 2011). Lack of strategic plans to deal with low water supplies for all users, including aquatic ecosystems, will probably leave fishes as a low priority despite the potentially long-term effects of local extinction.

At catchment scales, the legacies from past disturbances can have persistent impacts on fishes and their supporting ecosystems. For instance, loss of calcium from catchments during the decades of the acid rain era still affects freshwater ecosystems (Jeziorski et al. 2008) through changes in water chemistry to productivity of prey species for fishes, to developmental abnormalities in fishes. The long legacies of logging on stream ecosystems are detectable decades later in changes to hydrology, alterations of physical structure (including loss of large wood), and diminished nutrient capital from catchments (e.g., Sweeney et al. 2004; Hassan et al. 2005; Zhang et al. 2009; Levi et al. 2011).

At valley and local scales, natural riparian vegetation and the stream corridor protect the integrity of freshwaters (Richardson et al. 2010b). The riparian area provides shade and thermal moderation, bank integrity, organic matter inputs, nutrient storage and transformation, supplies of terrestrial invertebrates, large and small wood, nutrient sequestration, and important habitat for freshwater and many terrestrial species (Naiman and Décamps 1997; Richardson et al. 2005; Richardson 2008). The environmental basis of freshwater ecosystem productivity depends strongly on inputs from the surrounding terrestrial landscape (Richardson et al. 2010a). Leaf litter from vegetation surrounding streams and lakes is one of the most important sources of energy to freshwaters (e.g., Fisher and Likens 1973; Richardson 1991; Wallace et al. 1999), and terrestrial invertebrates falling from riparian areas contribute about half of the diet of many commercially and recreationally important stream fishes (e.g., Wipfli 1997). Small streams may transport invertebrates and organic matter into larger, fish-bearing streams and contribute most of the energy to support the growth of fishes in those streams (e.g., Wipfli et al. 2007; Wipfli and Baxter 2010). Lakes and wetlands also receive most of their energy from organic matter inputs, largely in the form of particulate and dissolved organic carbon from the surrounding landscape (Carpenter et al. 2005).

In some catchments, especially around the north Pacific Rim, including Alaska, western Canada, and the northeastern United States, resource subsidies of salmon returning from the ocean with most of their body mass derived from ocean food webs contribute enormous amounts of nutrients and energy to stream and lake food webs (e.g., Gende et al. 2002; reviewed by Janetski et al. 2009). These have been shown to affect numerous links in riparian food webs, including stream algae (Verspoor et al. 2010), aquatic invertebrates (Verspoor et al. 2011), riparian plants (Hocking and Reynolds 2011), and breeding birds (Field and Reynolds 2011). Watersheds above natural barriers, or beyond human-created

obstructions such as dams without fishways, can be relatively unproductive in comparison with streams and lakes where eggs and carcasses of migratory fishes augment the energy basis of freshwater (Wipfli et al. 1998; Chaloner et al. 2004).

vi. Biodiversity can enhance ecosystem resiliency and productivity

Biodiversity encompasses all levels of biological organization, from individuals to communities and ecosystems. Fish populations can contain distinct groups displaying unique phenotypes, each of which contributes to the productivity of the population by exploiting a different suite of available resources (e.g., Kerr et al. 2010). Populations can also be composed of mixed stocks that share habitats but vary spatiotemporally in resource use and are genetically distinct, increasing productivity through biocomplexity (Hilborn et al. 2003). Failure to protect such distinct units can lead to reduced abundance and the productivity of a fishery and its supporting food web (Villasante 2012). At the community level, many aquatic systems contain fish communities that are spatially distinct yet biologically linked (e.g., warm water – cold water; lentic–lotic), which combine to enhance productivity across habitats. For example, warm-water prey species can be an important food for cold-water predators (Vander Zanden et al. 1999). More is not always better though, and a distinction must be made between intact native faunas and diversity achieved through biomanipulation. Intentionally introduced species can have unpredictable negative effects, particularly in the absence of thorough risk assessments (Cambray 2003; Leprieur et al. 2009).

Among the ecosystem services provided by freshwater biodiversity, maintenance of resiliency and productivity are among the most important in sustaining fisheries resources. Ecological resiliency was originally defined by Holling (1973) as “a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables”. Resilient ecosystems can withstand disturbance without shifting state (Folke et al. 1996; Awiti 2011). Ecosystems can exist in alternative stable states (Carpenter et al. 1999; Scheffer et al. 2001) and species perform diverse functions, which together act as a set of mutually reinforcing processes (Peterson et al. 1998). Numerous empirical examples are available of state shifts in freshwater systems following the removal of a species, particularly in systems where diversity is low and functionally similar species do not exist (e.g., Schindler 1990; Findlay et al. 2005), though the effects of species loss are often difficult to predict. The potential ecosystem-level consequences of species loss are rarely known, and may depend on whether alternate species with similar ecological roles remain in the ecosystem or other changes to its abiotic attributes (e.g., highly eutrophied systems).

It has been argued that functional biodiversity is more important than species richness per se in maintaining ecosystems (Grime 1997; Cardinale 2012). Yet, even when additional species do not increase functional diversity, they do provide redundancy. In the face of disturbance and the extirpation or reduction in abundance of a species, functionally similar species can compensate by maintaining ecosystem function (Johnson et al. 1996; Johnson 2000). Resiliency increases further if species with similar ecological function differ in their response to environmental conditions. In this instance, disturbances that negatively affect one species may benefit others, limiting changes to ecosystem function (Chapin et al. 1997; Elmqvist et al. 2003). Redundancies are routinely incorporated into the design of city infrastructures to prevent major societal disruptions in the event of a disaster, such as an accident closing a major roadway. Likewise, biodiversity provides redundancy for ecosystems (Folke et al. 1996), preventing catastrophic shifts to alternative stable states not favoured by humans.

Biodiversity can also contribute to maintaining and enhancing the productivity of freshwater fisheries. Diverse communities contain a variety of functional traits and are able to efficiently use heterogeneous resources under varying conditions (Chapin et al. 1997; Cardinale 2012). Indeed, the productivity of producers along with primary and secondary consumers (often the targets of fisheries) increases with biodiversity (Tilman et al. 2001; Balvanera et al. 2006), though relatively few studies of the relationship between biodiversity and productivity have been conducted in freshwaters (compared to grasslands). Productivity can also be enhanced through maintenance of multiple stocks of fishes which thrive under different conditions; thus, a diverse portfolio of stocks can lead to enhanced and more consistent fisheries yields (Schindler et al. 2010).

Given the regulating and supporting services provided by the full community of an ecosystem and the uncertainty regarding ecosystem-level effects of species loss, policies and management strategies for freshwater ecosystem and fishery protection should incorporate protection for all species. The loss of species that play key roles in supporting ecosystems resiliency, including keystone species, ecosystem engineers, and primary prey species, may lead to the greatest changes to ecosystem structure and function and ultimately to fisheries productivity (Kenchington et al. 2013). However, considerable uncertainty remains surrounding the potential response of freshwater systems to the loss of individual species. Adopting a precautionary approach to protecting freshwater ecosystems by maintaining biodiversity will likely help to maintain fisheries sustainability and productivity because all species depend, directly or indirectly, on intact and diverse food webs in their ecosystems.

vii. Global processes affect local populations

Large-scale regional and global processes can have major effects on local populations (Matthews 1998). These effects can be indirect, such as climate change affecting hydrology. For example, changes in the amount of water vapour in the atmosphere can affect the timing and magnitude of flows. Indeed, seasonal discharge is decreasing in some watersheds in association with climate change (Leppi et al. 2012). Global processes can also interact; global warming and acidification can combine to reduce dissolved organic carbon in lakes, increasing UV-B penetration (Schindler et al. 1996).

Global warming is the ultimate example of a global process affecting local populations. The aquatic environment is very sensitive to changing climate, and fish, as ectotherms are powerful indicators of this change (McFarlane et al. 2000). Since the seminal work of Fry (1947, 1971), fish biologists have recognized that, among the most important local environmental factors influencing fish directly and indirectly, none are more important than temperature, which varies globally. Large-scale climatic variations can restrict and alter habitat, affecting fish-community structure and species abundance, especially near the edge of geographic ranges (Chu et al. 2005). Response to such variation depends upon the thermal requirements of each species (Casselman 2008). Changes in thermal conditions can have dramatic effects on both recruitment and growth (McCauley and Kilgour 1990), and even on the viability of local populations (Shuter and Post 1990). Cheung et al. (2013) projected that, over the next 50 years, changing climate will cause a significant decrease (average maximum body weight 14%–24%) in growth potential of fish assemblages in the aquatic environment. About half of this will be due to changes in distribution and abundance, with the other half associated with physiology. Morrongiello et al. (2011) demonstrated that, with a changing climate, growth of fish can decline with decreasing water levels and droughts but can also be enhanced by increasing length of the growing season. Regional declines have been observed for cold-water species in association with warming temperatures (Winfield et al. 2010), and range-wide declines are pre-

dicted as the amount of suitable habitat shrinks as the climate warms (Rieman et al. 2007).

Ample empirical evidence supports the effects of climate change on local fish populations. It wasn't by coincidence that scientists independently studying precision and accuracy in the interpretation of age and growth from fish calcified structures (e.g., Beamish and Harvey 1969; Casselman 1974) were among the first to report the effects of global warming on fish populations (e.g., Beamish 1995; Casselman 2002). Their early insights arose from detailed examination of calcified structures of various fish species that showed synchronous growth and recruitment across disparate regions. Extremes provide additional insight; for example, warm-water species recruitment is enhanced during warmer summers in the northern part of their range, whereas in cold-water species, it is enhanced during colder falls and winters in the southern part of their range (e.g., Casselman 2002). Distinctly different growth sequences document that growth is affected by wide-ranging climatic events (e.g., El Niño, La Niña, and volcanic eruptions such as Mount Pinatubo) (Pereira et al. 1995; Casselman et al. 2002; Smith et al. 2008). It is now well understood that a global climate regime shift in 1977–1978 had a dramatic effect on fish and fisheries in both freshwater and marine ecosystems in the northern hemisphere (e.g., Casselman 2002; Powell and Xu 2012).

Other important broad-scale effects associated with global processes include atmospheric loading of mercury and other persistent bioaccumulative toxicants (Blais 2005), as well as ultraviolet radiation. Mercury accumulation in fish from atmospheric emissions is an increasing concern (Power et al. 2002; Trudel and Rasmussen 2006). It has recently become apparent that ultraviolet radiation poses a threat, affecting fishes in unexpected ways, for example, directly through increasing metabolism (Alemani et al. 2003) and indirectly through interaction with other changing climatic factors (Häder et al. 2003). Radionuclides from atomic bomb testing of the 1950s and 1960s broadly contaminated aquatic ecosystems; their deposition in fish calcified tissue has been well documented and used in a novel way for validating age assessment (Campana et al. 2008). These other broad-scale effects may be important but probably less so than temperature.

Global processes and stressors can significantly affect fish populations, both globally and locally, and must be taken into consideration as a key principle when protecting freshwater ecosystems and using and managing fisheries sustainably. Their effects on fish and fisheries can be quite apparent, indicating broad-scale linkages (e.g., climate, synchronous growth, and year-class strength), and if human-induced, may require active mitigation efforts to counteract. Restoration of degraded habitats can help to mitigate climate-induced losses, including losses in more pristine areas of a watershed (Battin et al. 2007).

viii. Anthropogenic stressors have cumulative effects

A major concept of applied ecology and conservation biology highlights the importance of cumulative environmental effects, i.e., the significant accumulation of multiple human-induced stresses over time and space (Spaling 1994; Lindenmayer and Hunter 2010). The concept recognizes not only that multiple minor stresses (e.g., numerous small habitat alterations; Christensen et al. 1996; Jennings et al. 1999) can add up to create significant threats to biotic resources and their ecosystems (Langer 2000), but also that different anthropogenic disturbances (e.g., fisheries interactions combined with thermal stress; Johnson et al. 2012) can combine in complex ways to produce aggregate effects that may differ from the additive effects of individual activities (CEAA 2012; Master et al. 2009). It also recognizes that complex human impacts (e.g., climate change, dams, forestry, and urbanization) can affect multiple features of ecosystems via interacting and often indirect processes (Mesa 1994; Schindler 2001; Harvey and Railsback 2007; Scrimgeour et al. 2008; Troutwein et al. 2012). For fishes, Healey

(2011; see also Harrison et al. 2011) recently called attention to yet another form of cumulative effect when anthropogenic impacts propagate (or carry-over) across life stages, seasons, habitats, and even generations. Clearly, cumulative effects are important and pervasive and ultimately influence goals of environmental sustainability (e.g., protecting habitat, maintaining productivity and other ecosystem services, and preserving biodiversity; Kennett 1999; Gavaris 2009).

Unfortunately, cumulative effects are not as easy to understand or manage as individual, short-term, and local impacts of human activity. First, monitoring for them needs to be comprehensive, long-term, and regionally based. Cumulative effects often involve smaller, indirect, and (or) sublethal stressors that may be ignored because their local-level consequences to focal species are not obvious (Calow and Forbes 1998). Managing cumulative impacts may be conceptually straightforward if the component stressors combine in a straightforward, additive way. Even then, there can be surprises due to threshold responses: an ecosystem can reach a tipping point where an additional small stressor can generate a large effect. Threshold responses can involve changes to ecosystems ('state shifts') that are difficult to predict or reverse (Scheffer et al. 2001; Duinker and Greig 2006; Lindenmayer and Hunter 2010).

Stressor interactions can also be nonadditive; stressors are considered synergistic or antagonistic when their combined effect is larger or smaller, respectively, than predicted from the responses to each stressor alone (Folt et al. 1999). Indeed, both nonlinear and nonadditive interactions have been reported empirically (Gergel et al. 2002; Miltner et al. 2004) and emerge regularly from simulations (Rose 2000; Harvey and Railsback 2007). To help understand and predict such interactions, Vinebrooke et al. (2004) suggested that we examine the correlation (cotolerance) between the abilities of species in a community to tolerate a pair of stressors. A positive cotolerance should increase a community's resistance to a second stressor as a result of exposure to one stressor. With negative cotolerance, however, exposure to one stressor synergistically increases the community-wide impact of the second stressor.

Recognition of cumulative effects alerts us to the risks of unintended consequences arising from anthropogenic stressors (Lindenmayer and Hunter 2010), necessitating conservative, precautionary management that focuses on maintaining ecosystem resilience (Duinker and Greig 2006; Gavaris 2009; Healey 2011). Because aggregate stresses ultimately determine impacts, cumulative effects should be incorporated into risk assessments and resource management (e.g., Kennett 1999; Duinker and Greig 2006; Scrimgeour et al. 2008). As noted at least as far back as Bedford and Preston (1988), this will require both perceptual and practical shifts to larger scales. Unfortunately, there still appears to be a disconnect between the science and practice of cumulative effects assessment (Seitz et al. 2011).

ix. Evolutionary processes can be important

Fish species are distributed across landscapes as a mosaic of genetically divergent units, interconnected by various degrees of gene flow (Soulé 1986). Restricted gene flow, for example through strong site fidelity or from physical barriers between waterbodies, promotes rapid genetic adaptation to local environments according to climate, flow regimes, and habitat types (Philipp 1991). Indeed, adaptations to local environments can form the basis for the stock concept (Berst and Simon 1981) and evolutionarily significant management units (Allendorf 1995). Loss of local adaptation, for example through genetic bottlenecks caused by fishing, pollution, or habitat loss, reduces a population's capacity to adapt to environmental changes (Lewin et al. 2006). Fish may evolve in response to any of these processes. Failure to recognize this fundamental principle can lead to unintended consequences.

Consider stocking programs, many of which ignore regional genetic variation and local adaptation (Philipp et al. 1993; Hendry et al. 2011). The resultant mixing of previously isolated populations causes rapid homogenization of previously distinct gene pools and can lead to the loss of local adaptation (Campton 1987; Thornhill 1993). Hatcheries can be a major culprit here, as fishes evolve rapidly under hatchery selection, even when such selection is unintentional (Araki et al. 2008). Understanding the potential for genetic adaptation is increasingly important in the face of rapidly changing environments, as driven by climate change and other alterations to habitat (e.g., Somero 2010).

The potential for evolutionary impacts of fishing has been the focus of a great deal of research. We usually target the largest fish with size-selective gear and we fish at nonrandom times and places. This selectivity is often combined with mortality that is over twice as high as natural mortality. Anyone who breeds livestock would expect his or her animals to evolve under such intense selection. Many fishers worry about this, yet fisheries management often ignores this fundamental process.

Life-history traits that can be altered by fishing include growth, age at maturity, and body size (reviews include Jørgensen et al. 2007, Law 2007, Hard et al. 2008, and Darimont et al. 2009). A key challenge has been to quantify how much of the observed changes reflect genetic responses to selection (i.e., evolution), as opposed to purely phenotypic changes due to plasticity of traits. But the overall weight of evidence for the existence of rapid evolutionary impacts of fishing is strong. The same results have been found in both commercial and recreational fisheries (e.g., Lewin et al. 2006; Cooke et al. 2007; Philipp et al. 2009).

One reason to suspect that evolutionary responses to fisheries are widespread is that the two key ingredients for evolutionary responses are widespread, namely strong selection and heritability of key life history traits such as growth rates and body size. For example, Hard et al. (2008) reviewed selective fishing in salmonids, where mortality rates have often exceeded 70% annually. Changes in life histories found in 74 published analyses largely matched expectations from differential mortality, combined with evidence of significant heritability of many of the traits. Note that we can expect selection for earlier age at maturity even if fishing is not biased toward larger or older individuals, simply because any increase in mortality will select for early maturing individuals (Roff 1992).

Our understanding of evolutionary impacts is backed by experimental evidence. For example, Conover and Munch (2002) showed strong evolutionary responses within just four generations of high knife-edge selection for either small or large individuals in Atlantic Silversides (*Menidia menidia*, Atherinopsidae). A lake-wide experiment with Rainbow Trout (*Oncorhynchus mykiss*, Salmonidae) found that a gill-net fishery removed nearly twice as many fish with a fast-growing genotype as those with a slower growing phenotype (Biro and Post 2008). This was in spite of the fact that the fish of each genotype were the same size at the time of the experiment. The effect was attributed to differences in the behaviour of the fishes. Genetic correlations between behavioural and life-history traits are widespread, and breeding experiments have shown that susceptibility to angling can be a heritable trait (Philipp et al. 2009).

Evolution toward smaller, slower growing, and earlier maturing fish can lead to reduced fisheries yields (Law and Grey 1989; Conover and Munch 2002; Jørgensen et al. 2007; Enberg et al. 2009). Impacts on population persistence and recovery are less clear for some species (Kuparinen and Hutchings 2012).

The jury is still out on how much of the changes in life history and behaviour we see in fished populations is due to genetic change versus plasticity. For example, while some reviews have found changes consistent with an evolutionary explanation in a wide variety of studies (e.g., Hard et al. 2008), other reviews have found much less support (e.g., Hilborn and Minto-Vera 2008). But

the ingredients for evolutionary changes are clearly in place in many fisheries, and a precautionary approach cannot ignore this issue. To counter these and other effects of artificial selection, we need to adopt principles from evolutionary ecology into conservation and management (Ashley et al. 2003; Hendry et al. 2011). This is true for both effective fisheries management and the development of recovery plans for endangered species (Vrijenhoek 2005).

Integration, application, and future direction

We reviewed the key ecological principles describing the functioning of freshwater ecosystems and the fisheries they support, from principles representing predictable local relationships to those describing interactive landscape- and global-scale processes (Table 2). Failing to consider all principles presented here is problematic because they are inherently linked. Focusing policy or management efforts solely on one of the principles (or even addressing most but leaving one out) is unlikely to lead to success.

Implications for policy and management

The ecological principles presented in this review provide a template of essential attributes and the context that must be considered when crafting policy and making management decisions (Table 3). These principles, although constrained by knowledge gaps and uncertainties, are often embedded in specific evidence-based management actions. There are many such management tools and approaches available, each tied to one or more of the nine principles (Table 3). For example, fishing regulations to minimize habitat damage (iii) or impose size limits related to maturation and age structure (ii); maximum harvest and effort limits to prevent collapse or extirpation (i, ii) or selection of undesirable life-history traits (ix); protected areas to maintain habitat supply (iii); restoration to reconnect lakes to watershed stream networks (iv); or species removal and biological control to protect native species (vi). Our approach to considering policies and management is broad, covering all fishing sectors (i.e., recreational, commercial, and subsistence), and recognizes that inland systems are inherently complex with multiple uses and threats, many of which compete with fisheries (e.g., agriculture, hydropower, urbanization, climate warming; Beard et al. 2011). The higher level strategies and needs (e.g., governance, institutions, management paradigms) outlined in Table 3 provide a roadmap that can guide evidence-based development of management actions and policy with the precautionary approach to address gaps and uncertainties (Table 2). Of course, the success of management strategies for aquatic ecosystems and fisheries cannot be assessed without clearly defined and quantifiable, society-wide management objectives that are assessed and monitored over time (Richardson and Thompson 2009). Indeed, good management can be thought of as a process where credible evidence is used to achieve agreed common goals and objectives (Krueger and Decker 1993).

Typically, management actions focus on one or more of the three components of the fishery ecosystem: (1) the habitat, (2) the fish (and other relevant biota), and (or) (3) the actors directly and indirectly involved in the fishery (Nielsen 1993). As noted by FAO (2012), the primary goals of inland fisheries management will often involve some variant of the goals of the Convention on Biological Diversity (CBD): (1) conservation of biodiversity, (2) biologically sustainable use of its components, and (3) equitable sharing of benefits among diverse stakeholders (Welcomme 2001). Indeed, the principle-based policy and management actions that we identified here (Table 3) address one or more of the three components of fisheries systems and one or more of the three goals of the CBD. Inland systems are commonly managed for multiple fish-related goals (e.g., maintaining a trophy recreational fishery for Muskellunge (*Esox masquinongy*, Esocidae), maximizing sustainable yield of Walleye (*Sander vitreus*, Percidae) for commercial and aboriginal fishers, and restoring imperiled Deepwater

Table 2. List of key principles, including their components, along with aspects known with relative certainty (i.e., those supported strongly by empirical evidence).

Key principle	Aspects known with relative certainty	Knowledge gaps or uncertainties	Management recommendations
i. Laws of physics and chemistry apply to ecology	<ul style="list-style-type: none"> • Laws of thermodynamics • Laws governing gases, liquids, and solids 	<ul style="list-style-type: none"> • The upper bounds to human alterations of ecosystem processes beyond which higher forms of life cannot be sustained • Extent to which organisms overcome thermodynamic barriers such as activation energy costs to mobilize resources (e.g., sulfate reduction, methanogenesis, nitrogen fixation) 	<ul style="list-style-type: none"> • Set and live within limits on the cumulative impact and intensity of all human activities • Acknowledge aggregate limits to the exploitation of ecosystem services when attempting mitigation, compensation, or enhancement measures
ii. Population dynamics are regulated by reproduction, mortality, and growth	<ul style="list-style-type: none"> • Importance of density-dependent regulation for fish-population dynamics 	<ul style="list-style-type: none"> • Functional form of density-dependent regulation • Nature of population-specific density-dependent feedbacks 	<ul style="list-style-type: none"> • Be precautionary by minimizing unnecessary mortality in the face of uncertainty • Employ long-term studies to characterize the key population parameters of growth, fecundity, and survival
iii. Habitat quantity and quality are prerequisites of fish productivity	<ul style="list-style-type: none"> • Habitat quality and quantity and their distribution can vary in space and time within watersheds • Different geologies and climates create different habitat types and amounts 	<ul style="list-style-type: none"> • Key physical processes and conditions that create and maintain various habitat types • Critical habitat requirements of many species and life stages • Duration of effects of watershed changes on fish habitats 	<ul style="list-style-type: none"> • Maintain or restore key geophysical (e.g., watershed, stream geomorphology) and chemical processes that maintain habitats • Document critical habitat areas and understand how they are maintained
iv. Connectivity among habitats is essential for movements of fishes and their resources	<ul style="list-style-type: none"> • Links among essential habitats required to maintain viable populations • Access to upstream habitats can increase spawning and (or) rearing capacity • Habitat connectivity occurs both longitudinally and laterally in rivers and these can have a seasonal importance 	<ul style="list-style-type: none"> • Instances where connectivity may be detrimental (e.g., ecological traps, invasive species) • Fish-passage science and practice imperfect • Effects of barriers both longitudinal and lateral on all species and life-history stages 	<ul style="list-style-type: none"> • Prevent habitat fragmentation • Restore connectivity to essential habitats (e.g., through dam removal or effective fish-passage facilities) • Ensure linkages back into flood margins and seasonal edges
v. Freshwater species and their habitats are linked to surrounding watersheds	<ul style="list-style-type: none"> • Habitat is created by physical and chemical processes operating within watersheds • Catchments integrate all land-use effects, which affect downstream freshwater habitats • Ecosystem-scale effects can have large spatial and long-lasting consequences because habitats are controlled by processes operating at various spatial scales 	<ul style="list-style-type: none"> • The magnitude and direction of cumulative ecosystem effects are difficult to predict because of complex interactions (antagonistic, synergistic, or additive) and potentially long lag times 	<ul style="list-style-type: none"> • Ecosystem-based management must be considered for the effective conservation of fishes and fisheries

Table 2 (concluded).

Key principle	Aspects known with relative certainty	Knowledge gaps or uncertainties	Management recommendations
vi. Biodiversity can enhance ecosystem resiliency and productivity	<ul style="list-style-type: none"> Species with similar ecological niches contribute to community stability through competition Diverse stocks and phenotypes contribute to productivity 	<ul style="list-style-type: none"> Degree to which biodiversity contributes to resiliency, stability, and productivity Additional benefits of redundancy in diversity of functional roles Degree of genetic diversity and prevalence of mixed stocks 	<ul style="list-style-type: none"> Protect species that contribute to functional diversity and redundancy Protect all stocks and phenotypes in a population First priority is to protect and restore native species as the foundation for biodiversity management
vii. Global processes affect local populations	<ul style="list-style-type: none"> Large-scale climate processes can condition local population dynamics Contaminants are transported across regions and continents 	<ul style="list-style-type: none"> Interactions among global-scale stressors and between global- and local-scale processes 	<ul style="list-style-type: none"> Build resiliency into the watershed to allow all populations to adjust to global changes
viii. Anthropogenic stressors have cumulative effects	<ul style="list-style-type: none"> The accumulation of multiple minor stresses can be significant and push ecosystems past thresholds Complex human activities can affect multiple features of ecosystems Impacts can carry over across life stages and generations Different stressors can interact synergistically or antagonistically Anthropogenic stressors tend to be chronic versus natural stressors or perturbations which tend to be stochastic 	<ul style="list-style-type: none"> Lack of integrated, regional monitoring programs; thresholds are challenging to identify a priori and may be context-dependent Incomplete understanding of indirect effects of stressors Poor understanding of cascading life-history interactions Poor understanding of how multiple stressors interact 	<ul style="list-style-type: none"> Create an integrated regional monitoring plan to track multiple stressors, incorporate cumulative effects (and thresholds) into assessments Include uncertainty in risk assessments Incorporate “carry-over” effects into risk assessments Incorporate stressor interactions into risk assessments; employ “top-down” approach to risk assessment
ix. Evolutionary processes can be important	<ul style="list-style-type: none"> We place strong selection pressures on key life history traits that are heritable 	<ul style="list-style-type: none"> The relative role of evolutionary responses versus phenotypic plasticity in observed changes 	<ul style="list-style-type: none"> Maintain genetic diversity Avoid artificial selection, particularly selection leading to smaller size

Note: Knowledge gaps are listed along with aspects that are uncertain (e.g., supported by some empirical evidence or where contradictory evidence is available). Specific management recommendations are provided to address each key principle.

Table 3. Key components of successful fisheries management plans, with examples from Canada.

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
Protect and restore habitat as the foundation for fisheries	iii, iv, v, vi	<ul style="list-style-type: none"> Sustainability of a fishery depends on the availability of adequate interconnected habitats (combining physical, chemical, and biological attributes of the environment) for all life stages of species and their food resources (Minns 2001; Orth and White 1993) Assumes a reasonable knowledge of habitat requirements for fishes (Minns 1997; Rosenfeld and Hatfield 2006) 	<ul style="list-style-type: none"> Knowledge of fish–habitat relationships limited to very few fish species and life stages Must include ephemeral habitats and connections among habitats (e.g., movement corridors) Must not only protect habitat for fishery species, but also for all species given the functional roles they play in supporting ecosystem resiliency and productivity Need to understand and protect the physical dynamics of systems that create and maintain habitat over time Need to consider seasonal habitat use, particularly for the under-studied winter period (Cunjak 1996) Habitat alterations need to be considered in a cumulative framework to prevent “death by 1000 cuts” (e.g., shoreline development; Jennings et al. 1999) It is less expensive and more effective to protect habitat than to try to rehabilitate it after it has been altered Efforts still needed to improve the science and practice of restoration (Roni et al. 2008) Quigley and Harper (2006) and Cohen (2012) demonstrated that the “No Net Loss” principle in Canada’s habitat policy was not implemented properly, resulting in a slow net loss of habitat and productivity 	<ul style="list-style-type: none"> Mantzouni et al. (2010) showed how population dynamics and hence productivity are contingent on the quality and quantity of habitat available to various North Atlantic Cod (<i>Gadus morhua</i>, Gadidae) stocks Christie and Regier (1988) showed that sustainable yield of four commercial fish species in Canadian lakes is determined by the quantity of thermal growth space In cases where initial protection has failed, many examples demonstrate rehabilitation of aquatic habitats with concurrent increases in fish populations (e.g., Cowx and Welcomme 1998)

Table 3 (continued).

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
Protect biodiversity	vi, ix	<ul style="list-style-type: none"> Biodiversity at all levels of biological organization is of fundamental importance to ecological and evolutionary processes Protection of biodiversity is often in conflict with other management goals, leaving it essential for governments to protect biodiversity on behalf of the public good, even at the occasional expense of other management goals (e.g., improving a recreational fishery through stocking) Management for biodiversity in inland systems is increasingly being considered, particularly in highly diverse areas (e.g., Brazil; Agostinho et al. 2005) 	<ul style="list-style-type: none"> Regulations and policies related to species and habitat protection must extend beyond economically important species Once lost, recovery of biodiversity is nearly impossible (Westman 1990) With climate change and other stressors, maintaining biodiversity is essential to ensure maximal adaptive potential and resiliency in the face of future change (Sgrò et al. 2011) Managing for biodiversity is more prevalent in other systems (e.g., terrestrial; Sayer et al. 1995), providing opportunities to learn from those experiences At the federal level in Canada, implementation success has been limited in aquatic ecosystems and scientific advice is often ignored (Mooers et al. 2010) Recent changes to the Canadian Fisheries Act 2012 focus protection on fishery species and those that directly support it, contrary to biodiversity protection 	<ul style="list-style-type: none"> Canada has species at risk legislation (the <i>Species at Risk Act</i>) and a collection of protected areas and parks Most Canadian provinces have complementary laws and parks or reserves
Implement ecosystem-based management (EBM)	All	<ul style="list-style-type: none"> EBM is the basis of integrated management of natural resources in a human-altered world and is particularly relevant to freshwater ecosystems given the complexity of systems and diversity of users (Beard et al. 2011) EBM accounts for larger spatiotemporal scales and cumulative effects 	<ul style="list-style-type: none"> Disconnect between the concept of EBM and its application because the concept is complex and difficult to grasp and understand Current regulatory system is based on dissecting the ecosystem to focus management on distinct, “simple” aspects 	<ul style="list-style-type: none"> Canada has made progress with marine EBM; Pitcher et al. (2009) reviewed progress in 33 countries with Canada ranking 5th on principles, 5th on indicators, 1st on implementation, and 4th overall; Canada has made no similar efforts in its immense freshwater ecosystems

Table 3 (continued).

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
Identify and account for threats to ecosystem productivity	i, ii, vii, viii, ix	<ul style="list-style-type: none"> EBM acknowledges how activities in the landscape (catchment; riparian; wetlands) affect freshwater ecosystems (i.e., related to concepts of watershed management and integrated catchment management; see Heathcote 1998) Provides linkages between biodiversity and fisheries productivity as well as biotic and abiotic components Includes development of multispecies management programs Ample research on how anthropogenic activities influence fish habitat and thus fisheries production (Minns et al. 1996), largely studied in a limnological context (Arlinghaus et al. 2008) Failure to identify and account for threats to ecosystem production makes it difficult to predict consequences of development activities and management responses Efforts to factor cumulative impact assessment into decision-making have largely failed in Canada (Duinker and Grieg 2006) 	<ul style="list-style-type: none"> Governance structures must enable managers to adopt the EBM approach Impossible to take an ecosystem approach when multiple levels or regions of government each has a separate part of the system to manage and fail to cooperate The use of “ecosystem management” in many program titles is often misleading Need to account for synergistic and cumulative effects Need to develop models to predict consequences (including emerging threats such as nanoparticles, estrogenic compounds, and diseases) of activities on fishes and fish habitat rather than simply documenting changes after they occur 	<ul style="list-style-type: none"> Chu et al. (2003) provided a national assessment of freshwater-fish diversity, the carrying capacity of ecosystems, and the extent of cumulative human development pressures Minns (2009) showed how sustainable fisheries yield in Canada's lakes may be affected by human development pressure, compounded by effects of climate warming
Account for all ecosystem services provided by aquatic ecosystems	ii, v, vi	<ul style="list-style-type: none"> Not simply provisioning of fishes (Holmlund and Hammer 1999) Similar to habitat, the protection of ecosystem services should encompass protection of productivity and resiliency When quantified (e.g., Cowx and Portocarrero 2011), the concept of ecosystem services has much promise in inland fisheries given the potential to identify and examine trade-offs in management (Beard et al. 2011) 	<ul style="list-style-type: none"> Proper valuation of fisheries along with all the other services provided by inland water ecosystems is difficult to accomplish, but is critical for making well-informed management decisions (Beard et al. 2011) Nonmarket economic evaluation of ecosystems must be included in all cost-benefit analyses of resource development Decisions are only effective if they protect the long-term ecological and economic value of natural systems, yet this requirement conflicts with short-term political decision and feedback scales 	<ul style="list-style-type: none"> Carpenter et al. (2011) assessed the global status of freshwater ecosystem services with case studies from North America, providing a framework for more focused national and regional assessments Rothlisberger et al. (2012) showed how nonnative species have impaired ecosystem services in the Great Lakes

Table 3 (continued).

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
Adopt the precautionary approach to management (PA)	All, especially vi, vii, viii, ix	<ul style="list-style-type: none"> Intended to represent public in policy and management decisions made in the face of scientific uncertainty Focuses on protecting humans and the environment in a risk-management framework (Kriebel et al. 2001) Basic principles are laid out in the Ashford framework for PA (Hornbaker and Cullen 2003) Four central components to the precautionary approach (Kriebel et al. 2001): taking preventive action in the face of uncertainty; shifting the burden of proof to the proponents of an activity; exploring a wide range of alternatives to possibly harmful actions; and increasing public participation 	<ul style="list-style-type: none"> Must recognize that when there is substantial scientific uncertainty about the risks and benefits of a proposed activity, policy decisions should be made in a way that errs on the side of caution (Kriebel et al. 2001) Policies and regulatory frameworks must explicitly include mechanisms for operationalizing the precautionary principle PA should be employed unless there is relative certainty regarding outcomes The burden of proof for this certainty should be placed on the proponent (for both biological and socioeconomic components) but carries a need for rigorous evaluation of information generated by the proponent PA should be used to protect resources but is often only used to protect institutions and personnel The precautionary principle is not without controversy (Foster et al. 2000), particularly from proponents of activities that feel unduly burdened and (or) constrained 	<ul style="list-style-type: none"> More developed in marine systems (e.g., protected areas, Lauck et al. 1998, managing fisheries mortality; Garcia 1994; Gonzalez-Laxe 2005), providing opportunities to learn from those examples and formally extend to freshwater fisheries and habitats The Canadian government has adopted a PA (PCO 2003), but unfortunately the principles of the approach are severely compromised by the added qualifier “society’s chosen level of protection” and requiring that implementation be cost-effective
Define metrics by which fisheries resources and management success or failure will be measured	All	<ul style="list-style-type: none"> Metrics with multiple possible definitions make compliance with regulations difficult The decision-making process can be dysfunctional when definitions render metrics difficult to estimate 	<ul style="list-style-type: none"> Definitions must be clear and include metrics that are measurable and relevant in different types of environments Standard methods must be developed and adopted across regions to adequately estimate metrics, enabling communication, sharing, comparisons, and data integration (Bonar and Hubert 2002; Bonar et al. 2009) 	<ul style="list-style-type: none"> Minns et al. (2011) provided evidence of significant progress with respect to defining “productive capacity” and framing the evidence for success with respect to fish habitats

Table 3 (continued).

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
Embrace adaptive management (AM)	All	<ul style="list-style-type: none"> Without agreement on clearly defined, measurable metrics, the extent to which fisheries objectives are met and fisheries management decisions are successful cannot be assessed (Krueger and Decker 1993) AM is a structured, iterative process of robust decision making in the face of uncertainty, with an aim to reduce uncertainty over time and improve efficiency via system monitoring (Walters 1986) Differs from PA in that an experimental framework is used to inform management actions Involves feedback between monitoring and decision making such that learning occurs in an iterative manner In general the approach is under-used (or improperly applied) which is unfortunate given that it provides a systematic process for improving fisheries management policies and practices 	<ul style="list-style-type: none"> Increase accountability with regular state-of-the-resource reporting to determine management successes and failures Outcomes measured against shifting baselines can lead to management cycles where past mistakes are repeated Biological and human-dimensions studies should be used as the baseline for development of AM approaches Structured decision making in an AM framework (e.g., Hammond et al. 1999) can improve transparency and stakeholder support Institutions must be willing to engage in complex, spatiotemporally large-scale AM experiments (including monitoring) Requiring decision makers to admit and embrace that uncertainty can lead to the perception of incompetence (Walters 2007) AM failures can occur as a result of institutional limitations (Walters 2007), particularly budgetary Most claims that AM or its companion ACM is being implemented are false, given that full adoption of necessary components is never achieved (Rist et al. 2012; Plummer et al. 2012) 	<ul style="list-style-type: none"> There is little evidence to suggest that governments and institutions have made serious efforts to implement true AM or adaptive co-management (ACM), and most government institutions are risk-averse by nature
Engage and consult with stakeholders	All	<ul style="list-style-type: none"> Engage stakeholders through citizen science (Cooke et al. 2013), regional fisheries and watershed advisory groups, formal co-management structures (Pinkerton 2011) 	<ul style="list-style-type: none"> Must be at the appropriate level to be effective and productive 	<ul style="list-style-type: none"> The Ontario Ministry of Natural Resources has developed multistakeholder fisheries management councils in the province which work collaboratively with managers to develop and realize management objectives

Table 3 (continued).

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
		<ul style="list-style-type: none"> • Be transparent and accountable • Formalize use of scientific evidence in decision-making process • Transparency and meaningful participation in co-management will encourage understanding of local values and flexibility in local management systems (Wilson et al. 2003) • Builds support for management actions and encourages resource stewardship • Promotes a realization of the obvious need and (or) benefits of public outreach, awareness, and education (Cooke et al. 2013) 	<ul style="list-style-type: none"> • Process for selecting those to engage in co-management must be fair and transparent, and participation of some stakeholders will require financial support • Management institutions, governance structures, and associated processes require modification to enable more opportunities for engagement of stakeholders (Pomeroy and Berkes 1997; Wilson et al. 2003) • Require formal co-management frameworks that could be implemented at a variety of scales (Wilson et al. 2003) • Need for more stewardship programs to engage the public (requires stewardship coordinators; Cooke et al. 2013) • Need for better ways to evaluate and integrate stakeholder and traditional ecological knowledge (Huntington 2000) 	<ul style="list-style-type: none"> • Joint Fisheries Management Committee (legal responsibility held by British Columbia and federal governments) formed for the Nass Watershed following the 2000 Nisga's treaty ratification related to development of science and management capacity within the Nisga'a tribal government (Garner and Parfitt 2006)
Ensure that agencies have sufficient capacity, legislation, and authority to implement policies and management plans	All	<ul style="list-style-type: none"> • Even when good policies or management tools exist, governance and application can be wanting (Symes 2006) • Ensuring minimum protection will be insufficient most of the time • Governance structures are often complex and involve multiple agencies and organizations, creating confusion for stakeholders and agency staff 	<ul style="list-style-type: none"> • Requires surveillance, monitoring, and enforcement along with judicial follow-through to be effective • Requires sufficient resources for staffing and operations • Requires creative funding mechanisms (public, resource users, polluters and (or) proponents) 	<ul style="list-style-type: none"> • Effluents entering aquatic ecosystems from Canadian pulp and paper and mining operations are effectively monitored via the Environmental Effects Monitoring (EEM) program (Dumaresq et al. 2002; Walker et al. 2002), despite ongoing reductions to the size of all government operations, particularly those responsible for ecosystem conservation and protection

Table 3 (continued).

Management strategy	Associated principles	Context, needs, and benefits	Implementation needs and challenges	Evidence of success or progress
		<ul style="list-style-type: none"> Institutions that lack clear missions and are subject to political influence are impeded from true evidence-based decision making 	<ul style="list-style-type: none"> Agency staff require diverse training in topics that extend beyond traditional fisheries science (e.g., law, conflict resolution, public policy) Requires clear frameworks to identify responsible agencies, particularly where there is jurisdictional overlap or delegation of authority (Gerlak 2004) Authority should only be delegated in instances where capacity is insufficient (McCay and Jentoft 1996) 	

Note: The primary principles that are encompassed by each management strategy are listed (see Table 2 for descriptions of the principles associated with each numeral).

Cisco (*Coregonus johanna*, Salmonidae) populations) as well as for multiple other goals (e.g., drinking water, industrial and agricultural processes, waste disposal, transportation, recreation); thus, a diverse set or portfolio of policies and management tools is needed. The ecological principles identified here are inherently present in strategies such as protection of habitat and biodiversity, as well as an ecosystem-based management approach which addresses linkages among principles.

Research and monitoring needs

To improve understanding of these fundamental ecological principles and inform management and policy, data can be generated or obtained from many sources (e.g., stakeholder and traditional ecological knowledge, stock assessments, habitat inventories, creel surveys; see FAO 2009). Of particular importance is long-term systematic monitoring, which is necessary to establish regional baselines, detect and understand change, including climate variability, cumulative effects, and regime shifts, and prevent the adoption of shifting baselines (Pinnegar and Engelhard 2008) where the past is forgotten and the changing present becomes the sole reference for future expectations of each generation (the slide to the bottom approach). Baseline data should represent ecosystem conditions presumed to exist in the absence of modern human activities, or at least at some predetermined highly functional state. Unfortunately, such data are rarely available because of inadequate historical records predating the industrial era, insufficient historic knowledge to reconstruct original community attributes, and a lack of research and monitoring funds to study often remote ecosystems for a sufficient period prior to development (e.g., Post et al. 2002). This limitation is particularly germane to the biotic components of ecosystems such as fishes, which are found in low abundance and are subjected to high exploitation and introduction rates. Without baseline information, it is extremely difficult to develop fisheries management objectives, assess effects of human development on freshwater ecosystems, measure the efficiency of management decisions, engage in adaptive management (Walters 2007), and identify the extent to which fisheries have been protected (or not).

Given the strategic importance of baseline ecosystem information, multidisciplinary teams of scientists (e.g., climatologists, geologists, hydrologists, geo-morphologists, ecologists, modellers) should be involved in assessments and monitoring prior to development in a given area, with needs determined in part by the scale and scope of development activities. In large countries such as Canada that are rich in freshwater surface waters, and ecologically, climatically, and geologically diverse, it is impossible to routinely assess and monitor all systems (Cooke and Murchie, In press); however, landscape approaches to assessment and management based on representative units that capture the ecological principles driving ecosystem productivity can be defined (based on similar geology, climate, and zoogeography; Lester et al. 2003), which enables monitoring to be concentrated in a reasonable number of waters defined with statistical sampling designs and standard sampling techniques (Bonar and Hubert 2002) with robust data management and sharing programs (FAO 2009). Such monitoring programs provide data at spatial and temporal scales large enough for valid assessments of complex interrelationships between local and larger scale phenomena, including cumulative effects (Dubé and Munkittrick 2001; Seitz et al. 2011). Long term data and broad-scale monitoring provide considerable insights, helping us better understand variability in factors affecting fish production, such as year-class strength, growth, and survival. It is imperative that these broad-scale effects be taken into consideration as a key principle in managing sustainable fisheries.

Systematic reviews and meta-analyses represent powerful tools for synthesizing existing scientific knowledge and identifying the significance and direction of theoretical relationships, along with the range of variability to be expected (Pullin and Stewart 2006;

Roberts et al. 2006). Similarly, the Canadian Science Advisory Secretariat coordinates working groups involving government and academic researchers, along with other stakeholders, who review knowledge and provide recommendations on specific issues based on the best available science (e.g., Smokorowski and Derbowka 2008). Such tools can be used to resolve many of the uncertainties identified here, where considerable knowledge exists but has not been formally synthesized. Where sufficient empirical evidence does not exist to support systematic reviews of ecological relationships, focused research efforts can be prioritized. Formal, quantitative reviews can help to identify and bound uncertainties surrounding ecological processes. This can help inform assessments of ecological risks and improve how such uncertainties are accounted for in decision-making processes (Bartell 1998; Liu et al. 2011).

In addition to biological monitoring, human dimensions surveys (i.e., Wilde et al. 1996; Dutton 2004) are needed to understand stakeholder perspectives and identify barriers to policy compliance or address conflicts among resource users (e.g., conflict among aboriginal, recreational, and commercial sectors). Economic information can be used to identify market segmentation, values of fisheries, and willingness to pay for various management options (Loomis 2006). Indeed, inland fisheries are closely coupled social-ecological systems with dynamics that depend upon human behaviour, societal norms, and environmental quality, so it is necessary to combine traditional fisheries science, ecosystem theory, stock assessment, environmental impact assessment, environmental economics, human dimensions scenario-based global biophysical modelling, and multicriteria decision analyses (Beard et al. 2011).

Evidence-based decision making

Beyond having scientific information and principles (see earlier in the paper) on which to base decisions, it is essential that scientific evidence actually be used to inform important policy and management decisions (Sutherland et al. 2004; Sullivan et al. 2006). There has been much criticism levied towards managers for not using the appropriate types of evidence to inform decision-making processes (Sutherland et al. 2004). Even when scientific advice is available, there is a tendency for policy makers to focus more on experience than science (Pullin et al. 2004) — a concept referred to as faith-based fisheries management by Hilborn (2006). Worse still, questionable science or spurious results can be used to support predetermined decisions when evidence-based management is replaced with agenda-based management.

There have been calls for the environmental and conservation world to draw upon techniques used in the medical realm to synthesize information such that decisions are based on objective scientific evidence (Pullin and Knight 2001). Systematic reviews ensure accessibility of the best available evidence and should yield a more efficient and less biased platform for decision making (Pullin and Stewart 2006), such that managers do more good than harm (Pullin and Knight 2009). Indeed, broad consultation, peer review, and use of systematic reviews to facilitate evidence-based fisheries conservation and management are essential yet lacking despite a receptive scientific community and the existence of frameworks for doing so (i.e., Pullin and Stewart 2006).

Conclusions

The ecological relationships and community-, population-, and individual-level metrics described earlier in the paper can be used to estimate whether given anthropogenic activities pose a considerable risk to ecosystem health and the persistence of sustainable and productive fisheries. Individual physiological impairment, reductions in population abundance, or changes in fish-community structure can affect ecosystem function. Activities expected to alter fish abundance, body sizes, or growth rates may do so to levels that impair the sustainability or future profitability of a

fishery. Yet, despite our knowledge of biological responses to specific stressors, many unknown and unintended consequences arise from anthropogenic activities, as demonstrated by the evidence of cumulative effects from multiple minor stressors (Lindenmayer and Hunter 2010). The high uncertainty regarding the effects of anthropogenic activities necessitates conservative, precautionary management that focuses on maintaining ecosystem resilience (Duinker and Greig 2006; Healey 2011).

The protection and rehabilitation of ecosystem health require clearly defined conservation objectives, which constitute the basis of laws and policies, measure the success of management plans, and modify the regulatory framework if objectives are not achieved. The protection of fisheries requires the preservation of biodiversity and, therefore, the habitats required by aquatic organisms to successfully complete their life cycle. Protection efforts restricted to the prevention of major activities that directly alter aquatic systems will fall short of maintaining sustainable fisheries and healthy aquatic systems. In addition, concurrent efforts to rehabilitate or restore previously altered systems are required. Clearly, multiple minor alterations can have cumulative effects, and the health of aquatic systems is inseparable from the condition of the surrounding watershed. Protection and rehabilitation must extend beyond the water and political boundaries, and encompass impairments that are not immediately and intuitively apparent to uninformed stakeholders (and managers). Global stressors are equally important; and although they cannot be regulated by regional policies or laws, management plans must acknowledge their existence and plan for protection under a framework that accounts for externalities.

The ecological principles reviewed here are all linked and cannot be addressed in isolation: the exclusion of even one threatens freshwater ecosystem health and fisheries sustainability. Together, these principles are akin to the bricks in the foundation of a building; without all of the bricks, the building is unstable and cannot be expected to stand solidly. The broad management strategies identified here provide the mechanisms for addressing all of the ecological principles. Together, the ecological principles and management strategies offer a holistic template for science-based policy creation, both in developing nations without clear policies protecting freshwater ecosystems and fisheries and in nations seeking to revise existing policies to provide more effective measures for protection and restoration.

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