



A macrophysiology approach to watershed science and management

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ARTICLE INFO

Article history:

Received 17 June 2017

Received in revised form 7 January 2018

Accepted 8 January 2018

Available online xxxx

Editor: Daniel Wunderlin

ABSTRACT

Freshwaters are among the most imperiled ecosystems on the planet such that much effort is expended on environmental monitoring to support the management of these systems. Many traditional monitoring efforts focus on abiotic characterization of water quantity or quality and/or indices of biotic integrity that focus on higher scale population or community level metrics such as abundance or diversity. However, these indicators may take time to manifest in degraded systems and delay the identification and restoration of these systems. Physiological indicators manifest rapidly and portend oncoming changes in populations that can hasten restoration and facilitate preventative medicine for degraded habitats. Therefore, assessing freshwater ecosystem integrity using physiological indicators of health is a promising tool to improve freshwater monitoring and restoration. Here, we discuss the value of using comparative, longitudinal physiological data collected at a broad spatial (i.e. watershed) scale (i.e. macrophysiology) as a tool for monitoring aquatic ecosystem health within and among local watersheds to develop timely and effective management plans. There are emerging tools and techniques available for rapid, cost-effective, and non-lethal physiological sampling and we discuss how these can be integrated into management using fish as sentinel indicators in freshwater. Although many examples of this approach are relatively recent, we foresee increasing use of macrophysiology in monitoring, and advocate for the development of more standard tools for consistent and reliable assessment.

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1. Introduction

Humans require territory and resources, and have therefore expanded to occupy nearly the entire terrestrial world (Vitousek et al., 1997). Many settlements aggregate around waterbodies and extract from, modify, and pollute fresh water. Expanding human populations continue to exert stress on lands and adjacent waters with significant disturbances imparted on ecosystems (Daily, 2000). Fresh water is constantly impacted by human activities, creating a myriad of potential stressors such as modified flows, destabilized riparian zones (e.g. bank erosion, turbidity; Hasenbein et al., 2016), pollution, overfishing, and biological invasions (Carpenter et al., 2011; Dudgeon et al., 2006; Vörösmarty et al., 2010). These stressors are responsible for biodiversity loss and biotic homogenization in many ecosystems, which may lead to the impairment of ecosystem services provided by freshwater (Olden et al., 2004). Although local impacts of urbanization, modification, and eutrophication of watersheds are pressing and have received attention (Jeffrey et al., 2015), there are also broad scale stressors on ecosystems that operate across landscapes. The broad-scale stressors are primarily

traceable to a dense human population that is over-extracting abiotic (e.g. water, aggregate) and biotic (e.g. fisheries) resources, and burning fossil fuels that alters global patterns in precipitation, temperature, and ocean circulation (Karl and Trenberth, 2003; Solomon et al., 2009; Walther et al., 2002). In addition, human populations are projected to increase (Cohen, 2003) and further strain resources, generating continued threats to biodiversity, inland ecosystems and the services that they provide (Carpenter et al., 2011; Geist, 2015).

Part of the explanation for why threats to biodiversity, manifested in declining number of species and populations, continue despite past conservation efforts is that a focus on habitat or population-level metrics rely on indices with poor resolution to the factors that are most relevant to the functioning of the ecosystem (Rose, 2000). Indeed, projecting future animal population changes using higher scale assessments, such as organism abundance data, can be challenging without underlying data such as fecundity and survival (Van Horne, 1983). Population declines, therefore, can be difficult to predict without also defining mechanistic causes, making it difficult to predict biodiversity loss. Additional tools and techniques that could be incorporated into management plans to help with conservation actions to minimize biodiversity loss, including higher scale conservation paradigms that reach across landscapes, would therefore be a valuable supplement to traditional monitoring programs.

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Physiology is emerging as a tool that provides information about animal populations at a scale that is relevant to projecting systemic impairment or predicting population declines, particularly when applied at broad spatial and/or temporal scales (i.e., macrophysiology; Chown et al., 2004). An individual's health status is reflected in its internal biochemistry, and individuals living in poor quality environments will therefore reflect that in their physiology (Box 1). Just as physiological assays can diagnose illness in an individual before clinical signs emerge (Ackerman and Iwama, 2001), macrophysiological indicators precede demographic responses of populations. Physiological traits are also inherently linked to life history phenotypes of organisms (Ricklefs and Wikelski, 2002), and are therefore scalable to population demographics, range sizes, and abundance measures but may manifest more rapidly (Gaston, 1996; Somero, 2010). Macrophysiology (Chown et al., 2004), in particular, focuses on developing and scaling concepts from biochemical and physiological scales to populations, species, and communities (Gaston et al., 2009; Osovitz and Hofmann, 2007) by comparing physiological metrics among individuals rather than focusing on the individual responses to stressors. Macrophysiological frameworks of ecosystem function that contrast physiological functioning among populations or stocks can provide crucial information to many conservation and management initiatives, particularly because they can effectively scale research to manageable units (e.g. populations, watersheds) for conservation practitioners (Cooke et al., 2014; Cooke and O'Connor, 2010).

In this essay, we provide an overview of concepts related to why macrophysiological tools have the potential to supplement traditional management actions (i.e. common, field-based abundance/distribution monitoring, habitat rehabilitation) to reverse biodiversity loss, followed by examples and opportunities in which macrophysiology has provided, or can begin to provide, crucial information about inter- and intraspecific variation of species to inform conservation practices and priorities (Box 1). Macrophysiology has been advocated as a tool to help with conservation challenges on land (Chown et al., 2004; Gaston et al., 2009) and in the marine environment (Osovitz and Hofmann, 2007), which are highly connected contiguous environments. Now, there are increasing examples of macrophysiological approaches providing vital information to aid freshwater ecosystems (e.g. Adams and Ham, 2011; Blevins et al., 2013; King et al., 2016, 2016), which are highly separated from one another across terrestrial landscapes, heavily impacted by growing human populations, and often among the most degraded habitats on Earth. Incorporating macrophysiological tools into freshwater biodiversity conservation requires similar promotion to demonstrate

Box 1

Summary of discussion points advocating for macrophysiology as a tool for freshwater monitoring and conservation.

Natural selection acts on individuals and the health of individuals is of paramount importance to the status of a population and the community to which it belongs. Macrophysiology applies tools used to measure individual animal status at cellular and biochemical levels to broader scales.

Whereas many metrics used to evaluate freshwater health focus on population metrics such as life history traits and demographics, changes to individuals manifest more quickly and can be applied to diagnose ecosystem health.

The watershed is a relevant scale at which to investigate freshwater systems and it is possible to make macrophysiological contrasts between and within watersheds to assess local health.

Fish are relevant ecological indicators of freshwater quality because they are pervasive and play nearly every role in the trophodynamics in freshwater.

The health of individual fish is influenced by its environmental quality; therefore, the selection and measurement of physiological variables can be used to estimate the quality of the habitat.

Macrophysiology has the potential to supplement and enhance demographic measurements of freshwater ecosystem health such that conservation and restoration activities can be allocated effectively.

There are many possible physiological metrics that can be used to assess the health of individual fish, and more research is needed to rank and value them such that a standard suite of measurements can be developed and applied across watersheds to reliably assess ecosystem health.

the diversity of questions that can be addressed and the utility of these findings and paradigms to management of freshwater ecosystems. Although macrophysiology can be applied to other freshwater organisms, our emphasis is on the restoration of freshwater fish populations, which are among the most imperiled taxa on the planet (Jelks et al., 2008), are relevant ecological indicators (Fausch et al., 1984) and provide a number of critical ecosystem services (Colin et al., 2016; Holmlund and Hammer, 1999; Lynch et al., 2016; Box 1).

2. Freshwater ecosystems in a watershed context

Freshwater systems are effectively conceptualized in the context of the watershed, the branched network of water collected from headwater sources, groundwater inputs, minor and major tributary creeks and streams, and drainage runoff from adjacent lands (Hynes, 1975). Watersheds are dynamic and changing, with significant interactions with surrounding lands (Allan and Johnson, 1997; Gregory et al., 1991; Junk et al., 1989; Vannote et al., 1980; Ward, 1989). Freshwater ecosystems are therefore closely connected within their watershed and are inseparable from the surrounding area (Fisher and Likens, 1973; Ward, 1989). Indeed, the title of Noel Hynes' Edgardo Baldi Memorial Lecture was "The stream and its valley," which cogently described the inherent connectedness of those two watershed elements (Hynes, 1975). Disturbances within the watershed, including habitat modification (e.g. urbanization; Walsh et al., 2005), damming, and pollution, can have cumulative or synergistic effects on biota, particularly for the lower reaches of a watershed (Johnston, 1994) as the inputs at different points in the watershed affect both the downstream quantity and quality of water (Box 1). The mounting demand for fresh water resources has contributed to significant degradation of freshwater and imperilment of many species (Carpenter et al., 2011; Schindler, 1987). There is accelerating concern about the status and health (Meyer, 1997) of global freshwater ecosystems as human activity increasingly contributes to habitat modification and degradation of these ecosystems (Norris and Thoms, 1999; Box 1).

Traditional methods for assessing watersheds have predominantly relied on environmental sampling including water quality monitoring or environmental data such as temperature, flow, riparian stability, and vegetation or substrate indices. Stream health is alternatively measured using biotic metrics including the index of biotic integrity, which sample fish communities to assess population/community metrics such as abundance, diversity, and richness (Karr, 1981, 1991; Fausch et al., 1984) gathered from netting or electrofishing surveys. Water samples can now be collected to sequence environmental DNA (eDNA), which has been shown to be an effective alternative to netting surveys (Shaw et al., 2016).

3. Sick fish and healthy fish

In a broad sense, fish residing in a given ecosystem will exist on a continuum of health that spans from 'healthy' to 'sick' (Box 1). Sickness is a physiological state of being in which the body is compensating for a stressor. A stressor could be any stimulus that disturbs a fish's homeostasis (Chrousos and Gold, 1992); an individual will mount a stress response (Wendelaar Bonga, 1997) to cope with stressors that are encountered. Most stressors are acute and the stress response is an adaptive solution; however, prolonged exposure to stressors results in a chronic stress response that diverts energy from growth, reproduction, or immunity (see Pickering and Pottinger, 1989; van Weerd and Komen, 1998). These conditions are measurable and, when quantified across broad spatial or temporal distributions with sufficient interindividual replication, can provide an index of a population's health. However, where an individual fish falls on the sick-healthy continuum will be a product not only of the environment in which it is residing, but also its genes and its previous exposure to biotic and abiotic challenges. The combination of these factors and their cumulative impacts will be

reflected in a fish's internal biochemistry (e.g. metabolites, hormones, pH) and physiology, and be demonstrated in both labile metrics that can change over short time scales (e.g. blood physiology), as well as more resilient metrics that accumulate over longer periods of time (e.g. telomere length). Together, these physiological metrics or variables can be measured and incorporated into macrophysiological frameworks as biomarkers that can both define individual health and condition, and be used to predict changes to the status of both individuals and populations (Adams and Ham, 2011).

Healthy individuals in a population are expected to reside in relatively high-quality habitats in terms of the physical integrity, chemical composition, access to resources, and the stability of these physicochemical conditions in space and time. The health of individual fish should be reflected by moderate rates of energy consumption, particularly at rest (i.e., resting or standard metabolic rate; RMR, SMR), low concentrations of circulating stress hormones, and, consequently, low secondary and tertiary indices of stress and broad scope for stress responsiveness (King et al., 2016, 2016). Identifying appropriate baseline conditions would be useful and analogous to panels, which are combinations of physiological metrics used to evaluate wildlife health in veterinary medicine (see Madliger et al., 2016). Healthy fish should also exhibit low concentrations of leukocytes circulating in plasma (Davis et al., 2008), low indices of oxidative damage (Birnie-Gauvin et al., in press), long telomeres (Debes et al., 2016; Simide et al., 2016), and an abundance of nutritional indices in plasma such as lipids and cholesterol reflecting a good nutritional condition (King et al., 2016).

A myriad of challenges in an animal's life, can disrupt homeostasis and shift an animal away from a 'healthy' state towards 'unhealthy.' For example, many external challenges can activate the primary and secondary stress responses, which are comprised of neuronal, cellular, and hormonal signals (Barton, 2002) that mobilize energy for fight/flight responses. Chronically stressed organisms may also develop an altered scope for stress responsiveness, be incapable of increasing the circulation of stress hormones by concentrations considered to be normal for the species (King et al., 2016), impairing the capacity to cope with added challenges when living in degraded habitat (i.e., multiple stressors). McConnachie et al. (2012) simulated the stressed state characteristic of fish in degraded habitat with exogenous cortisol implants and observed a more pronounced response to starvation than in sham-treated bluegill (*Lepomis macrochirus*). Unhealthy individuals may also exhibit increased free radical production. A number of challenges may be reflected within cells by transcriptional responses upregulating the production of proteins such as heat shock proteins (e.g. *hsp70*, *hsp90*; Iwama et al., 2004). Many of these changes can be identified through either a direct quantification of the end product of a pathway (e.g., measuring heat shock protein expression in a tissue or the amount of cortisol in plasma, Dennis III et al., 2016), or through assessment of genomic/genetic pathways upstream of protein expression (e.g., gene expression patterns or quantification of RNA production; e.g. Gracey et al., 2001). Parasites on healthy fish tend to be low in abundance but high in diversity and health can also be approximated through parasitism assays (Chapman et al., 2015).

The shift from a 'healthy' to 'unhealthy' state has a number of important implications, both for individual fish, as well as for fish populations. Chronic innervation of the stress axis results in sustained elevation of glucocorticoids and the corresponding depletion of energy stores, distracting energy needed for growth, reproduction, or immune defense to maintenance of the stress response. Habituation to repeated stressors may eliminate the capacity for a fish to respond correctly to challenges with an acute stress response that facilitates fight or flight (e.g. King et al., 2016). Chronic endocrine stress, however, renders individuals prone to disease through immunosuppression (Pickering and Pottinger, 1989). Indeed, Chapman et al. (2015) observed high abundance of parasites on fish living in degraded habitats relative to individuals from more pristine habitats. Stress and parasitism are both factors that have been linked to increases in metabolic demand, elevating the

standard metabolic rate of infected individuals (Santos et al., 2010). Corresponding to increases in metabolic rate can be increased production of free radical reactive oxygen species (Loft et al., 1994), which can be defenced by synthesizing antioxidant enzymes at further metabolic cost, or possibly leading to oxidative damage that reduces growth or lifespan (Slos and Stoks, 2008). Fish experiencing chronic endocrine stress may also have impaired fitness because their lives will be shortened by the energetic demands of stress and production of reactive oxygen species (Birnie-Gauvin et al., in press). The impacts of sustained stress manifest in the energetic storage, nutritional status, or reproductive condition of individuals (e.g. Campbell et al., 1992; King et al., 2016), which can also be measured to index the response of animals to environmental quality. Ultimately, declines in physiological condition can lead to impairments in fitness if stress induces mortality, impairs fecundity, or if stress is endowed to gametes negatively affecting offspring, such as when there is a mismatch between the maternal provisions and the environment (Sheriff and Love, 2013).

4. Macrophysiological patterns relevant to fish

Many stressors negatively impacting ecosystems are the result of human activities. Anthropogenic disturbances result in impoverished water quality from waste water dumping, toxic leaching, nutrient loading, or acid rain deposition to create broad-scale changes in environmental quality that have the potential to affect fish across landscapes (Holden, 1966; Smith et al., 1999; Sharma et al., 2009; Snucins et al., 1995). Differences in depth, flow, gradient, riparian cover, and other local watershed characteristics can buffer or delay stressful conditions (e.g. higher flow may distribute pollutants more quickly, shallower streams heat up more rapidly), providing an opportunity for comparison among local systems in different states of degradation (Adams and Ham, 2011). Macrophysiology need not focus on each species in a community but can use sensitive or ecologically important sentinel species for which baseline data are available (Lower and Kendall, 1990). However, indicator species should be chosen carefully and studies should ideally use multiple species where possible (Mueller and Geist, 2016; Siddig et al., 2016). In a macrophysiological context, longitudinal sampling of biomarkers can be used to identify trends in the functioning of organisms across landscapes. In doing so, physiological responses can reveal locations where, or conditions under which, stressors are operating and have the potential to predict declines in abundance or diversity resulting from poor survival or low fecundity/recruitment (Box 1). However, longitudinal comparisons in individual condition are challenging and should be undertaken cautiously given that many differences naturally exist across space and time that may yield spurious correlations to environmental quality. Where possible, controlled experiments can be useful to overcome these challenges and supplement field data.

5. Applications and examples

Although macrophysiological approaches are better developed in terrestrial (Chown et al., 2004; Gaston et al., 2009) and marine (Osovitz and Hofmann, 2007) environments, there are emerging applications in freshwater. Within watersheds, reaches and tributaries can differ greatly in their adjacent land use, with varied impairments in physical habitat and water quality. Comparing physiological samples to baselines must account for background changes in the environment that could be influencing physiological responses. For example, Robinson et al. (2010) found that low conspecific density buffered the negative effects of high water temperature on brook trout (*Salvelinus fontinalis*) growth. Common garden experiments have been used to compare the physiology of populations, for example, Anttila et al. (2014) reared Atlantic salmon (*Salmo salar*) smolts from rivers near the northern and southern edges of their latitudinal distribution to compare their responses to warming as a function of their genetic origin and

their acclimation to one of two different temperature regimes. Although experimental approaches to macrophysiology are less common, they could be powerful for detecting main effects, particularly when conducted in parallel with field experiments to ensure that results are relevant in wild settings.

There are recent empirical examples of macrophysiology revealing how the environment influences fish physiology that showcase how it may offer innovative methods for monitoring watersheds. Blevins et al. (2013) compared the circulating glucocorticoids and resting metabolic rate in response to a thermal challenge (i.e. stress responsiveness) of creek chub (*Semotilus atromaculatus*) from forested and agricultural reaches of a central Illinois, USA and found depressed responsiveness of chub from the agricultural region. This was supported by King et al. (2016), in which the stress responsiveness, nutritional status, and oxidative damage were compared from blood biopsies withdrawn from largemouth bass (*Micropterus salmoides*) captured among watersheds draining into the St. Lawrence River across a gradient of land use (e.g. gradient of forested and agricultural land uses). Again, fish in forested areas were observed to have better physiological condition, having less oxidative damage and higher nutritional status, than those living in areas surrounded by agricultural areas. Largemouth bass from wetland areas also had better glucocorticoid function than in riparian or agricultural areas. This is consistent with findings from Wang et al. (1997), in which forested areas supported higher biotic integrity than reaches where the riparian zone was dominated by agricultural lands. In combination, these studies illustrate how physiological samples can be compared among reaches to determine how habitat interfaces with fish condition, ultimately revealing the quality of the habitat. Knowing that fish in forested areas are in better condition is beneficial but it is also relevant to understand the mechanisms that allow individuals to persist in degraded habitats where condition is impoverished.

Macrophysiology can also explain trends in species abundance and community richness that can assist with conservation. Paradigms such as latitudinal variation in resilience are explored using macrophysiology to predict how species' ranges will respond to climate change (e.g. Anttila et al., 2014). Projecting the effects of temperature increases in watersheds, for example, must draw on physiological tolerances of resident biota (as in marine systems; e.g. Somero, 2002), however, refugia in some watersheds might facilitate persistence. The identification of reach- or tributary-specific physiological phenotypes can also be promising for conservation purposes because intraspecific variation within watersheds is key to persistence via source-sink dynamics should some stocks become extinct (e.g. sockeye salmon *Oncorhynchus nerka*; Eliason et al., 2011). Latitudinal comparisons of species in freshwater have revealed that northern populations have greater energetic demands on activity (e.g. reproduction), which can have consequences for growth (Gravel et al., 2010), maturation (L'Abée-Lund et al., 1989), and parity (Jonsson and L'Abée-Lund, 1993). Macrophysiological clines in energy demand have diverse impacts on populations (e.g. vulnerability to fisheries; Mogensen et al., 2013), can be applied in the context of assessing changes in thermal habitat in watersheds, and can be scaled directly to predictions of demographic and community dynamics that are more relevant to managers.

Macrophysiology is also promising for assessing habitat quality in the context of climate change and non-native species establishment/invasion (Chown and Gaston, 2008). Native species are often best adapted to local disturbances such as seasonal flooding, drought, or freezing regimes that might provide an advantage against non-native species that are introduced; measurements of physiological tolerance or plasticity can enhance understanding of invasiveness that threatens watersheds. Warming of freshwater and reduction in winter conditions will facilitate success of introduced exotic species that would otherwise perish (Rahel and Olden, 2008), although Kiernan and Moyle (2012) suggested that hydrographical changes projected for California might favor native species. Impending changes associated with climate change will increase temperatures in watersheds and will certainly alter fish assemblages.

6. Unresolved issues, challenges and future research needs

Although macrophysiology holds promise for improved understanding of watershed health and augmented conservation programs, there are challenges to implementing and operationalizing macrophysiology for monitoring and informing management. Using physiology can be challenging in practice because the generalized stress response is not specific to any particular stressor. Therefore, it can be difficult to identify a mechanism responsible for driving declines in fish health without experimentation. However, this is also a challenge with metrics derived from community sampling (Connon et al., 2012). A potential solution is to assay a suite of physiological metrics that can collectively assist in identifying the source of stress as well as evaluating the downstream impacts on the organism. For example, field sampling of a fish species, coupled with *in situ* monitoring of water temperature, could identify thermal stress via the stress response, perhaps also gene expression of heat shock proteins (Werner et al., 2005). Whether this thermal stress affects growth or reproduction can be further explored by assaying growth hormones or sex steroids of the target population relative to a reference site or using laboratory studies for support. Of course, it can be difficult to establish the cause-effect of these integrated responses to stressors, and often it is beneficial to have validation with experimental approaches to extrapolate to the wild animals.

Macrophysiology is unique from other physiological approaches in that measurements are made across time or space to evaluate the status of populations through the lens of the individual. This requires consideration of how biomarkers may differ as a function of external variables beyond an analyst's control. For researchers, selecting the correct biomarkers can be a challenge given the plethora of possibilities (see Adams and Ham, 2011 for examples), and testing of possibilities may be prohibited by time or funds but the selected biomarkers must be relevant to the scale of study (Cooke and O'Connor, 2010). Specifically, the value of metrics requiring terminal sampling relative to those that can be withdrawn by non-lethal biopsy must be evaluated to minimize the extent of lethal sampling to develop macrophysiological frameworks (Maceda-Veiga et al., 2013).

Macrophysiological approaches will be well supported by a canon of research on biochemical pathways and physiology of fishes, but many of these systems have been developed in experimental settings where stressors are isolated (Barton, 2002; Sopinka et al., 2016). In the field, understanding how these physiological pathways operate is more challenging. For example, there may be diel variation in response variables collected at different times of the day (Cousineau et al., 2014), and seasonality can also influence the internal biochemistry of animals preparing for migration, smoltification, reproduction, or other life history events that are characterized by changes to an animal's physiology. Environmental conditions may be difficult to simulate, for example, finding shelter reduces metabolic costs associated with camouflage or predator vigilance (Enders and Boisclair, 2016), which may be difficult to observe in captivity. Another example is that fluctuating temperatures may have higher metabolic costs than constant temperatures (Enders and Boisclair, 2016), which may be difficult to simulate in experiments.

Physiological specializations or plasticity may allow individuals to cope with local environmental conditions; in such cases, differences in physiological functioning would reflect this natural plasticity rather than information about environmental quality. For example, Lawrence DeKoning et al. (2004) showed how killifish (*Fundulus heteroclitus*) from different habitats expressed the endocrine stress response differently (see also Schulte, 2014). Incorrectly assigned variation in physiology may arise from inadequate spatial or temporal sampling or from small sample sizes in which outliers bias findings and interpretations. Of course, individual variation is inherently useful as a component of individual-level assessments (Bennett, 1987) and can be exploited in an analytical sense (Williams, 2008). A solution to this variation may be an experimental design with a high degree of experimental unit

replication, both within and between sites, to account for natural variation among individuals and identify differences in physiological function with a causal link to the environmental quality. Early life stage fish may be more sensitive to disturbance and could therefore be important to incorporate into macrophysiological studies; however, small amounts of individual tissue may require pooling samples from multiple individuals (see Cavallin et al., 2015).

Multivariate analyses (e.g. principle components analysis) can assist in creating ordinated hybrid variables of multiple physiological measures that in combination suggest health status (Mueller and Geist, 2016); however, uncertainty can easily undermine efforts to identify sick and healthy fish. This is even more difficult because although we have so far described macrophysiological tools as capable of identifying sick and healthy individuals, and thereby populations, health operates along a spectrum and is not dichotomous, and can therefore be challenging to identify, particularly in early stages of degradation. Because many factors simultaneously operate to determine the physiological status of a fish, the more variables measured the more likely assessments are to accurately attribute variation in health status to habitat quality. Analysts must also be cognizant of natural zoogeographical differences in physiology that emerge among populations as a natural consequence of stream depth, width, gradient, etc. (Fausch et al., 1984).

7. Conclusions

Ecosystem health can be characterized through proxies such as biotic metrics (e.g., diversity, abundance, presence of intolerant species), and ecosystems may be resilient or tolerant to changes of certain types and magnitudes (Schindler, 1987). Freshwater biodiversity conservation often draws on paradigms that posit high species richness, diversity, and abundance as equivalent to good health (Cardinale et al., 2012), or at least a suitable substitute in some ways if integrated into proper frameworks (e.g. Index of Biotic Integrity; Karr, 1981, 1991). Augmenting traditional watershed management with macrophysiological tools is particularly urgent given that human society is heavily reliant upon fresh water as a source of potable water, irrigation, food, and potential energy (Fitzhugh and Richter, 2004; World Water Assessment Programme, 2003). Notwithstanding numerically abundant species or diversity of an assemblage, a watershed can be in poor health as a result of biotic (e.g., biological invasions, disease) or abiotic (water quantity or quality) disturbances in the watershed (Box 1). Diagnoses of the ecosystem as unhealthy and the prescription of restorative or remedial conservation actions (e.g., habitat restoration, stock enhancement, etc.) may not occur until subsequent samples identify the demographic changes emerging from periodic sampling. Physiology underlies life history phenotypes (Ricklefs and Wikelski, 2002) and therefore environmental changes that eventually affect the range, abundance, and demographics of species and thereby the richness, diversity, and length of food chains will first manifest in physiological changes to the functioning of individuals (Box 1).

The ability of traditional field-based sampling and monitoring programs to predict and prevent biodiversity loss have regularly been revisited and questioned (Field et al., 2007; McDonald-Madden et al., 2010; Mueller and Geist, 2016). Physiology provides an accessible scale for detecting or forecasting impending changes in aquatic communities and assigning health status to a watershed while testing hypotheses about aquatic community health (Box 1). Because direct measurement of environmental variables does not provide precise information about the suitability to biota (i.e. because they may be resilient to the conditions or find refuge; e.g. Wilkens et al., 2015), physiological metrics can support assessments of ecosystem health by providing an index of the status and health of organisms (Depledge and Galloway, 2005; Jeffrey et al., 2015).

A macrophysiological approach to watershed conservation and management shifts focus away from demographic responses of

organisms to disturbance to emphasize the importance of individual-scale responses to stressors. Recognition that healthy ecosystems support healthy fish requires the tools and understanding for assessing individual health, which we distinguish in this paper from population-scale metrics such as abundance, and also calls for a more proactive approach to identifying and restoring degraded habitats in a timely way. How to operationalize such a shift is a challenging question, particularly when prioritizing “sick” systems against defaunated systems; specifically, macrophysiology may be able to identify sick fish living in relatively poor habitat that are at risk of population or community scale impairment, but this may not be the priority of conservation practitioners if they wish to first address those systems that have gone beyond the state of being sick. We argue that the restoration of degraded ecosystems is less effective, and likely more expensive, than effective protection against declines (Leung et al., 2002; Roni et al., 2008). Identifying these systems is made possible by using macrophysiology and reversing these declines can be accomplished by restoration, which can be easier and more cost effective than focusing on systems at a later stage of degradation.

Physiological functioning operates at small organizational scales and can be effective for developing ecosystem approaches, which aim to conserve ecosystem integrity and functioning (as opposed to single-species conservation efforts; Mueller and Geist, 2016). However, operationalizing macrophysiology as a standard monitoring tool for watersheds will require continued demonstration of the links between individual physiology and the downstream impacts on fitness and population-level responses (Bonier et al., 2009). Although macrophysiology relies on indicator individuals, findings are used to develop conservation plans for the watershed with benefits extending to the population, species (i.e., conservation efforts that focus on populations will ultimately protect species; Ceballos and Ehrlich, 2002), and ultimately the habitat and community.

Questions of various scale can be posed and answered by testing hypotheses using macrophysiological approaches by measuring the physiological responses of freshwater organisms to natural (e.g. drought, flood) and anthropogenic (e.g., pollution, channelization) disturbances to habitat can provide a reliable index of ecosystem health (Allan et al., 1997; Norris and Thoms, 1999). Implementing macrophysiology to reveal how various stressors operate from a mechanistic perspective can contribute to conservation prioritization, habitat restoration, or water quality remediation by identifying hotspots where it is most needed.

Acknowledgments

Lennox was supported by an NSERC graduate scholarship. Lennox and Cooke are members of Ocean Tracking Network Canada. Cooke is supported by NSERC and the Canada Research Chairs Program.

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