



A macrophysiology approach to watershed science and management

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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

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