Expanding the “toolbox” for studying the biological responses of individual fish to hydropower infrastructure and operating strategies

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Abstract: To date, few studies have evaluated sub-organismal responses (e.g., physiological or energetic consequences) of individual fish to hydropower infrastructure (e.g., fishways, turbines) or operations (e.g., fluctuating flows, low flows). The field of “conservation physiology” (i.e., the use of physiological information to enhance conservation) is expanding rapidly and has great promise for hydropower research. However, there is a need to both expand the “toolbox” available to practitioners and to validate these tools for use in this context. This synthetic report details the behavioural, energetic, genomic, molecular, forensic, isotopic, and physiological tools available for studying sub-organismal responses of fish to hydropower infrastructure and operating procedures with a critical assessment of their benefits and limitations. Furthermore, this paper provides two case studies where behavioural, energetic, and physiological tools have been used in hydropower settings. Progressive and interdisciplinary approaches to hydropower research are needed to advance the science of sustainable river regulation and hydropower development. The expanded toolbox could be used by practitioners to assess fishway performance, migration delays, and fish responses to fluctuating flows through a more mechanistic approach than can be offered by only focusing on population metrics or indices of community structure. These tools are also relevant for the evaluation of other anthropogenic impacts such as water withdrawal for irrigation or drinking water, habitat alteration, and fisheries interactions.

Key words: anthropogenic impacts, pacific salmonids, telemetry, genomics, enzymes, ions.

Résumé : Jusqu’à maintenant, peu d’études ont évalué les réactions suborganismiques (p. ex. conséquences physiologiques ou énergétiques) des poissons individuels aux infrastructures hydroélectriques (échelles à poisons, turbines) ou aux opérations (fluctuations de débit, faibles débits). La "conservation physiologique" (p. ex. l’utilisation des informations physiologiques pour favoriser la conservation) constitue un champ en développement rapide et possède un avenir prometteur pour la recherche sur les impacts des usines hydroélectriques. Cependant, on doit élargir la "boîte à outils" disponible aux praticiens, et valider l’utilisation de tels outils dans ce contexte. Cette synthèse fait état en détail des outils comportementaux, énergétiques, génomiques, moléculaires, isotopiques, physiologiques, et de preuves, disponibles pour étudier les réactions suborganismiques des poissons aux infrastructures hydroélectriques et aux modes d’opération, avec une évaluation critique de leurs bénéfices et de leurs limitations. De plus, cette synthèse présente deux études de cas où les outils comportementaux, énergétiques et physiologiques ont été utilisés pour l’Installation d’ouvrages hydroélectriques. On a besoin d’approches progressistes et interdisciplinaires pour la recherche sur l’hydroélectricité afin de faire avancer la science sur la régulation durable des rivières et le développement hydroélectrique. La "boîte à outils" élargie pourra être utilisée par les praticiens pour évaluer la performance des échelles à poissons, les délais de migration, et les réactions des poissons aux fluctuations des débits, grâce à une approche impliquant uniquement les indices ou les mesures de la structure des communautés. Ces outils s’avèrent également pertinents pour évaluer d’autres impacts anthropiques comme le prélèvement d’eau pour l’irrigation ou la consommation, l’altération des habitats et les interactions avec les pêcheries.

Mots-clés : impacts anthropiques, salmonidés du Pacifique, télémétrie, génomique, enzymes, ions.

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Introduction

Globally, hydropower facilities contribute 17% of the electricity needed by humans, and further developments are planned to meet the growing demand for clean energy (Yüksel 2007). In fact, over 50% of the Earth's freshwater river systems have been altered for the generation of electricity (Rosenburg et al. 2000). Though hydropower is considered a clean and safe power source in comparison to fossil fuel and nuclear facilities, the infrastructure and operation of power generation facilities can have profound impacts on aquatic environments and the organisms that dwell in them. Given the importance of fish and fish habitat and the fact that freshwater fish represent some of the most threatened animals (Richter et al. 1997; Cowx 2002; Malmqvist and Rundle 2002; IUCN 2008; Jelks et al. 2008), there is a need to better understand how hydropower infrastructure and operations alter fish and fish habitat so that more appropriate guidelines can be developed to ensure the sustainability of the hydropower industry.

Hydropower infrastructure and the operational strategies used by power utilities have the potential to fundamentally change the local aquatic environment. These changes and their effects can be grouped into two main research topics: (1) *altered flow regime*, which encompasses numerous changes to river characteristics related to the amount of water present and its movement (Poff et al. 1997); and (2) *barriers and connectivity*, which include the hydropower infrastructure that prevents upstream and downstream movement of fish and the constructed passage facilities for fish designed to make hydropower infrastructure as "invisible" as possible to fish. Because both of these topics have been reviewed elsewhere (e.g., Poff et al. 1997; Murchie et al. 2008; Roscoe and Hinch 2009), we will not provide an in depth review of these topics, but we will incorporate relevant research into our 'tool' summaries where appropriate. In addition, there are other associated processes that can lead to similar changes to the local aquatic environment and necessitate similar research needs, such as water withdrawal, flood control, and temperature regulations. However, for the purpose of this paper, we will focus solely on hydropower infrastructure and operations, but readers should note similar research needs and opportunities exist elsewhere.

Much of the research on hydropower impacts on fish has focused on evaluating changes in community structure or population size by sampling individual fish (Murchie et al. 2008). However, the response times can be lengthy, often extending beyond the monitoring periods required by regulatory agencies. In a recent synthesis, Murchie et al. (2008) revealed that few studies have evaluated sub-organismal responses of fish to fluctuating flows associated with hydropower infrastructure, despite the fact that investigation into these effects can provide information on time scales that are consistent with most monitoring programs (Cooke and Suski 2008). In addition, it was apparent that few studies had included physiological or energetic endpoints (aside from several studies on the osmoregulatory consequences of dams on downstream migrants) or linked individual condition with behaviour and fate in a hydropower context. This is somewhat surprising as understanding organismal function and life history traits has been identified as an integral component of conservation and management initiatives (Young et al. 2006*a*). Also, the field of "conservation physiology" (i.e., the use of physiological information to enhance conservation [Wikelski and Cooke 2006]) is expanding rapidly and has great promise for research into the impacts of hydropower. Indeed, much of this work is possible because of the advent of tools that enable physiological research to take place outside of the laboratory. This sub-discipline is called "field physiology" and to date, has tended to focus on larger animals such as marine mammals and terrestrial vertebrates (see Costa and Sinervo 2004). However, there is a need to both expand the "toolbox" available to fisheries practitioners and to validate these tools for use in fish–hydropower research. In addition, for this toolbox to become practical in hydropower research, physiological endpoints need to facilitate regulatory action and (or) decision-making by utilities and regulators.

The objective of this paper is not to present an overview of the impacts of hydropower on fish, but to summarize 12 types of tools that show promise for research on fish and hydropower interactions. First, we provide a brief summary of the current state of knowledge regarding the tool and its usefulness in fisheries science and environmental management. Second, we assess whether the tool is useful for studying individual and sub-organismal responses to hydropower and discuss the benefits and limitations of using these techniques for the evaluation and monitoring of hydropower impacts on fish and fish habitat. Finally, we present two case studies to illustrate how the inclusion of individual-based information into hydropower research had helped to incrementally enhance the understanding of complex fish and hydropower issues.

Research tools for assessing possible individual level effects of hydropower infrastructure and operations

To assess the impacts of hydropower infrastructure and operations on individual fish, tools that measure sub-organismal responses should be developed and validated to measure physiological changes that have the potential to be harmful to fish. Currently, tools developed to measure gene expression, heat shock protein expression, enzymatic activities, sensory physiology, and stable isotopic ratios have not been widely applied to research involving hydropower systems. Likewise, tools designed to quantify biomolecules like ions, lipids, hormones, and metabolites in fish tissue have been rarely applied to hydropower settings (with some exceptions, e.g., Wagner and Congleton 2004). Other tools such as physiological telemetry, forensic techniques and conventional measures of condition have also not been exploited to their full potential. Here, we outline several investigative tools to measure the individual and sub-organismal responses to hydropower infrastructure and operations, as well we suggest how they could be contextually used (Table 1). Each tool is introduced by way of a general overview and is then discussed with respect to its actual or potential role for the study of individual and sub-organismal responses of fish to hydropower impacts.

Table 1. An assessment of possible research tools that could be used to measure individual level effects of hydropower infrastructure and operations on fish (see text for details).

Assessment tool	Examples	Potential use in a hydropower setting	Relative applicability	Advantages	Disadvantages
Genomics	cDNA microarrays from multiple tissues; gene receptors	Predictive biomarkers; responses to abiotic and biotic stressors	Applicable	Typically only requires a nonlethal gill or muscle sample	Expensive laboratory methods required Still considered a novel research area and requires further validation Species-specific (or family-specific) gene arrays required
Heat shock proteins (HSP)	Hsp70 expression in multiple tissues	Predictable fluctuations in abiotic environment (e.g., flows, water temperature)	Possibly applicable	Found in most tissues Validated for thermal applications	Expensive laboratory methods required Still considered a reasonably novel research area
Enzymatic activity	Na^+K^+ ATPase; aspartate aminotransferase; creatine kinase; lactate dehydrogenase	Tissue damage; energetics; growth; smoltification; effects of pollution	Very applicable	Laboratory methods are relatively easy to do Can often be done with a non lethal biopsy	Other variables (both endogenous and exogenous) can influence enzyme rates Some enzyme assays can be expensive
Sensory neurophysiology	Neural stimulation; scanning electron micrographs of neuromasts	Developing fish guidance tools; attraction and avoidance studies	Very applicable	Fundamental to understanding how fish locate and select migration paths around barriers	Rarely applied to hydropower issues Challenges in conducting field studies on this topic
Ions and minerals	Na^+; Cl^-; K^+; Mg^+, Ca^{++} osmolality	Exhaustive exercise; nutritional condition	Applicable (fish ladder assessment and nutrition)	Nonlethal sampling (blood sample) Easy to measure	Can be influenced by any factors that alter homeostasis Nutritional indicators can be influenced by feeding history
Lipids	Triglycerides; proximate body composition	Condition as it relates to habitat quality; energy expenditure; overwinter survival	Possibly applicable	Laboratory methods are well-defined	Some methods require lethal sampling
Endocrine measures	Catecholamines; corticosteroids; reproductive status	Effects of hydro-peaking; abiotic and biotic stressors	Very applicable (cortisol and reproductivehormones)	Very responsive Time lag between stressor and response (cortisol only)	Influenced by genetics, development and environment Habituation or desensitization can occur
Metabolites and tissue energy stores	Blood glucose; blood and muscle lactate; muscle glycogen, ATP, PCr	Indicate magnitude and duration of abiotic or biotic stress (e.g., fishway passage)	Very Applicable	Can be done using simple methods and (or) inexpensive meters Reasons for responses well-defined	Dependent on temperature
Biotelemetry and biologging	Electromyogram transmitters (EMG); tail-beat transmitters; temperature loggers	Tracking fish through a hydropower system; fish way attraction; energetics; habitat use; thermal biology	Very Applicable	Direct responses from organism Can determine fate Compare behavioural responses to physiological responses	Expensive if using large sample sizes Tracking is time intensive

Table 1 (*concluded*).

Assessment tool	Examples	Potential use in a hydropower setting	Relative applicability	Advantages	Disadvantages
Condition-based assessments	Length–weight relationships; hepatosomatic index; organ condition	Fish condition near facilities; growth rates	Possibly applicable	Simple, inexpensive methods	Gross indicator of organismal condition (may be influenced by many factors) With the exception of length–weight relationships, involves lethal sampling
Stable isotope analysis	$^{13}C/^{12}C$; $^{15}N/^{14}N$	Nutrient derivation; trophic position	Possibly applicable	Can reveal food webs and diets associated with various flows or other system level changes Nonlethal sampling	Expensive laboratory methods required
Forensic techniques	Fluorescein; Hemident	Tissue damage caused by turbines and fishways	Very Applicable	Ease of use Nonlethal sampling Relatively inexpensive	Not fully tested for effects on fish Requires further validation Not all false positives are known

Genomics

Overview

Genomics is the study of whole genome patterns and regulation of genes and implies the use of high throughput DNA- or RNA-based methods, often involving costly microarrays, and bioinformatic approaches (Wenne et al. 2007). More simply put, this tool uses computer analysis to determine the array of genes that are either up-regulated or down-regulated in a given tissue sample. There are three main types of genomic studies: comparative, functional, and environmental. Comparative genomics refers to the study of whole genomes and their gene content. Functional genomics relates to the biochemical and physiological role of gene products. Environmental genomics encompasses the molecular variation in populations and across taxa, especially in response to environmental conditions. Whole genome sequences exist for multiple model species (e.g., zebrafish [*Danio rerio*], fugu [*Takifugu chrysops*], and stickleback [*Gasterosteus aculeatus*]). However, only partial sequences exist for species at a greater risk to be effected by hydropower (e.g., Atlantic salmon [*Salmo salar*], rainbow trout [*Oncorhynchus mykiss*]; Thorsen et al. 2005; Palti et al. 2004; Wenne et al. 2007). Genomic studies involving fisheries management have typically been undertaken to discriminate between different populations, assess immune response and disease susceptibility, and to investigate the effects of chemical contaminants and life history strategies on gene expression (e.g., Koskinen et al. 2004; Aubin-Horth et al. 2005*a*, 2005*b*; Hook et al. 2006; Purcell et al. 2006; Roberge et al. 2006; Fisher and Oleksiak 2007). To date, no studies have directly applied genomic techniques to fish exposed to a hydropower-related stressor.

Potential

Genomics could be used in a hydropower setting to develop biomarkers to predict if fish can successfully navigate through a hydropower impacted system, and to assess genome level responses (up- or down-regulation) to hydropower related stressors (for studies associated with the impact of hydropower on genetic variation please see Fagan 2002; Meldgaard et al. 2003; Alò and Turner 2005; Jager 2006). For instance, recent work by Miller et al. (2007) aims to develop predictive biomarkers for fate and entry times of Pacific salmon (*Oncorhynchus* spp.) by using cDNA (complementary DNA) microarrays from multiple tissues. If these techniques are to be used to understand gene expression of fish that successfully pass through hydropower infrastructure and deal with variable hydropower operations, it may be possible to understand, at a very basic level, the predictive biomarkers for successful navigation through a hydropower setting.

Other ways in which genomics could be used to assess the impact of hydropower infrastructure and operations on fish are to analyze the gene-level responses to abiotic and biotic stressors. Little is known about the genetic mechanisms present in fish to deal with acute changes to multiple environmental variables. Some recent studies have measured gene expression in relation to changes to habitat. For example, San Martín et al. (2007) quantified the expression of the prolactin gene receptor in response to seasonal changes to habitat in carp (*Cyprinus carpio*). In another study, Ju et al. (2007) found that a number of genes were up-regulated and down-regulated in Japanese medakas (*Oryzias latipes*) exposed to hypoxia. As hydropower infrastructure and operations can result in many changes to the surrounding habitat, genomic tools may be an effective way to assess the impact of these changes on fish. However, there is still a need to develop species-specific tools, as well as link changes in gene expression to facility operations, before wide-use of genomic techniques in hydropower settings will be effective.

Heat shock proteins

Overview

Heat shock proteins, also known as stress proteins, are a unique group of highly conserved cellular proteins that are found in living cells of animals (see reviews by Iwama et al. 1998; 1999; and Basu et al. 2002). Briefly, there are two types that are primarily studied in fish, Hsp70 and Hsp80. Hsp70 is most often used in fisheries research, although more studies are needed to validate its use as a stress indicator, as it is not expressed in some cold water species (Barton et al. 2002; Iwama et al. 2004; Zakhartsev et al. 2005). Heat shock proteins are up-regulated in cells exposed to environmental (e.g., adverse levels of metals and contaminants, chemical toxins, physical and chemical water properties, and natural change), pathophysiological (e.g., crowding, handling, confinement, etc.), and biological stressors (e.g., pathogens, parasites, etc.). Consequently, heat shock protein expression is a possible indicator of stress. However, heat shock proteins are still considered a developing research tool and the methodology is fairly intensive (i.e., Western blotting or enzyme-linked immunosorbent assay). Heat shock protein expression has never been used in a hydropower setting, but represents a promising tool for quantifying the possible effects of hydropower infrastructure and operating strategies on the cellular stress of individual fish.

Potential

Studies aimed to understand the sublethal effects of crowding near fish passageways, the use of side-channel refuge habitat, and on individuals exposed to pulse flows may benefit greatly by using heat shock protein expression tools. Coupling heat shock protein expression techniques to local environmental monitoring and habitat assessment would allow researchers to bridge the gap between hydropower impacts and the stress response in fish. Certain attributes of heat shock proteins make them amenable to this type of research. To start, heat shock proteins are expressed in numerous tissues (blood, muscle, liver, fin). Another essential intrinsic characteristic of heat shock protein expression is that there are minimal effects on expression when fish are handled (Vijayan et al. 1997). Furthermore, quantification of heat shock protein expression permits the indication of only definitive stressors; as heat shock protein expression likely occurs in a threshold manner, rather than in a graded way (Currie and Tufts 1997; Vijayan et al. 1998).

Enzymatic activity

Overview

Measuring the rates of enzymatic reactions involves the quantification of a particular rate limiting enzyme or reagent. With the development of commercial assay kits and spectrophotometers, enzyme activities can be measured with relative ease, though some can be costly. Some disadvantages of using enzymatic activities is that typically a variety of enzymatic activities need to be measured to fully understand the processes being measured, and results may be influenced by a number of endogenous and exogenous factors (McDonald and Milligan 1992; Wagner and Congleton 2004). Activities of a number of enzymes have been used to measure tissue damage (e.g., Wagner and Congleton 2004; Morrissey et al. 2005), energetics (e.g., Garenc et al. 1999; Martínez et al. 2003; Kaufman et al. 2006), growth (Pelletier et al. 1995; Lamarre et al. 2004; Imsland et al. 2006), smoltification (e.g., VanderKooi et al. 2000), and the effects of pollution (e.g., Ahmad et al. 2006; Tejeda-Vera et al. 2007).

Potential

Measuring enzymatic activities of fish in hydropower settings can be used for a number of applications, although perhaps the most relevant use is the measurement of tissue damage. When cells are damaged or die, the intracellular enzymes are released into the blood. By measuring the levels of alanine aminotransferase (ALT), aspartate aminotransferase (AST), creatine kinase (CK), and lactate dehydrogenase (LDH) in the blood, inferences to the magnitude and type of tissue damage can be made (Grizzle et al. 1992; Wagner and Congleton 2004; Morrissey et al. 2005). In hydropower settings, tissue damage in fish can occur in passageways, turbines, or during high flow conditions.

Other ways in which the measurement of enzymatic activities would be useful in a hydropower setting would be to evaluate energetics, growth, osmoregulatory preparedness (i.e., smoltification for downstream migrating salmonids and preparedness for freshwater migration in upstream migrants), and pollution. By measuring LDH (an enzyme used in anaerobic respiration to convert lactate to pyruvate and vice versa; and LDH is an indicator of burst swimming capacity [Garenc et al. 1999; Martínez et al. 2003]), Kaufman et al. (2006) were able to judge how active walleye (*Sander vitreus*) were in different habitats with varied food resources. It is possible that fish exposed to variable flows or in areas with fish ladders could have elevated levels of LDH. Growth is another process that could be measured using enzyme activity (Pelletier et al. 1995; Lamarre et al. 2004;). Imsland et al. (2006) found that growth positively correlated with pyruvate kinase (PK) and LDH (both indicators of glycolytic activity) in spotted wolffish (*Anarhichas minor*). Enzymes such as PK and LDH could potentially be used to compare growth rates between reference sites and areas affected by hydropower development. Smoltification is the process of adaptation to a marine environment (measured using Na^+/K^+-ATPase; Zaugg and McLain 1972; Giles and Vanstone 1976). In fact, the measurement of Na^+/K^+-ATPase activity has been used in several studies associated with hydropower impacts (Giorgi et al. 1988; Tiffan et al.

2000). Giorgi et al. (1988) found a relationship between gill Na^+/K^+-ATPase activity and their susceptibility to guidance through gatewells at dams located on the Snake-Columbia River system. Tiffan et al. (2000) found no link between travel time through a hydropower impacted stretch on the Columbia River and gill Na^+/K^+-ATPase activity. In general, enzymatic activities can offer very direct measurements of the effects that hydropower infrastructure and operations have on fish.

That being said, there are numerous reasons why enzymatic activities may change near a hydropower facility. It will be important to validate field studies by using multiple tools from our proposed toolbox, researchers should be able to predict the causes of enzymatic activity change. For example, lactate may be elevated following severe exercise (Garenc et al. 1999; Martínez et al. 2003), in resting fish within close proximity of each other (Pickering and Pottinger 1987), or following tissue damage (Wagner and Congleton 2004). To distinguish the cause of the change in enzyme activity, biotelemetry could be used to understand if the change in lactate is due to activity rates (see case study 1), and forensic techniques could be used to assess epithelial tissue damage (Colotelo et al. 2009).

Sensory neurophysiology

Overview

Sensory neurophysiology concerns the study of how animals perceive and react to the ambient environment using their nervous system. However, little is known about the interactions between the structure of the sensory organs of fish, the environmental cues that fish are subjected to while moving, and the behavioural decisions fish adopt particularly when they encounter barriers. With reference to fish passage, sensory physiology can yield information on the roles of visual, auditory or mechanical (including the lateral line), and tactile (including temperature sensors) sensory systems in fish movement (Hara and Zielinski 2006). For example, scientists can understand lateral line mechanosensory ability by observing the neural response of superficial neuromasts to changing water velocity (Bleckmann et al. 2000). Ablated superficial neuromasts have been shown to have a strong connection to rheotactic behaviour across several fish species (Montgomery et al. 1997) and it is likely that rheotactic behaviour has an important role in successful passage by fish through fishways.

Tools that researchers can use to measure sensory neurophysiology vary widely. Manipulation studies can be completed by altering the sensory ability of fish. For example, Partridge and Pitcher (1980) blinded fish by creating temporary blindfolds using painted film, and altered lateral line function by cutting the lateral line. Observation and measurements of superficial neuromasts can be done by fixing tissue for view under scanning electron microscopes (e.g., Marshall 1996). Chagnaud et al. (2006) connected electrodes to the lateral line of gold fish and recorded afferents caused by stimulations made by a steel rod using an electrode amplifier connected to a digital audio tape recorder.

Potential

Understanding the sensory physiology associated with fish movement has great potential for the design of behavioural guidance technologies. By measuring lateral line sensory ability and fish swimming muscle activity, engineers may be able to construct fish passageways that guide fish through hazardous areas, making hydropower developments as invisible as possible to fish. By placing objects in the path of flowing water costly movement through fishways can be avoided, as fish may be able to sense and use water that decreases the cost of locomotion (Liao et al. 2003). Thorstad et al. (2003) located fish near hydropower water outflows and suggest that this may cause migration delays and could be energetically costly. By understanding how fish sense different flows, engineers may be able to prevent movement towards water outputs by developing guidance technologies that exploit lateral line mechanics or other sensory functions.

Ions and minerals

Overview

Typically in studies aimed to quantify the magnitude or physiological consequences of stress in fish, the concentrations of specific ions (e.g., Na^+, Cl^-, and K^+) or minerals (e.g., total calcium, total magnesium, total phosphorous) are measured to understand the secondary effects of stress (Mazeaud et al. 1977; Wendelaar Bonga 1997) and nutritional condition (Wagner and Congleton 2004); the primary response being the release of stress hormones. Plasma ions are often used to understand the ability of an organism to deal with stress responses, such as acidosis, a secondary response that is the result of lactic acid build-up caused by anaerobic respiration (e.g., Wood 1988, 1991). Following exhaustive exercise, ion concentrations may be disturbed over a period of 4 h–24 h before returning to baseline levels (McDonald and Milligan 1997). In some cases, severe ion imbalances can lead to mortality (Wood et al. 1983; Wood 1988, 1991). Measures of plasma ion balance (plasma osmolality) have typically been used to measure the stress effects of catch-and-release angling (a practice that results in brief exhaustive exercise and subsequent release of the angled fish) on fate and physiology (e.g., Brobbel et al. 1996). Measuring minerals (e.g., Ca^{2+}, Mg^+, phosphorous) can also yield valuable information on the nutritional condition of fish (Wagner and Congleton 2004). Calcium is present in the plasma as both ionized and bound forms; however declines in plasma calcium are correlated to declines in plasma protein because the majority of plasma calcium is bound to proteins (Andreasen 1985). Magnesium may be associated with lipid metabolism (Wagner and Congleton 2004). Methods to determine ion and mineral concentration are not difficult or expensive; some can even be done using handheld instruments. Measuring the secondary stress responses associated with ions and minerals will give researchers a better understanding of the proximate causes of fish mortality associated with hydropower impacts. Currently, few studies have applied measurements of plasma ion and mineral concentrations to assess fish dealing with hydropower infrastructure and operations.

Potential

Fish experience periods of brief exhaustive exercise when near hydropower systems, as passage of fish through fish ladders is analogous to brief periods of exhaustive exercise (not always the case, for example, the Seton study; see case study 1) (Gowans et al. 2003). It is likely that passage up a fish ladder results in changed levels of plasma ion concentrations indicative of physiological stress, but after a recovery period, the levels of plasma ions would return to normal levels (Wood et al. 1983; Wood 1988, 1991). In many incidences, fish likely do not successfully ascend fish ladders on the first try, and must make multiple attempts to pass (Bunt et al. 1999; Moser et al. 2002; Castro-Santos 2004). Elevated ion concentrations are likely indicative of passage problems, as fish making several attempts to successfully pass likely incur a physiological cost. Managers may be able to use plasma ions and minerals in a predictive model (once cause and effect are determined) to assess fish upon arrival as to whether they are "physiologically capable" of successfully passing through hydropower infrastructure and dealing with hydropower operations (especially if passage is known to require multiple attempts). Minerals reflective of nutritional condition could be used to evaluate habitat quality associated with restoration of altered habitats (Cooke and Suski 2008). Another possible use of ions relates to temperature, as ion concentrations tend to decrease in response to heat stress (Wood 1991) and this could be related to hydropower (stranding in side channels that get warm or warm water epilimetic releases from dams).

Lipids

Overview

Lipids have widely varied structures and biological function. They are vital to the formation of biological membranes and are storage molecules for metabolic energy. Lipids are the primary store for energy and often are a major factor in proximate body composition. Proximate body composition is defined as a whole body energetic metric that measures the amount of lipids, proteins, organic ash, and water present in an animal and can indicate condition. Fatty acids are the simplest type of lipid and are aliphatic monocarboxylic acids that can be either saturated or unsaturated with hydrogen (further information is provided in the hormone section). In fish, triglycerides are the primary form of stored energy (Higgins and Talbot 1985) and are stored in the muscle, liver, subdermal tissue, and the mesenteries. In salmonids, triglycerides are primarily stored in the adipose tissues (Henderson and Tocher 1987). Cholesterol is another blood borne lipid that can easily be measured using nonlethal approaches and simple laboratory methods. Blood cholesterol levels indicate body energy stores. Energy stores and lipid content are important for fish health as they have been linked to overwinter survival; energy allocation strategies; reproductive performance; early life history strategies; and environmental stress response (Henderson and Tocher 1987; Jobling et al. 1998; Adams 1999). Lipid content in general can easily, and at a modest cost, be quantified using destructive extraction techniques that require relatively large pieces of tissue (usually requires lethal sampling; Bligh and Dyer 1959) or by various nonlethal electronic devices (e.g., handheld microwave energy meter, Crossin and Hinch 2005; bioelectrical impedance analysis, Kushner 1992). Lipid analysis has only recently begun to be used in river systems altered by hydropower infrastructure and operations (Wagner and Congleton 2004; Cleary 2006).

Potential

Lipid analysis can likely be a robust tool to use in predictive models relating to fish response to hydropower infrastructure and operations because it has been shown to be indicative of numerous variables such as habitat quality, energy use, nutrition and overwinter survival. Assessments of habitat quality are imperative in understanding fish response to hydropower, and lipid analysis has revealed strong connections between habitat quality and lipid reserves in marine fish (Lloret et al. 2005). Energy use is also important in hydropower systems, as changes in flow rates can cause fish to compensate or seek refuge when faced with altered flow. It is likely that fish in an energetic demanding system would have less lipid reserves and researchers could exploit lipid analysis to judge the energetic requirements of a specific hydropower operational strategy. Lipid assessments may be especially useful in studies examining dam passage of anadromous Pacific salmon, as these species cease feeding prior to river entry and rely on energy stores to power migration, sexually mature, and spawn (Brett 1995; Magnoni et al. 2006).

Endocrine measures

Overview

Stress hormones can be useful indicators of hydropower induced effects (Adams 1990; Wendelaar Bonga 1997). Stress hormones are an endocrine response to perceived changes in the surrounding environment. For fish, stress responses occur for a number of reasons including elevated temperature, toxins, and handling (e.g., Mazeaud et al. 1977; Strange and Schreck 1978; Hontela et al. 1992; Fagerlund et al. 1995; Wendelaar Bonga 1997). Because of the stress response in fish being linked to environmental change, it is likely that hydropower impacts may be manifested in the response (see review by Fagerlund et al. 1995). Two main types of hormones commonly used to measure stress are catecholamines and corticosteroids (Wendelaar Bonga 1997; Barton 2002). Plasma catecholamines are released rapidly in response to perceived ambient disturbance and are linked to tissue oxygen delivery and fuel mobilization for tissue metabolism. However, because catecholamines are very rapid acting, sampling fish in a manner that would be reflective of concentrations of catecholamines during the stressful event, and sampling control fish without inducing a catecholamine response would be difficult. Cortisol on the other hand may be a good indicator of the magnitude and duration of acute stress because there is a time lag between the stressor and the response (Barton 2002; Barton et al. 2002).

Reproductive hormones are typically fatty-acids secreted as thyroid hormones, growth hormones, or metabolic hormones and may also be relevant to hydropower applications. Specifically, some examples that have been studied in fish include: testosterone, 11-ketotestosterone, 17α,20β-dihydroxy-4-pregnen-3-one, 11-beta-OH-testosterone, and 17-beta-estradiol (Brantley et al. 1993; Pankhurst 1995).

Often reproductive hormones are used to link reproductive behaviours, reproductive development, and the effects of endocrine disrupters on fish maturity (Pankhurst 1995; Arcand-Hoy and Benson 1998; McKinley et al. 1998). Quantifying reproductive hormones is well understood and can be done using a variety of laboratory techniques using small blood samples.

Potential

Cortisol and reproductive hormones are probably the most useful hormones to measure and quantify stress induced by hydropower infrastructure and operations. Cortisol has been used to link hydropower operations to sub-organismal stress, as Flodmark et al. (2002) found that the amount of plasma cortisol changed due to a simulated hydro-peaking event. However, fish can become desensitized to cortisol and other variables like development stage, genetics, and environment could influence cortisol levels (Gamperl et al. 1994; Barton 2002). Other hormones that have been used to understand the impact of hydropower infrastructure are reproductive hormones such as testosterone and 17β-estradiol (both fatty acids). McKinley et al. (1998) found that hydropower development caused delayed reproductive development because of impingement or entrainment. However, hormones can change naturally or as a result of non-hydropower related effects (Carruth et al. 2000), and so care should be used when interpreting these measures in making assessments of hydropower effects.

Metabolites and tissue energy stores

Overview

With the onset of a hormonal response to stress, numerous secondary effects occur (Wendelaar Bonga 1997). Mainly, metabolites such as glucose, lactate, glycogen, and numerous other reactants and products of metabolism change to meet energetic demands to fuel the stress response (Mazeaud et al. 1977). In field studies, blood samples can be taken rapidly and non-lethally by caudal puncture (and (or) gill puncture) and plasma glucose and lactate can be measured using inexpensive portable devices or simple laboratory methods. Increases in either glucose or lactate can indicate a metabolic response to stress. Plasma glucose is an indicator of mobilization of energy reserves, and plasma lactate a by-product of anaerobic respiration. Other, more invasive techniques can be used to measure tissue glycogen or tissue lactate. Tissue glycogen is an indicator of the metabolic reserves stored in the liver and muscle and is a good indicator of muscular activity, but is highly dependent on temperature and when the fish last fed.

Potential

Fish experiencing acute changes in hydropower infrastructure and operations often exhibit a stress response (see case studies). It is likely that by measuring specific metabolites, indications of the magnitude and duration of stress can be found (Barton 2002). However, few studies have measured metabolite responses to hydropower infrastructure and operations (e.g., Flodmark et al. 2002). Fish swimming up a fish ladder likely experience a rise in lactate, as exhaustive exercise typically leads to anaerobic respiration (e.g., Schwalme and Mackay 1985; Wood 1988, 1991). Plasma or tissue lactate could also change if fish are exposed to hypoxic water (e.g., if water is released from the hyperlimnion) (Morrissey et al. 2005). Glucose and glycogen would also likely change in hydropower systems in relation to exhaustive exercise, however Flodmark et al. (2002) found no change to plasma glucose in fish exposed to simulated changes to water flow. Metabolites would likely be a good indicator of short-term effects of hydropower systems, such as the energetic costs of pulse flows, fish ladder use, and water discharges. Metabolites should be used in studies investigating the impacts of hydropower infrastructure and operations, as the techniques can be informative, non-invasive, and inexpensive.

Biotelemetry and biologging

Overview

The term “telemetry” encompasses a variety of technological instruments that can be used to assess the physiology, behaviour, and energetic status of free-living animals (Cooke et al. 2004*a*). Conventional telemetry involves the use of transmitters and listening devices (i.e., radio-antennas, hydrophones) to locate the tagged animal in space and time (for simplicity, we also include the use of passive integrated transponders [PIT tags] in this definition as they are often used to locate fish [Burke and Jepson 2006]). There are two principal types of telemetry: radio and acoustic. Radio telemetry uses antennas to receive waves of energy that are emitted from implanted or attached transmitters. By using arrays of antennas, or by using manual tracking approaches, animals can be tracked with a high degree of confidence. Acoustic telemetry involves the use of hydrophones to position implanted tags that transmit sound waves through water to convey fish location. As with radio telemetry, acoustic transmitter can be tracked manually or using a fixed hydrophone array. Both radio and acoustic platforms can be used to transmit information such as temperature and pressure. In addition, there are a number of logging technologies (called “biologging” or archival loggers) that must be retrieved and downloaded to obtain data. The accuracy and confidence in telemetry and logging data depends on device choice, number of antennas, hydrophones, and loggers being used, and the method used to interpolate the location of the transmitters (i.e., triangulation vs. successive gain reduction). Telemetry studies can be costly; however, they can provide large datasets and detailed information about fish movements, habitat selection, behaviour and physiology, data that are often unavailable from free-swimming fish using any other technique.

Remote physiological techniques (either radio-, acoustic-, or archival logger-based) can provide measurements of in situ physiological variables such as heart rate, opercular rate, tail-beat frequency and muscle activity (Cooke et al. 2004*b*). Electromyogram (EMG) transmitters are becoming a more commonly used tool to assess the volitional movements of fish (Cooke et al. 2004*b*). Electromyogram equipped transmitters have electrodes that detect the bioelectrical voltage changes in the red muscle, which is proportional to the degree and duration of muscle tension (Sullivan et al. 1963) and is correlated with oxygen consumption (Weatherley et al. 1982; Weatherley and Gill

1987). Electromyograms can be calibrated to tail-beat rate to allow estimates of swimming speed, and (or) oxygen consumption, and the metabolic costs of activity. Electromyogram telemetry has been used to measure in situ metabolic rates at different temperatures and during seasonal and daily periods (Briggs and Post 1997*a*, 1997*b*), and has been shown to be useful in assessing energetic responses of fish to hydropower infrastructure and operating strategies (Gowans et al. 2003; Thorstad et al. 2003; Murchie and Smokorowski 2004; Brown et al. 2006; Scruton et al. 2007*a*, 2007*b*). Forthcoming sensors including accelerometers may provide more opportunities for monitoring fish activity in the wild.

Potential

Conventional telemetry has been highly useful to track fish through hydropower systems (e.g., McKinley et al. 1998; Cooke et al. 2004*a*; Scruton et al. 2002, 2007*a*). For instance, by placing radio or acoustic receiving loggers throughout a hydropower impacted river system, detailed measurements of fish passage, fishway evaluation, turbine mortality, migration rates, survival, and habitat use have been made (Stier and Kynard 1986; Moser et al. 2002; Scruton et al. 2002; Behrmann-Godel and Eckmann 2003; Parsley et al. 2007). These methods are particularly important for assessing unanswered questions such as, how far fish will swim upstream when flows are high due to pulse flows, when temperatures vary because of water being released from below the thermocline, or to determine where fish spawn when hydropower systems have prevented passage to typical breeding grounds.

There are many applications of remote physiological devices (mostly telemetry) for assessing the response of fish to hydropower infrastructure and operations. Changing flow rates, fish passage, and habitat use can all be assessed in part by using physiological telemetry. Changing flow rates present an altered environment that can force fish to swim at high speeds for brief or extended periods of time. Physiological telemetry allows the researcher to track the location of individual fish, and collect data on swimming speeds and metabolic activity (see case study 2 for example; Murchie and Smokorowski 2004; Scruton et al. 2007*a*). Fish passage is also an important component of hydropower infrastructure. Fish often physically exert themselves to successfully pass through a fishway; thus by using physiological telemetry, the costs of such movements can be quantified (See case study 1; Gowans et al. 2003; Scruton et al. 2007*b*). Assessing habitat use may also benefit from physiological telemetry. The physiological data could help researchers make links between habitat quality and individual behaviour and physiology (this aspect can have large impacts on fish habitat modeling and management; Cooke et al. 2004*a*). Overall, physiological telemetry can be used in a number of ways to address the impact of hydropower infrastructure and operations on fish physiology and behaviour.

Condition-based indicators

Overview

Condition-based indicators encompass length–weight relationships, organosomatic indices, and necropsy-based assessments. These assessments range from being relatively non-invasive to lethal. Length–weight relationships are typically very easy to measure, as fish only need to be handled briefly and they are appropriate indicators of general health. However, changes may not necessarily be due to stress, as seasons (Adams et al. 1982), stage of development and sexual maturation (Medford and Mackay 1978) can also influence length–weight relationships. Organosomatic indices involve the comparison of a particular organ to body weight ratio (e.g., hepatosomatic index [liver:body weight, HSI], gonadosomatic index [gonads:body weight, GSI], viscerosomatic index [entire viscera:body weight, VSI], and splenosomatic index [spleen:body weight, SSI], see Barton et al. 2002). These indices can be used to measure stress, as values that are lower or higher than normal indicate that energy allotment to organ maintenance and growth is altered (Kebus et al. 1992). Another condition-based indicator is necropsy-based. This method involves autopsies of sacrificed fish and linking the condition of internal organs to stress based on published guidelines as to the condition of normal organs (Barton et al. 2002). It is difficult to relate condition-based assessments to stress, as results could be influenced by a variety of variables (i.e., disease, pollution, genetics, etc.), thus caution should be used.

Potential

Condition-based indicators may be most appropriate for assessments of the effects of hydropower infrastructure and operations on fish habitat and fish health downstream of the installation. A number of previous studies have used condition-based indicators to directly assess the impacts of hydropower (e.g., McKinley et al. 1998; McKinney et al. 2001; Paukert and Rogers 2004; Sato et al. 2005). McKinney et al. (2001) used a length-specific mean-weight equation to assess the condition of rainbow trout below the Glen Canyon dam and found that smaller fish were more strongly affected by dam operations than larger fish. Likewise, Sato et al. (2005) measured Fulton's condition factor and gonadosomatic index and determined that female curimatá (*Prochilodus argenteus*) were in better physiological and reproductive condition than male fish. Studies that measure condition-based indicators typically require control sites, and controlled laboratory experiments (possibly using underwater video) may be needed to fully understand the environmental conditions that lead to changes to condition-based indices.

Stable isotope analysis

Overview

In aquatic ecosystems stable isotopes are useful for understanding the sources of fish diets and the trophic positions held by a particular fish in a food web (Peterson and Fry 1987). By using the ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$, diet source and trophic position, respectively, can be inferred (Deniro and Epstein 1978, 1981; Post 2002). Typically, researchers have lethally sampled the white muscle of fish (Pinnegar and Polunin 1999); but recent studies have promoted the use of fin clips and other tissues (e.g., blood, scales) to assess stable isotopes (Jardine et al. 2005) — mainly to sample species of conservation concern.

Potential

It may be possible to use stable isotope analysis in habitats downstream of hydropower facilities, as shifts in habitat caused by changes in flow and flooding events may alter food sources and trophic positions of fish. Recently, stable isotope analysis has been used to assess growth and feeding in yellow perch to understand site specific physical and chemical factors (Murchie and Power 2004), and to assess landscape-scale hydrological characteristics and carbon flow in river food webs (Hoeinghaus et al. 2007). In general, with the use of reference sites and (or) archived specimens, stable isotope may be a unique tool to assess how individuals alter feeding behaviour in hydropower systems. However, caution should be taken when considering stable isotopes as a tool, as recent criticisms about the use of stable isotopes have been proclaimed (Hoeinghaus and Zeug 2008).

Forensic techniques

Overview

Forensic techniques encompass tools than can be used to investigate external tissue damage, especially to the skin. These tools have recently been applied in fisheries to assess skin abrasion caused by nets. Researchers have used a combination of fluorescein bath and ultraviolet light exposure to assess tissue damage (Noga and Udomkusonsri 2002) in a variety of species such as walleye pollock (*Theragra chalcogramma*), sablefish (*Anoplopoma fimbria*), northern rock sole (*Lepidopsetta polyxystra*), and Pacific halibut (*Hippoglossus stenolepis*) (Davis and Ottmar 2006). Other chemical enhancers including Hemastix®, Hemident™, Phenolphthalein and Bluestar© may offer alternatives to fluorescein for detecting fish skin abrasion (Colotelo et al. 2009). The use of chemical enhancers as a common tool in assessing tissue damage in fish is likely a few years away, as much work is still needed to determine any negative effects of the chemicals on the fish and aquatic environments, as well as to determine the extent to which false positives or false negatives may influence conclusions.

Potential

Using chemical enhancers to aid the detection of skin injury may be useful to assess the impact of hydropower infrastructure on fish. Numerous infrastructures including turbines and fishways either cause or likely cause tissue damage in both migratory and non-migratory fish. A quick, non-invasive method for determining and quantifying injuries would be useful for understanding how different mitigative options affect individuals. Presumptive tests would also help researchers identify injury patterns that may lead to improvements in infrastructure and common practices. Davis and Ottmar (2006) used presumptive tests, including forensic techniques to understand the effect of fish nets on multiple fish species. It is highly likely that similar methods could be used in a hydropower setting to determine external injury in fish passing through hydropower barriers and fishways.

Using multiple tools

All of the above "tools" have the potential to provide useful information about the physiology of fish exposed to hydropower impacts. However, organismal physiology will be affected by other exogenous and endogenous factors. Many species that are affected by hydropower infrastructure are anadromous and semelparous (i.e., Pacific salmon). Depending on the species, stock, and location of the hydropower facility, these fish will have different maturation status and (or) nutritional status and will be also influenced by other factors such as fishing and thermal stress. For example, lipid levels are related to glycogen stores or vitellogenesis; ions and enzyme levels (Na^+/K^+ ATPase) are inherently linked to both nutritional and maturation status. We suggest that studies should use multiple tools to clearly determine the impacts of hydropower on fish to ensure that other exogenous and endogenous factors are appropriately considered.

Case studies

Here we present two brief case studies to illustrate how individual-based metrics can be used to understand fish responses to hydropower operations and infrastructure. Both case studies are based on data collected at hydropower facilities in British Columbia, Canada, by an interdisciplinary research team consisting of academic, government, and industry partners.

Case study 1: The Seton River

The Seton-Anderson watershed in the southern interior of British Columbia, Canada, is highly modified by hydropower development. Maturing sockeye salmon (*Oncorhynchus nerka*) returning to spawn in the watershed must pass a diversion dam via a vertical slot fishway (Fig. 1) and two powerhouse tailraces before reaching spawning grounds. In 2005 and 2007, studies were conducted using physiological biopsy (Cooke et al. 2005), and electromyogram (EMG) and conventional telemetry to evaluate physiological and behavioural responses to hydropower facilities in this system (Pon et al. 2006; Roscoe and Hinch 2008). Sockeye salmon were caught at the top of the Seton River fishway, blood sampled, and tracked by electromyogram, acoustic or radiotelemetry after release (fish were released downstream of the dam). Blood samples were analyzed for ion concentrations (i.e., Na^+, K^+, Cl^-), metabolites (lactate and glucose), and cortisol to assess the degree of anaerobic exercise and physiological stress associated with hydro-system passage.

All stress indicators examined from fish captured at the top of the fishway were comparable or lower than previously reported for migrating adult sockeye (Crossin et al. 2008; Young et al. 2006*b*). Thus, the physiological variables measured suggest that hydropower infrastructure passage was neither physically exhausting nor particularly stressful. However, when comparing successful and failed migrants it was found that fish that failed to ascend the fishway had lower plasma sodium ion concentrations ($P = 0.020$, Pon et al. 2009) and fish that failed to reach spawning grounds had higher levels of plasma lactate ($P = 0.007$, Pon et al. 2006). Although lactate and ion levels in failed migrants were still within the range of values reported elsewhere for migrating sockeye, the results suggest that physiological stress may inhibit successful migration.

To examine the physical effort required to ascend the fishway, fish were tagged with EMG transmitters. Record-

Fig. 1. Vertical slot fishway at the Seton river hydropower facility used to facilitate upstream migration of salmonids (photo source, L.B. Pon).

ings of EMG signals converted into swim speed estimates (see Hinch and Rand 1998) revealed that fish generally did not invoke anaerobic activity for extended periods of time in the fishway (Pon et al. 2009). Observations of low swimming intensity (i.e., aerobic activity), were consistent with low plasma lactate levels in fish caught at the top of the fishway and suggested that passage through the Seton River fishway is unlikely to be physically exhausting for migrant adult sockeye salmon. Electromyogram telemetry also revealed that some fish used reverse flows to minimize swim efforts while others did not. As a consequence, these fish were able to ascend the fishway in a more energetically efficient manner than other fish.

In using blood sampling to examine stress related to dam passage, there are several limitations highlighted by the Seton River dam study. For one, to obtain an accurate representation of fish condition, it is necessary to catch and sample fish in an expedient manner, so as to avoid biasing the blood sample with capture- and handling-related stress. At Seton River dam, fish could only be caught in such a manner by dip-netting individuals from the top of the fishway, and thus it was not possible to capture fish downstream of the dam. It is also important to consider the effects of natural variability on measures obtained from blood samples, as common stress indicators such as cortisol and ions change over the course of migration (Carruth et al. 2000; Shrimpton et al. 2005). At Seton River dam, individual cortisol measures ranged from 32.5 to 927.6 $ng \cdot mL^{-1}$ in fish caught over the course of August and September of 2005, making it difficult to distinguish between stress effects and maturation-related changes.

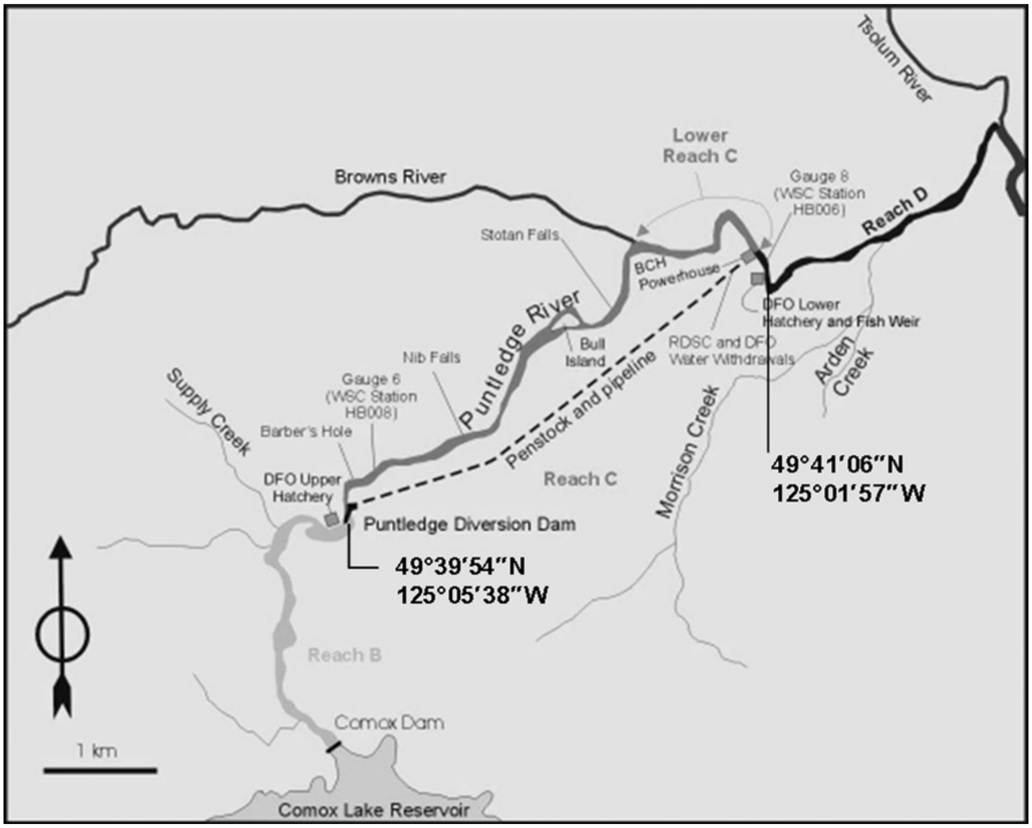
Electromyogram telemetry also has limitations, and should be used with care when making estimates of fishway passage efficiency. At the Seton River dam, a 40% drop-back rate was observed in EMG tagged fish, while only 20% of radio tagged fish failed to pass the fishway, a discrepancy that may be due in part to the additional stressors associated with EMG tag implantation (e.g., surgery). Also, as individual transmitters are relatively expensive, it may be cost prohibitive to tag a sample of fish sufficiently large enough to make statistical comparisons with a high degree of power.

Case study 2: The Puntledge River

The Puntledge River is a regulated river that has a number of natural and artificial barriers to the upstream migration of adult Pacific salmonids (*Oncorhynchus* spp.), particularly in reach C (Fig. 2). Throughout the reach there are a number of natural barriers, specifically Nib Falls and Stotan Falls. These two areas have a number of fish ladders (steps carved out of bedrock) built into the natural terrain of the river to facilitate upstream migration of fish. Beginning in 2004, experimental release of water from the diversion dam has occurred in an effort to mimic natural variation in river flow. These pulse flows lead to elevated water levels and increased flow rates, especially through the fish ladders (Fig. 3). Research is currently being conducted to understand whether these pulse flows have an effect on upstream migration of summer Chinook salmon. Techniques being used include biosampling, thermal logging (biologgers), and telemetry.

In the summer of 2007 male summer-run Chinook salmon were measured for total length and blood and gill samples were taken (blood parameters measured included triglycerides, calcium, glucose, phosphorous, and AST [aspartate transaminase]; gill sample was collected for future genomic work). A microwave energy meter (Crossin and Hinch 2005) was used to estimate gross somatic energy density. Following these procedures, fish were either implanted with an EMG transmitter or a conventional radio transmitter. Both

Fig. 2. Map displaying the Puntledge River and the locations of artificial and natural barriers (map source, E. Guimond).



types of transmitters were equipped with a thermal logger (DS1921Z, iButton, Maxim Integrated Products and Dallas Semiconductor, Sunnyvale Calif., USA) to record ambient body temperature every 20 min. Upon release, fish were tracked using multiple antenna telemetry arrays placed at the powerhouse, Stotan Falls, Nib Falls, and numerous other strategic locations throughout the study period. The arrays were complemented with manual tracking whereby each fish was tracked for at least 10 min twice daily, increasing to 4 times daily during pulse flows, to ensure collection of EMG data for all fish (i.e., fish not tracked automatically by the multiple antenna arrays). River temperature and flow was also measured hourly at numerous locations.

Pulse flows increased the flow of water through reach C of the river. Some Chinook salmon (e.g., Chinook salmon #29) were found to move upstream during the periods of increased water flow (Fig. 3). These movements are likely important, as migratory delays have been found to negatively affect spawning success (Quinn et al. 2000).

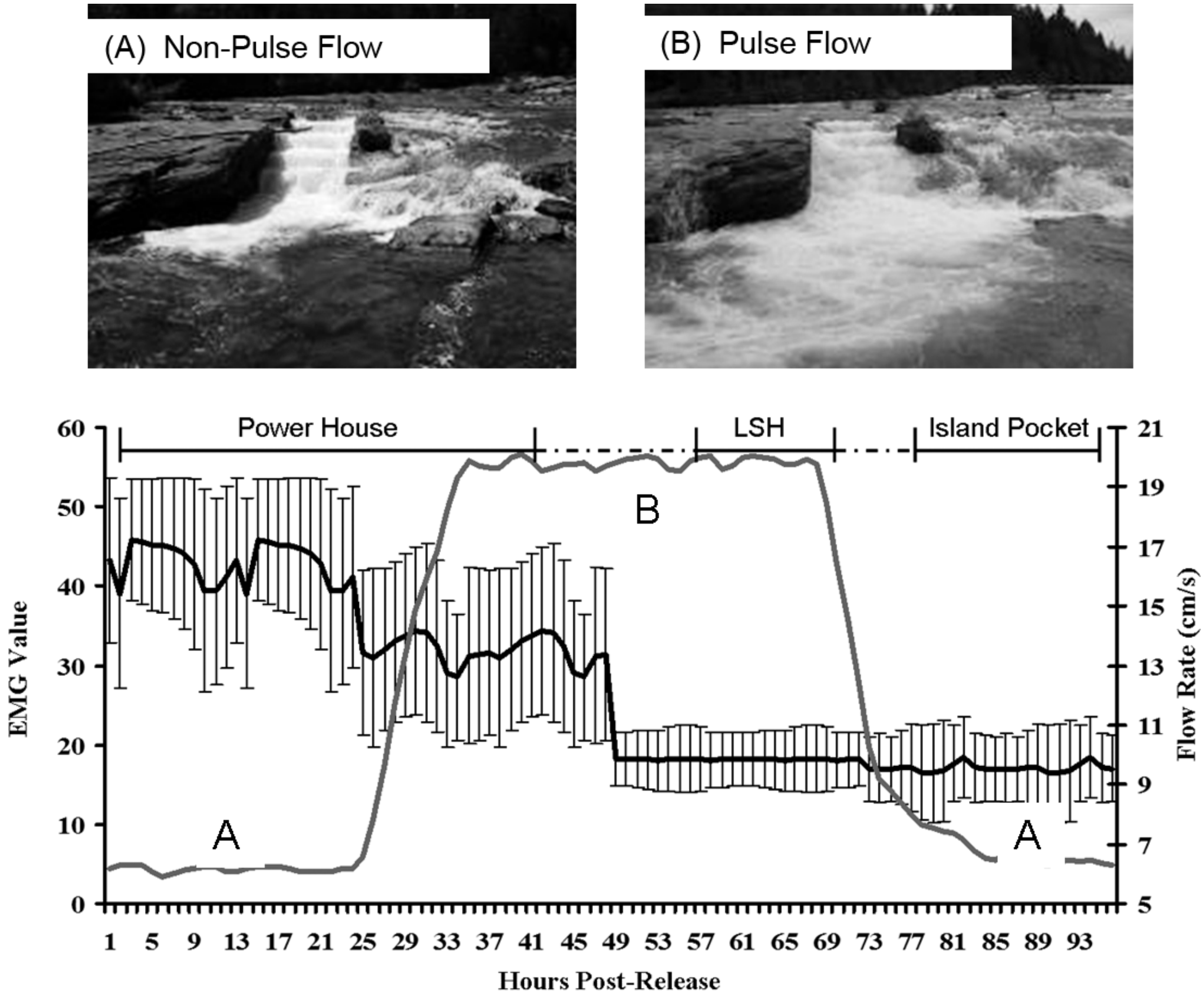
Fish were more likely to ascend Stotan Falls at lower flow rates. This finding will help managers select species-specific or community-specific (if multiple species are used) flow rates that increase the probability of successful ascent in difficult reaches. Also, in future studies we will investigate the thermal histories of tagged Chinook salmon using thermal loggers (e.g., Fig. 4) and attempt to understand the importance of thermal refuge to spawning success (similar to studies by T.P. Quinn, e.g., Berman and Quinn 1991). Temperature has previously been shown to affect migration mortality and travel rates in sockeye with long migrations (Keefer et al. 2008). If flow rates are combined with river temperature profiles, managers will be able to regulate rivers so that both flow and temperatures are optimal for upstream migration of Pacific salmonids (see Macdonald et al. 2007) and more closely resemble a natural flow.

Fish that were unable to move upstream during the pulse flows and were subsequently located downstream (though not necessarily as a result of the pulse flows) were found to have higher concentrations of plasma Ca^+ and lower levels of triglycerides. These fish were sampled at the time of release, and thus, physiological condition at time of fallbacks was not known and can only be inferred. There were no significant impacts of time-of-release physiology and spawning success, but there may be multiple physiological variables related to maximum distance traveled, as calcium and magnesium were strongly negatively correlated and gross somatic energy density was strongly positively correlated with maximum distance traveled. The future genomics research will enable us to determine if there are any biomarkers that yield information on the potential fate (i.e., ascent, survival and spawning) of individual fish. Such information would identify the extent to which fish were predisposed to failure independent of the hydropower facilities. Furthermore, genomic biomarkers could be used to make in-season decisions regarding flows or retention of fish for artificial spawning in the enhancement hatchery.

Implications for regulatory agencies and utilities

When results are obtained using sub-organismal tools, it may be difficult for regulatory agencies and utilities to di-

Fig. 3. The mean (whiskers represent standard error) EMG value for Chinook salmon #29 before and after the first pulse flow (black line) and the water flow measured at gauge 6 (blue). The physical location of the fish along reach C is also given (solid line indicates known location, dotted line indicates unobserved transition between known locations) (photo source, M.R. Donaldson).

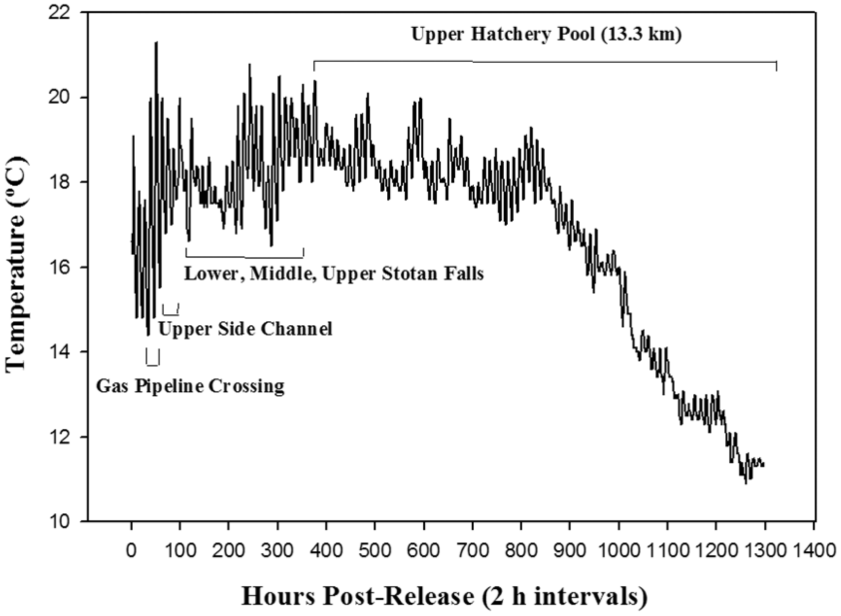


rectly relate these data to management issues at the level of the population, community, and ecosystem. However, we argue that sub-organismal responses are just as important as population and community level responses for several reasons (as reviewed in Young et al. 2006*a* and Cooke and Suski 2008), and should be used by regulatory agencies and utilities when engaged in management decisions. The primary basis for this assertion is the notion that organismal condition, health, and behaviour are influenced by both genetics and environments and that collectively these factors influence the fitness of an individual fish (Ricklefs and Wikelski 2002). In general, regulatory agencies responsible for hydropower operations should be making decisions based on a range of scientific data from the organismal level to the community level, ideally in an integrated manner.

Conclusions

Physiological indicators are sensitive and provide an integrative assessment of the condition of fish. Furthermore, energy is the currency of life and can be affected by a suite of factors including altered thermal environments, changes in food supply, delays in migration, and variable water discharge. Ecological genomics will provide an even more mechanistic understanding of the biological systems regulating fish behaviour and survival. Heat shock proteins and stable isotope analysis could be used to assess fish response to changing abiotic and biotic environmental variables once further research is completed. Quantification of enzymatic activity (e.g., LDH and CK), ions (e.g., Na^+ and K^+), hormones (e.g., catecholamines and corticosteroids), and metabolites (e.g., glucose and lactate) likely will provide insight into tissue damage, energetics, and overall stress that fish endure when dealing with hydropower. Information on the sensory neurophysiology of fish can be used to help develop effective fish guidance and attraction technologies to facilitate safe passage past hydropower barriers. Lipids and condition-based indices may be useful for assessing habitat linked body condition. Physiological telemetry will continue to help researchers understand how fish respond to hydro-

Fig. 4. Thermal history of a Chinook salmon (fish #28) in the Puntledge River with locations determined using conventional telemetry data.



power infrastructure and operations in real time. If researchers couple some or many of these tools, predictive models could be developed to assess how changes to fish habitat caused by hydropower infrastructure and operations will affect fish. The two case studies highlighted both the benefits and challenges of including individual-based metrics in studies of hydropower–fish interactions. Clearly, no single individual will possess the skills or expertise needed to mount a study that makes use of all of the tools identified in this review. Hence, implicit in expanding the "toolbox" is building more integrative and interdisciplinary teams to tackle complex hydropower questions. In summary, this paper should provide researchers with a comprehensive understanding of the tools available to understand individual and sub-organismal responses to a variety of hydropower activities (but these tools may be useful during environmental assessment periods as well). Furthermore, the expanded toolbox has the potential to provide the knowledge to move towards a more sustainable hydropower industry and provide regulators with additional tools for evaluating compliance and making more informed decisions.

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