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Developing a Mechanistic Understanding of Fish Migrations by Linking Telemetry with Physiology, Behavior, Genomics and Experimental Biology

The Value of Information in Fisheries Management

Fisheries

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301/897-8616 • fax 301/897-8096 • main@fisheries.org
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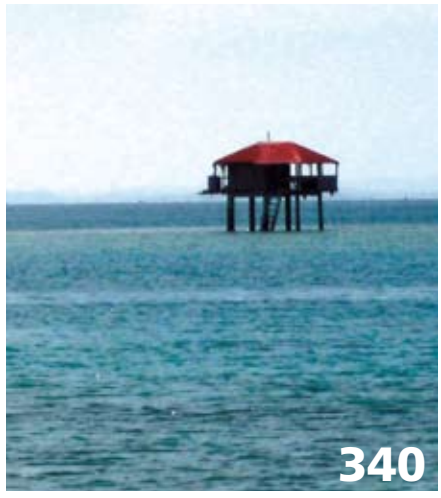

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COVER: Close-up of micro-array slide (background) illustrating differentially regulated genes for sockeye salmon that die prior to reaching spawning grounds (foreground).
CREDIT: Steven J. Cooke

FEATURE:
FISHERIES RESEARCH

Developing a Mechanistic Understanding of Fish Migrations by Linking Telemetry with Physiology, Behavior, Genomics and Experimental Biology: an Interdisciplinary Case Study on Adult Fraser River Sockeye Salmon

Steven J. Cooke
S. G. Hinch
A. P. Farrell
D. A. Patterson
K. Miller-Saunders
D. W. Welch
M. R. Donaldson
K. C. Hanson
G. T. Crossin
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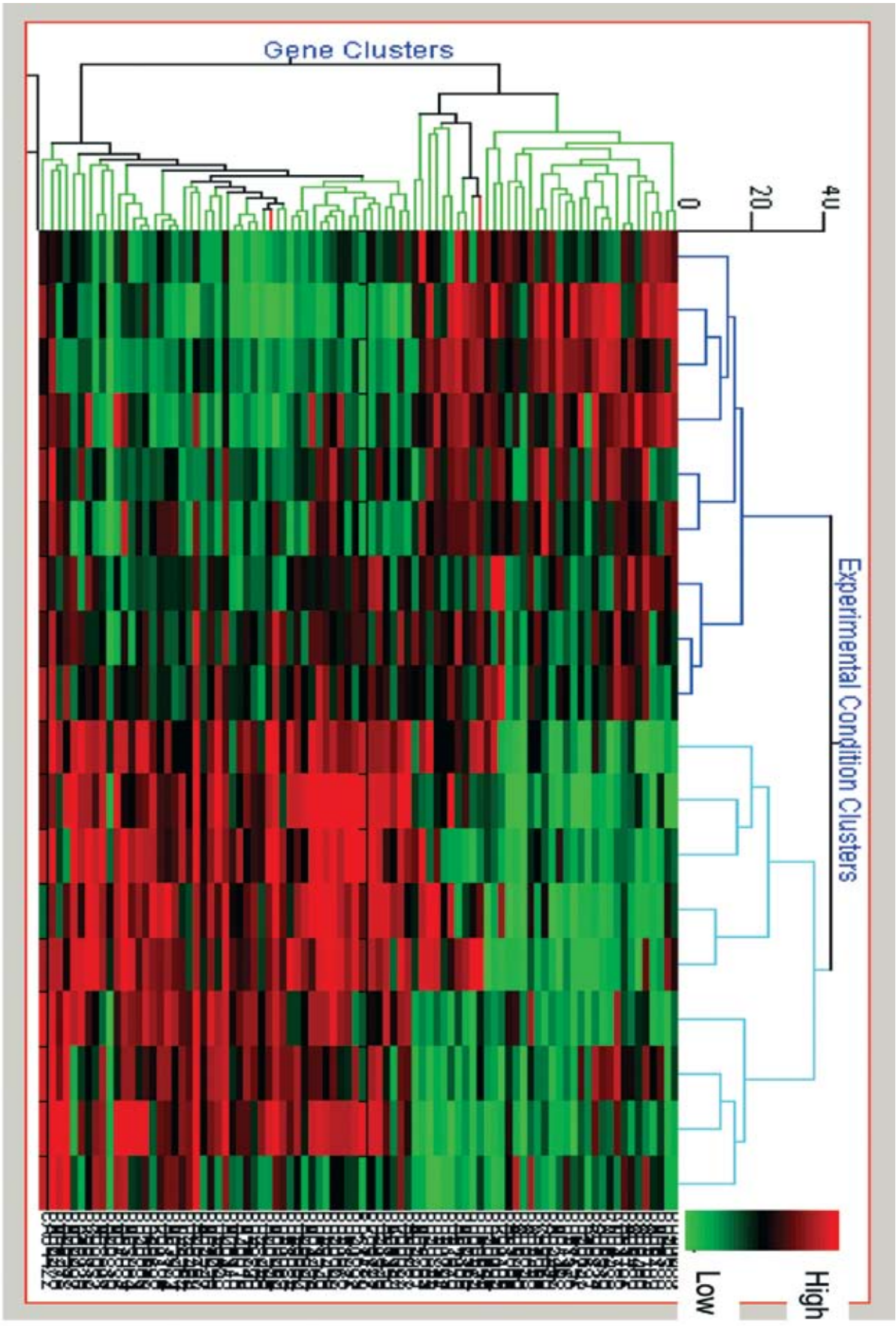
I. C. Olsson
G. N. Wagner
R. Thomson
R. Hourston
K. K. English
S. Larsson
J. M. Shrimpton
G. Van der Kraak

Cooke is an assistant professor at the Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, Ottawa, Ontario. He can be contacted at Steven_Cooke@carleton.ca. Hinch is a professor at the Pacific Salmon Ecology and Conservation Laboratory, Department of Forest Sciences and Institute for Resources, Environment, and Sustainability, The University of British Columbia, Vancouver. Farrell is a professor at the Centre for Aquaculture and the Environment, Faculty of Land and Food Systems and Department of Zoology, The University of British Columbia. Patterson is a research biologist at the Cooperative Fisheries Research Institute, Fisheries and Oceans Canada, Burnaby, British Columbia. Miller-Saunders is a research scientist at the Molecular Genetics Laboratory, Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia. Welch is president, Kintama Research, Nanaimo, British Columbia. Donaldson and Hanson are a graduate students at the Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario. Crossin, Cooperman, Mathes, Lotto, and Hruska are graduate students, biologists, and post-docs at the Centre for Applied Conservation Research, Department of Forest Sciences, University of British Columbia, Vancouver. Olsson is biologist at the Biology Department, Karlstad University, Sweden. Wagner is a research biologist at Rescan Environmental, Vancouver, British Columbia. Thomson and Hourston are a research scientists at the Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, British Columbia. English is vice president, LGL Ltd., Sidney, British Columbia. Larsson is a research professor, Institute of Marine Science, Umea University, Umea, Sweden. Shrimpton is an associate professor at the Department of Biology, University of Northern British Columbia, Prince George. Van der Kraak is a professor in the Department of Integrative Biology, University of Guelph, Ontario.

ABSTRACT: Fish migration represents one of the most complex and intriguing biological phenomena in the animal kingdom. How do fish migrate such vast distances? What are the costs and benefits of migration? Some of these fundamental questions have been addressed through the use of telemetry. However, telemetry alone has not and will not yield a complete understanding of the migration biology of fish or provide solutions to problems such as identifying physical barriers to migration or understanding potential impacts of climate change. Telemetry can be coupled with other tools and techniques to yield new insights into animal biology. Using Fraser River sockeye salmon (*Oncorhynchus nerka*) as a model, we summarize the advances that we have made in understanding salmonid migration biology through the integration of disciplines (i.e., interdisciplinary research) including physiology, behavior, functional genomics, and experimental biology. We also discuss opportunities for using large-scale telemetry arrays and taking a more experimental approach to studies of fish migration that use telemetry (i.e., intervention studies involving endocrine implants, simulated migration studies) rather than simply focusing on descriptive or correlational techniques. Only through integrative and interdisciplinary research will it be possible to understand the mechanistic basis of fish migrations and to predict and possibly mitigate the consequences of anthropogenic impacts. Telemetry is a tool that has the potential to integrate research across disciplines and between the lab and the field to advance the science of fish migration biology. The techniques that we have applied to the study of Pacific salmon are equally relevant to other fish taxa in both marine and freshwater systems as well as migratory animals beyond ichthyofauna. The interdisciplinary approach used here was essential to address a pressing and complex conservation problem association with sockeye salmon migration.


Gene Clusters
40
20
0
Experimental Condition Clusters
High
Low
Survivors
En Route Losses

Entendimiento Mecanístico de las Migraciones de Peces Relacionando Telemetría y Fisiología, Comportamiento, Genética y Biología Experimental: el Salmón Adulto del Río Fraser Como Caso de Estudio Interdisciplinario

RESUMEN: La migración de los peces representa uno de los fenómenos biológicos más complejos e intrigantes del reino animal ¿Cómo es que los peces migran distancias tan grandes? ¿Cuáles es el costo/beneficio de la migración? Algunas de estas preguntas fundamentales han sido abordadas mediante el uso de la telemetría. Sin embargo, por sí misma, la telemetría no puede ni podrá ofrecer un entendimiento completo de la biología de las migraciones de peces, no dará soluciones a problemas como la identificación de barreras físicas a la migración y tampoco permitirá entender los potenciales efectos del cambio climático. La telemetría, no obstante, puede complementarse con otras herramientas y técnicas para generar nuevos enfoques en la biología animal. Utilizando como modelo de estudia al salmón "sockeye" del Río Fraser (*Oncorhynchus nerka*) en el presente trabajo se resumen los avances logrados en cuanto al entendimiento de la biología de su migración mediante la integración del conocimiento de distintas disciplinas (i.e. investigación interdisciplinaria) como la fisiología, comportamiento, genética funcional y biología experimental. También se discute tanto la oportunidad de usar los diseños de telemetría a gran escala como el considerar análisis de carácter más experimental para estudiar la migración de los peces (i.e. estudios con implantes endócrinos, estudios de simulación de migraciones) en lugar de enfocarse sólo en técnicas descriptivas o de correlación. Solo mediante la investigación integrativa e interdisciplinaria será posible comprender las bases mecanísticas de la migración en los peces y predecir, y posiblemente mitigar, las consecuencias de los impactos de origen humano. La telemetría es una herramienta que tiene el potencial de integrar la investigación de diferentes disciplinas así como aquella proveniente del trabajo de campo y de laboratorio, con la finalidad de avanzar en la biología de la migración de los peces. Las técnicas que se han aplicado para el estudio del salmón del Pacífico son igualmente importantes para otros taxa de peces tanto marinos como dulceacuícolas, y para otros animales migratorios. El enfoque interdisciplinario que se usó en este trabajo demostró ser esencial para abordar una asociación de problemas crecientes de la conservación relacionados a la migración del salmón.

INTRODUCTION

Migration is one of the most complex and intriguing biological phenomena in the animal kingdom, and is observed in a wide variety of taxa including birds, mammals, insects, and fish (Dingle 1980). Ramenofsky and Wingfield (2007) characterized the changes in environmental conditions that regulate migration into three categories: (1) predictable seasonal changes in environment (e.g., temperature, photoperiod) which influence resources (e.g., food supply), (2) unpredictable changes associated with disturbance (e.g., weather, anthropogenic activity, predation), and (3) social relationships that tend to be life-stage related. In fish (Northcote 1984; Lucas and Baras 2000), and indeed most taxa, research efforts to date have focused primarily on the first category, where there are predictable movements between breeding and non-breeding areas. Irrespective of scale, migration is a remarkable activity that requires an understanding of both behavior (that is, what motivates a fish to migrate) and physiology (the capability for following through on its motivation; Hinch et al. 2006), and thus its study requires collaboration and integration between two or more distinct disciplines.

Early studies of fish migration relied on external marking to track individuals between different habitats in an effort to characterize timing and extent (Lucas and Baras 2000). However, spatio-temporal variation inherent to these kinds of studies can lead to biases against the detection of movement (i.e., the "restricted movement paradigm"; Gowan et al. 1994). Since the 1970s, a number of innovations in telemetry have enabled researchers to track individual organisms remotely in the wild using radio and acoustic platforms. Telemetry also includes devices that store data (archival data loggers—also called "biologging"; Block 2005; Ropert-Coudert and Wilson 2005) which are either downloaded upon recovery, or periodically transmitted to receivers, or some combination (Cooke et al. 2004a). Although telemetry devices can be expensive and cannot be used with all taxa or life stages (because the available tag sizes are inappropriate for the organism), they have provided biologists with unprecedented information on the spatial distribution and movement patterns of fish.

To date, the majority of telemetric studies examining migration have been either observational (describing patterns) or correlational (exploring relationships between environmental factors and migration timing or success). However, most of these approaches do not allow one to test hypotheses about mechanisms affecting migration. In fact, observational studies tend to generate more questions than answers, many of which cannot be addressed through telemetry alone. Nor does telemetry alone provide solutions to anthropogenic problems such as migration barriers and climate change impacts. Interestingly, migratory fish species are at twice the risk of extinction than non-migrating ones (Riede 2002) and are more susceptible to commercial and recreational exploitation (M.R. Donaldson, unpublished data). Given the complexity of migration and its role in a myriad of management and conservation situations, simply documenting

Figure 4. Unsupervised hierarchical clustering of expression intensity of 88 genes (gene codes listed on far right) that were significantly ($P < 0.001$) differentially regulated in gill tissue of 18 adult sockeye (each fish is a column) that were radio-tagged in the lower Fraser River in 2005 and were bound for the Chilko River (see Figure 1). The expression of a specific gene for a specific fish is reflected by each individually colored cell. The "high to low" grey scale (top right) indicates the direction of gene regulation in each cell—"high" means strongly up-regulated gene expression (red), and "low" means strongly down-regulated gene expression (green). Two-way (gene and sample) clustering was performed using Pearson's correlation as a density metric and centroid values for cluster linkage. Fish that survived the migration to reach spawning grounds ("survivors" $n = 9$) clustered together as did fish that perished during the migration ("en route losses" $n = 9$). A relationship scale indicating branch distance links for the fish cluster analysis is provided on the top left and reveals that survivors were more similar than en route losses in terms of gene expression. Cluster analysis on genes revealed two main groups with several smaller groups within each reflecting gene regulation of specific physiological pathways.

migration timing and extent is insufficient. For example, we need to understand the fundamental processes that enable some fish to migrate vast distances, the causes of mortality during migrations, and the factors that cause some fish to migrate and others not to. Telemetry alone will never yield a complete understanding of the migration biology of fish, but as we will show, by integrating positional telemetry with other disciplines (e.g., stress physiology, functional genomics, oceanography, experimental biology) we can start to test hypotheses that until recently were not practical or within reach of fish ecologists.

The objective of this article is to highlight opportunities for enhancing the study of fish migration by adopting a more interdisciplinary (Box 1) approach to telemetry studies. To do so, we review our studies of adult Pacific salmonids (*Oncorhynchus* spp.) with a focus on the spawning migration of adult sockeye salmon (*O. nerka*) where we have adopted an interdisciplinary approach. The work we describe is a combination of basic and applied research and uses a number of novel techniques that were spatially and temporally organized around telemetry studies. Based on our experience and progress, we feel that our interdisciplinary and integrated approach, which couples telemetry with other techniques, has the ability to enhance future research on fish migration and ultimately provide fisheries managers with the knowledge to better manage and conserve migratory fishes globally. We also acknowledge that there is a rich historical literature on the topic of salmonid migration and complete coverage is beyond the scope of this paper (see Groot et al. 1995 for a starting point to the historical literature). Here we have focused on contemporary and forthcoming research that is focused on Fraser sockeye salmon.

Box 1. What is interdisciplinarity?

For the purpose of this article, interdisciplinary research is defined as instances or opportunities where researchers from different disciplines collaborate in a tightly integrated approach (see Aboelela et al. 2007 for discussion on the challenges of defining interdisciplinarity). This differs from a multidisciplinary approach to research where specialists in different disciplines conduct self-contained research with little cross-fertilization. Although both approaches cross disciplinary boundaries, we have adopted an interdisciplinary approach for our research where we function as equal stakeholders in addressing a common challenge. Recently, an additional interface has been defined and is referred to as transdisciplinarity which adopts both a within and beyond discipline approach. However, there is less consensus regarding this term and usually involves more radical approaches including the dissolution of all disciplinary boundaries.

ADULT PACIFIC SALMON MIGRATIONS

The considerable information available on the migration of Pacific salmon, coupled with their importance to humans and ecosystem function, makes them a useful model organism to explore universal aspects of migration biology that extend well beyond salmonids. Pacific salmon life histories are varied, providing ample opportunity to explore inter- and intra-specific physiological and behavioral diversity (See Groot et al. 1995). Indeed, Hinch et al. (2006) recently used sockeye salmon as the model for the first life-history review of the behavioral physiology of fish migrations. Our research on sockeye salmon in the Fraser River, Canada's most productive salmon river, has focused primarily on adult spawning migrations in coastal and freshwater environments with a goal of gaining an improved understanding of physiological and energetic limitations. Adult salmon must transition from saltwater (where fish are hypoosmotic) to freshwater environments (where fish are hyperosmotic), which creates significant physiological challenge. They often traverse long up-river distances (e.g., exceeding 1,200 km) which is challenging because they cease feeding a week or more before entering freshwater and must fuel the migration and gonad maturation by endogenous energy reserves (Brett 1995) and must have enough remaining to spawn. Furthermore, river migration environments can be very inhospitable with fish facing variable, sometimes lethal temperatures and unpredictable flows, particularly now in our current era of climate warming. Because the coastal and up-river migration stage is naturally stressful, can involve high levels of mortality, and is when most fisheries on Pacific salmon occur, the need is great to understand movement and survival patterns. Not surprisingly, the majority of telemetry studies on salmon have focused on adult spawning migrations (reviewed in Hinch et al. 2006), but there is also a large body of work on outmigration of smolts with telemetry and PIT tagging (e.g., English et al. 2000; Venditti et al. 2000; Welch et al. 2004; Melnychuk et al. 2007), including several that couple different techniques from multiple disciplines to gain an improved insight into the mechanisms underlying outmigration biology (e.g., Martinelli-Liedtke et al. 1999; Aarestrup et al. 2000). Indeed, there are arguably more interdisciplinary studies on smolts than adults (see Hoar 1976; Høgåsen 1998). The focus of our article will be on the adult migratory phase.

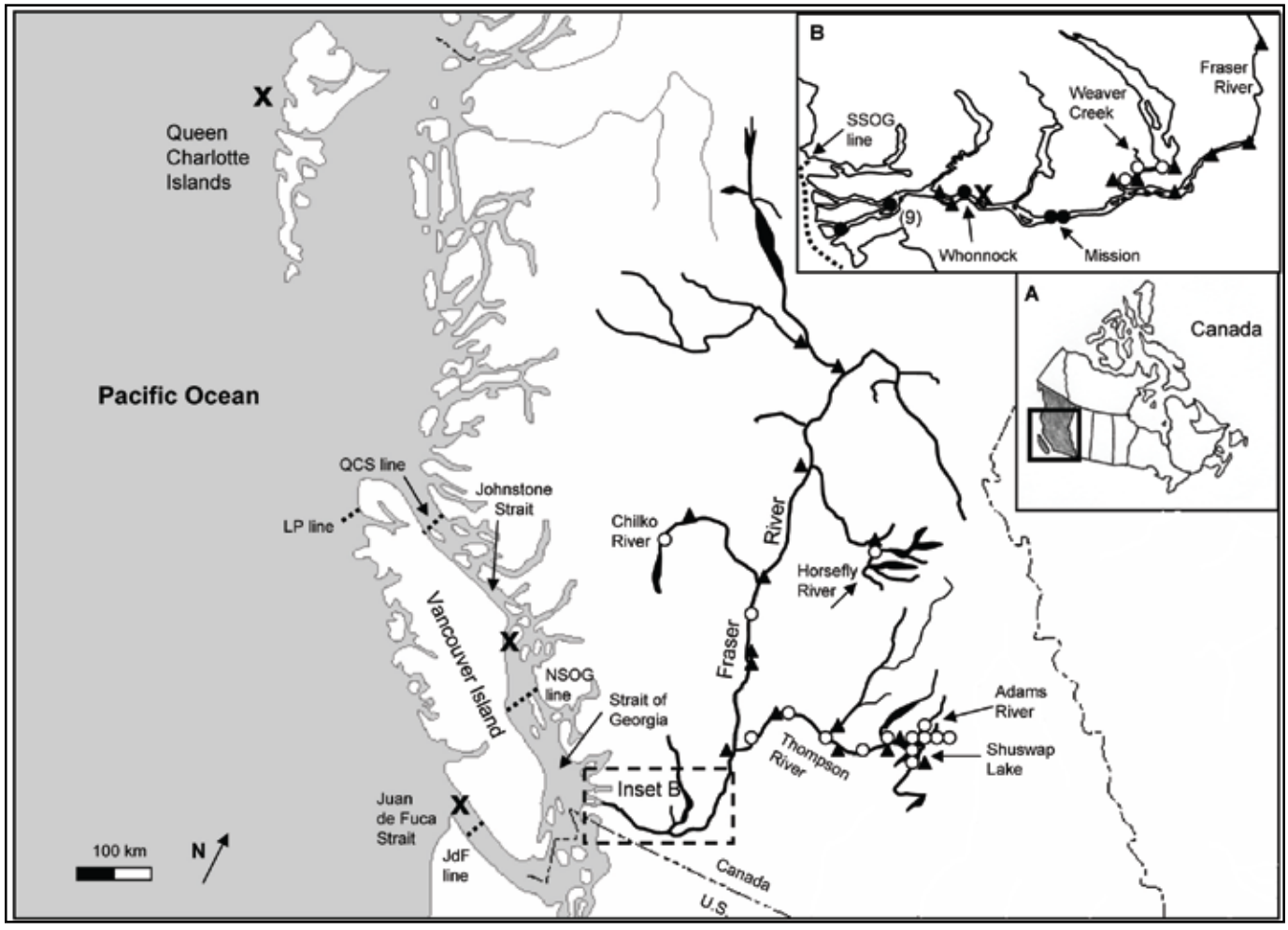
A further important impetus behind the development of an interdisciplinary approach to studying salmon migrations was a fisheries crisis associated with the late-run Fraser River sockeye salmon, an economically important stock complex that includes the famed Adams River stocks. Unlike other run timing groups in the Fraser River (i.e., early Stuarts, early summer, and summer runs), late-run fish were known for their holding behavior in the Strait of Georgia (Fraser River Estuary), where they stopped their migration for periods of three to six weeks prior to re-initiating migration up-river (Cooke et al. 2004b). Beginning in 1995, segments of the run entered the river with little or no delay in the Strait of Georgia (Figure 1), and mortality rates for early-entry migrants exceeded 90% in some years (Cooke et al. 2004b). While developing a long list of hypotheses to explain both this early-entry behavior and the associated high mortality (Cooke et al. 2004b), it became apparent that there was surprisingly little known about the factors influencing migration behavior for adult Pacific salmon. This article summarizes the development of an interdisciplinary and interagency research program to examine mechanisms of mortality and behaviors of salmon migrations, and is intended to emphasize the opportunity available to telemetry practitioners worldwide interested in the study of fish migrations that utilize telemetry simply by being creative and reaching out to other disciplines. We conclude by discussing the benefits and challenges to interdisciplinarity.

NOVEL OPPORTUNITIES FOR TELEMETRY IN FISH MIGRATION RESEARCH

Telemetry is revolutionizing how we study fish migration. However, by coupling telemetry with other tools and approaches,

Figure 1. Map of the Fraser River watershed and coastal waters of British Columbia showing 2006 telemetry array deployment locations.

Inset A shows this region in British Columbia (dark area) Canada.
Inset B shows more detail on the lower Fraser River.
Filled circles are acoustic receiver stations deployed by the Pacific Ocean Shelf Tracking Project (POST).
Nine acoustic receivers (Inset map B, filled circle 9) were positioned in the region where the four mouths of the Fraser River converged into one river.
Open circles are acoustic receiver stations deployed by the University of British Columbia and Carleton University.
Filled triangles are radio receiver stations deployed by LGL Ltd.
Dark dotted lines in marine areas are acoustic receiver lines consisting of multiple receiver units deployed by POST (Northern Strait of Georgia line, Southern Strait of Georgia line, Queen Charlotte Strait Line, Lippy Point Line, Juan de Fuca Line).
Fish capture and tagging locations are indicated by X.
Relevant town and waterway names are indicated.



it is possible to unravel some of the mysteries of migration biology (i.e., both proximate and ultimate questions) that would not be possible otherwise. For each subsection below we provide an overview of a specific methodological technique or approach and describe how each methodology has been implemented to advance an understanding of migrations. We begin with coverage of several topics that are central to our research program, specifically, the infrastructure needed to track migratory salmon across long distances (i.e., telemetry arrays), genetic tools needed for stock assignment of telemetered individuals, and non-lethal energetic and physiological biopsy techniques that enable us to collect tissues from telemetered fish.

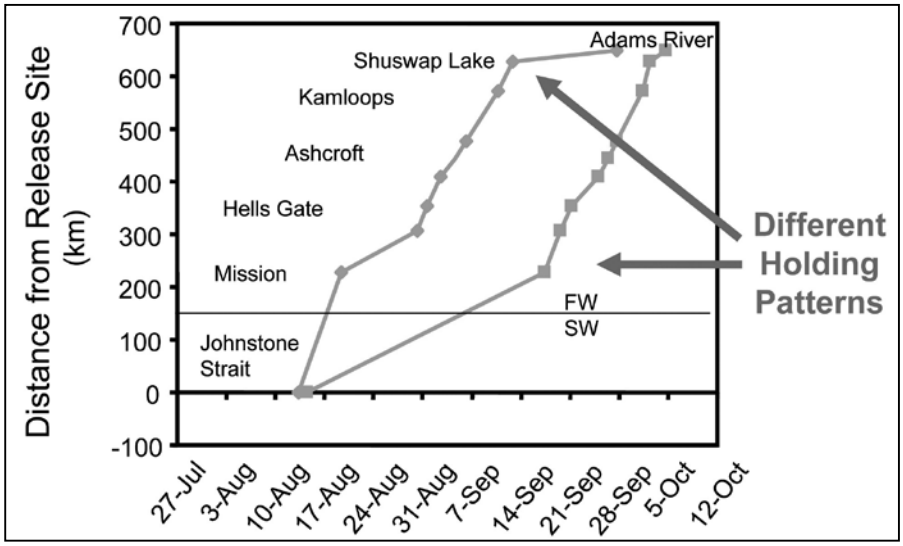
Large Scale Biotelemetry Arrays—Acoustic and Radio

Technological developments associated with the advent of cell phones and the demand for other low power electronics have made it possible to deploy very-large scale and permanent acoustic (e.g., Welch et al. 2002; Heupel et al. 2006) and radio (e.g., English et

A research team member surgically implants an acoustic telemetry transmitter into an adult sockeye salmon. The fish was also biopsied to obtain tissues for physiological, genomic, and stable isotope analyses.

al. 2005) telemetry arrays. Instead of manually tracking individual fish, which is labor intensive and can only be done at irregular intervals, large-scale arrays enable the continuous monitoring of individuals across hundreds or even thousands of kilometers. In 2002 and 2003 a radio-telemetry array was established on the Fraser River that extended from Mission (~80 km from the ocean) to terminal spawning grounds (up to 1,200 km from ocean; Figure 1). Migration histories of coastal tagged sockeye were reconstructed from telemetry data (English et al. 2003, 2004) detailing the abnormal entry timing phenomenon of some late run sockeye (Figure 2). This receiver array has been deployed annually from 2005–2007. A pilot version of the Pacific Ocean Shelf Tracking (POST) acoustic telemetry array was deployed in 2003 to extend telemetric monitoring to marine areas (Crossin et al. 2007) and into deep lakes of the Fraser watershed. In 2006, large elements of this array were expanded (Figure 1) and some of it is presently used in a multi-year deployment with year-round coverage representing the world's largest telemetry array. Coastal monitoring with this array has proven very effective at revealing how variable stocks and individuals are in the durations of estuarine holding periods prior to starting freshwater migration, and has revealed that once fish enter the river mouth, their migration becomes very directional (Crossin et al. 2007). Receivers (both radio and acoustic) have also been deployed in the vicinity of terminal spawning grounds (Figure 1) to determine migration success.

Figure 2. Representative migration history of two late run Fraser sockeye salmon (Adams stock) gastrically radio tagged on the same day in the ocean at Johnstone Strait (see Figure 1). Movement was monitored with an array of radio receivers (see Figure 1). One sockeye exhibits the typical holding period (2–3 weeks) in the estuary prior to entering the river. Conversely, the other individual enters the Fraser River within a few days of tagging and migrates upriver, however, this individual holds in their natal Shuswap Lake for two weeks prior to reaching the Adams River spawning ground such that the actual spawning date does not differ appreciably between these two very different migration strategies. See English et al. (2005) for more details on the radio telemetry study.



The information collected from the telemetry arrays provided an unparalleled opportunity to relate behavior and physiology of individual animals in the ocean with their subsequent migration survival and reproductive success. In addition, the data have proven very useful, when incorporated with a fisheries tag-recovery program, at identifying relative exploitation rates along migratory routes, and for the first time assessing natural mortality rates in coastal versus freshwater environments (e.g., Cooke et al. 2006a,b; Crossin et al. 2007). However, it is important to ascertain detection efficiency for any array to be certain that it is providing credible data on movements and survival. Detection efficiencies for radio-tagged sockeye in excess of 95% were common for most of the stations deployed along the Fraser River from 2002–2006 (English et al. 2003, 2004; Robichaud and English 2006, 2007). In only a few locations where the river was very wide and deep did the detection efficiencies drop below 90%. In 2006, we estimated that acoustic arrays deployed in the Strait of Georgia and Juan de Fuca Strait (Figure 1) detected 94–100% of the passing acoustic-tagged sockeye. In these studies, we thus interpret the numbers of tagged fish detected at a location as survival to that location. We caution that attrition between the monitoring locations (e.g., mortality) may also be caused by other processes other than "natural" mortality, such as tag loss, handling effects, or fishery removals. Tag retention for sockeye is believed to be high based on marine holding experiments (English et al. 2003, 2004) and high detection rates for in-river releases (Robichaud and English 2006). In 2006, 67% of acoustic-tagged sockeye released in Johnstone Strait survived to reach the SSOG listening line (Figure 1) and 49% released in Juan de Fuca Strait survived to the SSOG line (survival/day 91–92%; Table 1). Thus, in this example, large percentages of fish disappeared in coastal environments. Some were captured

Table 1. Number of acoustic tagged and released Fraser sockeye from Johnstone Strait (JS) and Juan de Fuca Strait (JdF), survival/day and mean travel time to the Southern Strait of Georgia acoustic line (SSOG, see Figure 1). Survival/day was estimated as S1/TMean, where TMean = mean travel time, and was adjusted for tag returns from the fishery.

Release locale	Number of tagged sockeye	Number survived to SSOG	Tagged fish returned from marine fisheries	Tags returned (%)	Overall Survival (%)	Mean travel time (days)	Survival/day
JS	108	72	3	3%	67%	4.7	92%
JdF	39	19	3	8%	49%	6.6	91%

and our reported tag recoveries are undoubtedly an underestimate of actual exploitation rates, and some likely perished from natural causes. But these results beg the question of what about these fish may have caused or contributed to their specific fate? Such questions provide the general context for the integrative work discussed below.

Incorporation of Genetic Tools

In order to gain the most from biotelemetry studies, researchers must know the population origin of animals being tracked. Animals are often tagged along a migration route instead of within the home or natal environment. Under these circumstances, it may be possible to use genetic markers to predict their population of origin. This has been done successfully in Fraser River sockeye salmon, as large genetic databases used for stock identification in fisheries management already exist. Hence, in sockeye salmon, which exhibit strong genetic structure due to their high degree of fidelity in homing to natal sites, small samples of tissues from the operculum or adipose fin (collected so as to avoid killing the fish) are sampled from fish at time of tagging. Genetic analysis of microsatellite loci provides highly accurate and rapid identification (in some cases 24 h) for individual fish (Beacham et al. 2005). With this information, researchers can determine timing and location for tagging efforts and rapidly identify if the targeted number of fish from the populations of interest have been tagged (English et al. 2005). Furthermore, knowledge of the population of origin of salmon allows researchers to determine the fate of fish during river migration (English et al. 2005; Robichaud and English 2006, 2007) and examine associations between physiological condition in the ocean and fate in river on a population-specific basis (Cooke et al. 2006a,b; Young et al. 2006; Crossin et al. 2007). Knowing the population of origin enables researchers to ask questions regarding stock-specific migration routes (e.g., distances and elevations of migration routes, which are highly stock-specific) and environmental conditions (e.g., migration routes and duration of migration in relation to water temperatures and flow conditions). Given the important role of genetics in the management and conservation of Pacific salmonids (Waples et al. 1990), the integration of telemetry and genetics has the potential to yield major advances.

Incorporation of Non-Lethal Physiological and Energetic Biopsies

Physiology and energetics are integral for long distance fish migrations (Hinch et al. 2006), particularly those involving a transition between marine and freshwater systems (Shrimpton et al. 2005) and reproductive maturation. In addition to incorporating physiological sensors into telemetry devices (see below), non-lethal tissue biopsies or other conditional assessments can be combined with positional telemetry. Positional (e.g., standard) transmitters are relatively inexpensive compared to physiological telemetry devices (e.g., electromyogram transmitters), providing opportunity to achieve reasonably large "physiology-telemetry" sample sizes with modest budgets. Although this approach does not provide real-time data on physiological or energetic status, it does provide an indication of the status of the animal upon release. By coupling assessments of animal position, movement, behavior, and survival with non-invasive physiological and energetic sampling, it becomes possible to test hypotheses associated with animal condition, behavior, and fate. The ability to link individual behavior and fate with energetics and physiology has eluded researchers until recently (Altmann and Altmann 2003; Goldstein and Pinshow 2006) and yet inter-individual variation is recognized as an important concept (Bennett 1987). Although the concept of releasing transmitter-implanted animals that have been biopsied for physiological variables is simple and the potential insight invaluable, there are only a few published examples where this approach had been employed to study fish migration, all within the last few years. Conventional lethal physiological sampling (see McKeown 1984 for a summary of previous physiology studies on fish migration) was ruled out as the only sampling method in our studies (although we did use it to complement non-lethal telemetry sampling) because sampling from a population that encounters natural mortality during its migration provides little insight into what happened to those that were unsuccessful and/or died because the sampling progressively becomes limited to those fish that have succeeded in completing a specific part of the migration. Assessments of the physiological condition for individuals with known fates and migration behavior are clearly preferred.

It is possible to rapidly and non-lethally collect a number of tissue samples including blood (usually via caudal puncture), gill tissue (using surgical tools), muscle (using muscle biopsy punch), fin tissue, and scales. Cooke et al. (2005) demonstrated that with practice it is possible to rapidly sample multiple tissues from un-anesthetized, transmitter-implanted (gastrically) fish without deleteriously affecting animal condition or post-release behavior. These tissue samples can be analyzed for a variety of parameters using a number of techniques including blood and muscle biochemistry (e.g., metabolites, ions, acid/base status), hematology (e.g., hemoglobin, hematocrit), endocrinology (e.g., hormone titres associated with reproduction or stress), genetics (e.g., stock identification; see above), genomics (e.g., gene expression; see below), and stable isotopes (see below). In addition, a number of new tools enable the non-lethal measurement of energy density using microwave signals (see Crossin and Hinch 2005) or total body electrical conductivity measures (i.e., TOBEC). Typically, fish are anesthetized prior to blood, muscle, and gill biopsies (e.g., McCormick 1993). However, in some cases (like migratory adult salmon) transmitter-implanted fish could be caught in fisheries and then processed for human consumption which could put anesthetics into the human food supply. Also, anesthesia may unnecessarily increase handling time, recovery, and post-operative care, risk of predation, as well as physiological disturbances arising from the anesthesia. Thus, we have developed protocols for physiological biopsy without the use of anaesthesia (Cooke et al. 2005).

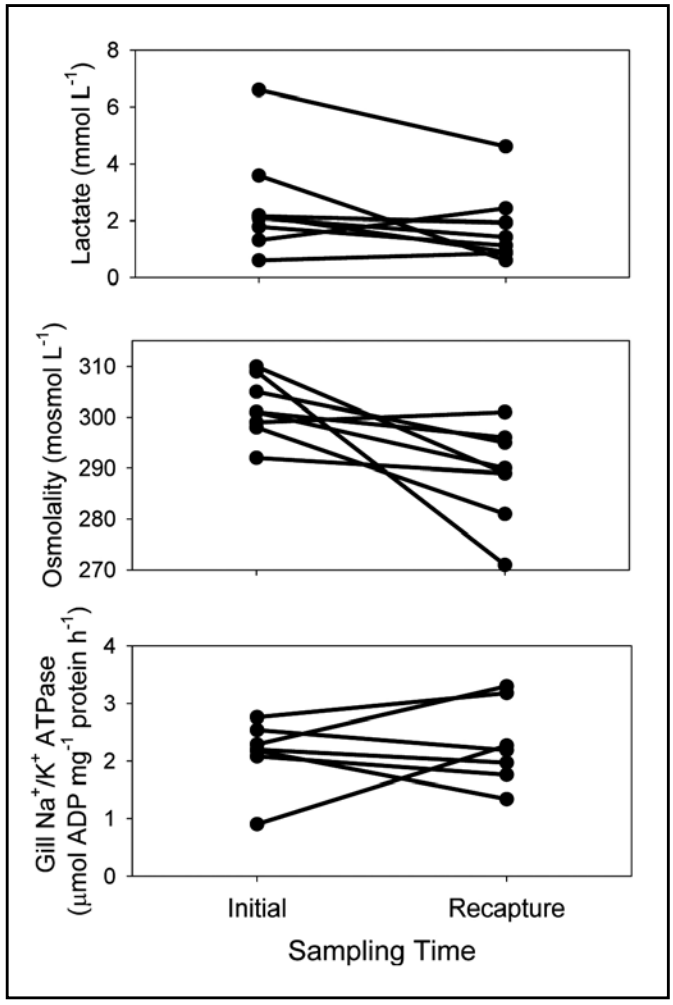
We have used this biopsy technique to sample fish in the Pacific Ocean and then to evaluate the physiological and energetic correlates of fate and behavior. One of our hypotheses explaining why late-run sockeye salmon were entering the river early was that they had a different physiological status. Specifically, we predicted that abnormally early migrants would have advanced maturation status (as assessed by reproductive hormones), be prematurely prepared for entry to freshwater, and/or have low energetic status. Any of these physiological differences could motivate the fish to enter the Fraser River and reach spawning grounds as quickly as possible (Cooke et al. 2004b). Indeed, our first prediction was correct in that abnormally early migrants tended to have elevated levels of reproductive hormones, including testosterone, 11-ketotestosterone, and estradiol (Cooke et al. 2008). However, since gill Na^+K^+ ATPase was not significantly different in early migrants, although more variable from normal timed migrants, we

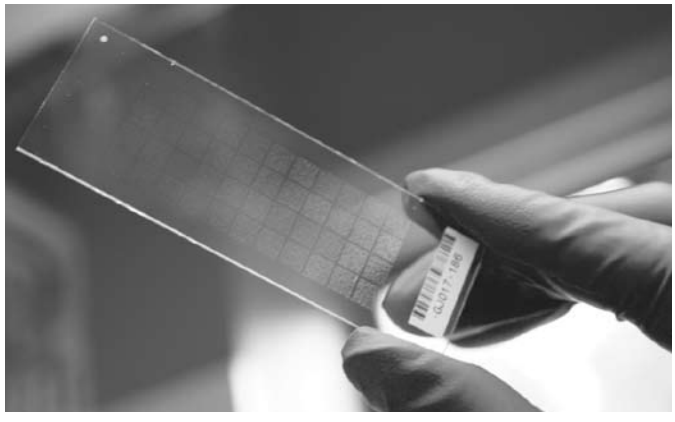
found limited evidence to support our second prediction regarding premature preparation for freshwater entry. Interestingly, converse to our prediction that early migrants had lower energy, motivating them to move more rapidly to spawning grounds, early migrants had higher energy densities than normal timed migrants. Using biopsies from fish tagged and released in the ocean, we found evidence that fish which failed to enter freshwater were characterized by elevated levels of stress indicators (e.g., elevated plasma lactate, glucose, and cortisol; Cooke et al. 2006a,b), whereas fish tagged during freshwater migrations (in the Thompson River; Figure 1) but failed to reach the spawning grounds had lower gross somatic energy and higher levels of plasma reproductive hormones than those that reached spawning grounds (Young et al. 2006). Recapturing previously biopsied individuals that are tagged with telemetry devices and evaluating temporal changes in physiological variables is an exciting approach that we have recently attempted. We captured, biopsied, and released acoustic-tagged Weaver Creek sockeye (Figure 1) during their migration, then re-captured some of these same individuals from spawning grounds several weeks later by using hand-held mobile acoustic receivers (Figure 3). Physiological measures evaluated included plasma lactate (an index of stress and recent anaerobic physical exertion) and plasma osmolality and gill Na^+/K^+ ATPase (indicators of ionic and osmoregulatory preparedness). The results reveal that some individuals physiologically respond to the migration in very different ways than the population trends. Such unique individuals may represent ones that perish before spawning or produce inferior offspring. Indeed, previous work by our group has revealed that sockeye salmon that tend to die en route in the freshwater migration phase are characterized by having higher levels of lactate (Young et al. 2006) and osmoregulatory dysfunction (Cooke et al. 2006b). This is potentially a very powerful assessment tool as it revealed just how individual-specific changes in physiological features can be and that average population-level changes are only a piece of the puzzle when trying to understand the mechanisms underlying behavior and fate.

Incorporation of Genomic Tools

Genetic studies generally are based on the variation at a small number of genes and gene families hypothesized a priori to be of importance, whereas genomic research typically encompasses thousands of genes, or even the entire genome, many with unknown connections to the traits of interest. Moreover, functional genomics research captures the interplay of genetic and environmental factors on the fate or behavior of an organism (Feder and Mitchell-Olds 2003), rather than viewing them as discrete processes. Gene arrays (also called microarrays) are a new functional genomics tool that can profile the expression of thousands of genes at once, enabling the assessment of response to environmental stressors on a genome-wide scale (Klaper and Thomas 2004; Thomas and Klaper 2004). In migration studies, microarrays can be used to determine the physiological switch points that occur en route, and to test hypotheses about the molecular pathways and regulatory elements involved in physiological change and maturation (Miller et al. 2007). Because gene arrays examine many more physiological pathways than is possible with conventional bioassays, gene arrays can also be a valuable data-mining tool to guide hypothesis development. For tissues sampled non-destructively, microarrays can be used in conjunction with biotelemetry studies to identify the physiological basis of behavior and/or fate. We used the salmonid GRASP microarray (i.e., 16,006 gene array; Von Schalburg et al. 2005), along with biotelemetry, to assess the genes associated with differential river entry timing

Figure 3. Physiological measures (plasma osmolality, plasma lactate, and gill Na^+/K^+ ATPase) for seven Weaver Creek sockeye salmon that were intercepted en route to spawning grounds, tagged, biopsied and released ("Initial") then recaptured upon arrival at terminal spawning grounds and biopsied again ("Recapture"). Each line connects initial and recapture biopsy measures for a given individual to indicate directional change.





Salmonid GRASP microarray (with 16,006 genes) used to reveal patterns of gene expression. Gill and white muscle samples (for gene expression analysis) were collected from fish before they were tagged and released with telemetry transmitters. This approach enables the assessment of genes associated with differential behavior and survival.

and in-river survival in adult sockeye. Using gill tissue collected from radio-tagged fish captured and released in the lower Fraser River (Figure 1) and tracked towards spawning grounds in 2005, we found a strong association between gene expression and freshwater fate. Statistical analysis revealed that 88 genes were expressed at a higher level in the fish that survived compared with fish that perished during migration (Figure 4, page 322). Profiles of survivors were more alike than that of mortalities (i.e., the dendrogram shows experimental condition clusters linking more tightly together among survivors) suggesting that fish die during migrations for several different physiological reasons but that fish survive because of a more common physiology. The gene clusters and physiological pathways that they regulate are presently being resolved, but regardless, these results demonstrate that some sockeye are physiologically predisposed at the start of river migration to survive and others to die—results consistent with our non-invasive biopsy results discussed above. The coupling of telemetry and genomics is going to yield unprecedented information on migration biology of fish. However, there will need to be a re-engineering of scientific attitudes, training, and institutions, to achieve extensive interdisciplinarity and understanding of the promise of ecological functional genomics before this becomes a reality (Feder and Mitchell-Olds 2003).

Incorporation of Physiological Sensors

Researchers studying migration have used travel times from telemetered fish between two known points as well as other creative techniques to estimate swimming speeds, which are then used to predict energetic costs. Although such information is useful, it does not provide insight into the fine scale behavior, swimming dynamics, or real energy expenditure as fish rarely swim in a straight line or at constant speeds and most telemetry devices operate with transmission rates that are significantly longer than burst swimming events. Failure to address such issues, particularly from short duration but high intensity burst swimming activity can yield dramatic underestimates of migration costs (Rand and Hinch 1998). Innovation in physiological sensor technology that can be adapted into biotelemetry (or biologging) platforms means that researchers can obtain information on physiologically and energetically relevant activity through the measurement of heart rate, opercular rate, or some indicator of locomotion (e.g., electromyogram [EMG], accelerometer, tail beat). Although all of these technologies have been used on fish, only EMG telemetry has been widely embraced by fisheries scientists (Cooke et al. 2004c). Electromyogram telemetry tags are commercially available and can be implanted intraperitoneally, enabling long-term deployments without impeding individual migration performance. Although most often deployed with radio telemetry output modules, acoustic devices have been recently developed. Electrodes placed in the axial swimming musculature detect bioelectric activity (generated by the muscle contractions), which is then collected, integrated, and transmitted providing an indication of locomotory activity. Once calibrated (in respirometer), the transmitters can be used to reliably estimate energetic activity or swimming speeds.

For the study of migration biology, EMG transmitters have most frequently been used in the Fraser River watershed by members of our team. We have found that swimming speeds, swimming pattern, and energy use of upriver migrating salmon is clearly associated with local environment and varies with size, gender, and species. For example, river locales with turbulent flow patterns cause inefficient and energetically expensive swimming patterns (Hinch et al. 1996; Hinch and Rand 1998; Standen et al. 2004). Females tend to be more energetically efficient during migration than males, possibly because they have less reserve energy that can be used for swimming as much more is devoted to their gamete development than in males (Hinch and Rand 1998). Although they are closely related and share many of the same migratory routes, pink (*O. gorbuscha*) and sockeye salmon exhibit very different migratory behaviors, with pink generally swimming at more constant speeds, rarely exhibiting burst swimming (Hinch et al. 2002). Interestingly, on average, individual specific energy use was very similar between these species for a given reach of the migration (Standen et al. 2004). EMG telemetry has also been used to study energetic costs of migration in other Pacific salmon species including Chinook salmon (*O. tshawtscha*) and steelhead (*O. mykiss*) in the Columbia River watershed (USA; Geist et al. 2000; Brown et al. 2006) and in systems in Japan (e.g., Ueda et al. 2000). Because they can be used to help predict migration mortality resulting from energy depletion (e.g., Rand and Hinch 1998), EMG data can be very useful for habitat management in determining optimal water discharge regimes in regulated rivers during periods of migration to reduce energetic costs of migration, and for aiding the design of habitat modifications that affect flow (e.g., bank configurations, gravel bar management). They can also aid fisheries management in decisions regarding balancing allocations of fish between escapement and harvest in light of expectations of natural mortality caused by energy depletion (e.g., Rand et al. 2006).

Incorporation of Environmental Sensors

A number of animal-borne environmental sensors can be combined with biotelemetry devices that measure parameters such as water temperature, depth, dissolved oxygen, and salinity (see Cooke et al. 2004a). Our group has focused primarily on the use of thermal sensors because water temperature controls and limits almost all physiological and behavioral parameters of fish migrations, including energetics (Lee et al. 2003), physiological stress (reviewed in Hinch et al. 2006), migration timing (Cooke et al. 2004b; Hodgson et al. 2006), migration rate (Goniea et al. 2006; Hodgson et al. 2006) and en route mortality (Gilhousen 1990; Macdonald et al. 2000). Migration studies that use telemetry often

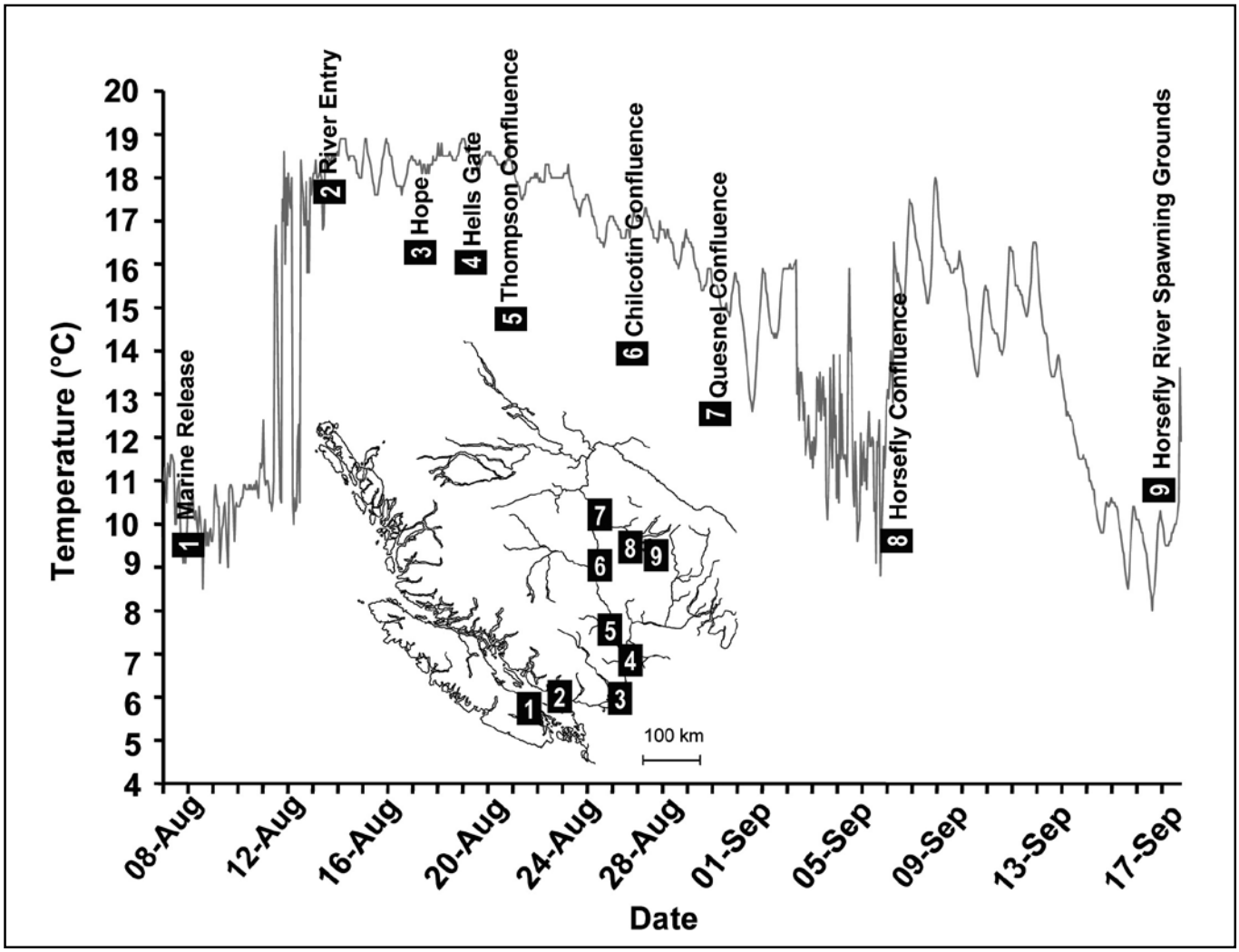
Adult sockeye salmon exposed to forced swimming in a mobile swim tunnel.

A thermal logger being affixed to a radio transmitter. The device will be waterproofed prior to deployment. Spatially-linked thermal histories can be reconstructed as per Figure 5.

record environmental temperatures from a series of stationary temperature stations and then correlate these data with receiver detections of telemetry tagged fish to estimate thermal exposures (Goniea et al. 2006). However, this approach does not permit an understanding of changes in individual body temperatures throughout complete migration routes. Remote temperature data can be obtained from free-swimming migrants by using temperature-sensitive telemetry transmitters that send thermal and positional data to receivers in real-time (Berman and Quinn 1991; Azumaya and Ishida 2005; Clabough et al. 2006). The disadvantage of this approach is that data are only transmitted when detected by a receiver, which can reduce the temporal resolution of the data. These transmitters can also be very expensive. Alternatively, combining positional transmitters with archival temperature loggers can yield high-resolution temperature data throughout entire migrations, and be much less costly. Temperature loggers permit data to be collected continuously (e.g., minutes, hours), but must be retrieved in order to download temperature data to a computer (Tanaka et al. 2000) and recovery rates can be quite low (e.g., < 15%; Newell and Quinn 2005; ~13% by our group in 2006).

Because salmon home to specific natal areas, there is some opportunity for retrieving thermal loggers for fish that survive migrations and which can be located on spawning grounds using telemetry, although this can be a challenging task. When linked with detection data from telemetry arrays, temperature loggers permit the re-creation of complete migration thermal histories for individual migrants. Thermal histories allow

Figure 5. A representative thermal history figure for an adult migrating sockeye salmon (summer run, Horsefly stock) that was gastrically radio tagged (with an archival temperature logger attached to the transmitter) in the marine environment at Juan de Fuca Strait in 2006. Individuals were tracked from river entry to spawning grounds using a fixed telemetry array in the Fraser River. Labels refer to detection locations (i.e., fixed telemetry arrays) throughout the Fraser River watershed and correspond to inset map. Temperatures were logged at hourly intervals.



for a fundamental understanding of thermoregulatory behavior (e.g., use of thermal refugia, holding patterns, diel temperature fluctuations) during migrations and permit links to be made with multiple endpoints (e.g., linking physiological stress or energetic status with stressful temperatures or accumulated thermal units). In an example from 2006 (Figure 5), a marine-tagged adult sockeye experienced relatively cool coastal temperature for a few days after tagging then a highly variable thermal environment for a day as it entered the river mouth (+/- 8ºC change; potentially related to tidal cycles). During its first week in the Fraser River, it experienced 17–19ºC, though daily cycles and other anomalies were detected. Passage past cool water tributaries and through the hyplimnion of lakes seems to offer thermal refuge prior to reaching spawning grounds. The main disadvantage of using temperature loggers is that thermal histories of fish which perish during a migration cannot be assessed. For situations where temperature information is needed on fish that likely will not survive migrations, it is possible to estimate thermal experience from migration depth information through using depth-reporting acoustic transmitters. We have used this approach in several inland lakes and have found that sockeye which utilized thermal refugia (i.e., below the thermocline) were more likely to survive the migration than those that did not (Farrell et al. in press; see also Newell and Quinn 2005; Newell et al. 2007). Management agencies can use this information to inform decisions about reducing harvest rates to account for expected thermal-based migration mortality and thus aid in achieving pre-season escapement goals. Thermal history data also provides information on the actual environmental conditions encountered by migrating fish enroute and, thus, allows for the validation of temperature-mortality models (e.g., Rand et al. 2006).

Integration with Oceanographic Data

The marine waters of British Columbia are a heterogeneous and complex biophysical system in which highly variable factors, such as temperature, salinity, dissolved oxygen, nutrient concentration, and currents generate a patchy distribution of marine animals. For anadromous migrating adult fish, oceanographic factors may not only influence travel distances and timing, but may also affect behavioral and physiological performances during up-river migration. Salmon migrations have been studied in coastal waters (e.g., Madison et al. 1972; Stasko et al. 1976; Quinn and terHart 1987; Quinn et al. 1989), but relatively less is known about salmon migration in the high seas. One example of how migratory behavior might be related to oceanographic conditions is the work conducted by Block et al. (2001) who found that Atlantic bluefin tuna (*Thunnus thynnus*) made trans-Atlantic migrations which could be linked directly to oceanographic processes such as productivity and sea surface temperature.

One hypothesis for unusually early spawning migrations in Fraser River late-run sockeye salmon is related to changes in coastal water properties. Changes in the marine environment, such as in surface water temperature, salinity, circulation, and mixed layer depth, may affect river entry timing by earlier "triggering" of certain physiological systems (e.g., accelerated maturation rates, freshwater preparedness). At present we are attempting to developing correlative links between the timing of up-river migration initiation of late-run Fraser River sockeye salmon and oceanic and meteorological measures from coastal waters of British Columbia (Thomson 2002). Preliminary results indicate that the proportion of late-run sockeye that enter freshwater early correlates with indices of coastal mixing (e.g., retention of freshwater layer). During homeward migration, Fraser River sockeye salmon encounter strong and fortnightly varying tidal currents in coastal areas and it is reasonable to believe that both the magnitude and the direction of the currents may also influence migratory behavior as has been documented for other salmonids (Metcalfe et al. 1990). Interestingly, Quinn et al. (1989) noted that Fraser sockeye did not exhibit behaviors indicative of selective tidal stream transport. Establishment of a clear cause-and-effect relationship between salmon river migration timing and their physical oceanic environment could provide a valuable tool for in-season management and conservation measures for Fraser River sockeye stocks. Although we have found strong correlations with several oceanic variables which make sense from a cause-and-effect perspective, we are not yet in a position to make definitive statements regarding the importance of the changing environment to fish response. Although there exist very few telemetry studies conducted with a focus on migratory fish ecology and the associated oceanography, such interdisciplinary studies could help us develop more suitable management plans for Fraser sockeye salmon (Hinch et al. 2006) and possibly other migratory fish species (Åkesson 2002).

Integrating Telemetry with Laboratory and Field-based Physiological Experiments

Swimming performance and oxygen consumption studies conducted in a laboratory setting could be relevant to field telemetry studies on fish migration. Such experiments provide an opportunity to determine ecologically relevant thresholds, such as the thermal optima (T_{opt}) for aerobic scope which has recently been related to migration success of sockeye salmon. For example, Lee et al. (2003) used swimming performance trials to generate T_{opt} values for Weaver Creek sockeye salmon. The laboratory-derived values from Lee et al. (2003) coincided with the most frequently encountered river migration temperature over the previous 60 years (Farrell et al. in press). The temperature when aerobic scope collapses to zero (T_{crit}) above T_{opt}, has rarely been encountered but an important exception occurred in 2004 when 70% of a stock that entered the Fraser River failed to reach the spawning grounds (Farrell et al. in press). Using T_{crit} as a cut off for failure to complete river migration, it was possible to explain over one-third of this disappearance (Farrell et al. in press). Unknown is the aerobic scope needed for up-river migration since zero aerobic scope simply allows to fish to rest and not migrate. Of course, the specific needs for aerobic scope will vary according to the migratory challenges faced by specific stocks of salmon. Given these findings, stock-specific characterization of T_{opt} for aerobic scope provides promise to link stock-specific migration mortality (as assessed by telemetry) with their physiology.

It is also possible to integrate the findings from telemetry studies and laboratory swimming performance assessments to test hypotheses regarding energy use. Hanson et al. (2008) used energy assessments from fish at capture and travel rate data from radio telemetry to assess migration speeds (used as proxy for swimming speeds), and to estimate reach-specific energy use (from

laboratory swim tunnel data; Lee et al. 2003) to reach sub-natal watersheds for summer run Fraser sockeye. The results revealed that fish generally displayed individually consistent swim speeds from reach to reach, and that those individuals that started with lower energy reserves did not swim proportionally faster or use proportionally different amounts of energy to reach spawning grounds than fish with higher initial energy reserves. These results suggest that energy reserve status may not be a primary determinant of migratory speed and highlights the value of linking field and laboratory results to broaden our understanding of fish migration behavioral energetics.

Laboratory studies have also validated findings from field telemetry studies where we documented high levels of mortality in late run sockeye salmon that entered the river several weeks earlier than normal. A laboratory study revealed that fish which accumulated more than 400 in-river degree-days (DD) tended to develop severe parasite infections (*Parvicapusa minibicornis*), which impaired swimming performance and led to significant physiological alterations (Wagner et al. 2005). Wagner et al. (2005) used data from telemetry studies (e.g., English et al. 2005) to calculate reach-specific degree-day accumulation of fish with different migratory behavior (i.e., early and normal timed migrants) and found that early migrants typically accumulated levels of degree-days that were consistent with severe *Parvicapsula* infections. Conversely, normal-timed migrants avoided the accumulation of sufficient degree days that would promote severe *Parvicapsula* infections by entering a cooler river and moving directly to spawning grounds.

Use of Intervention Experiments

Telemetry in and of itself generally leads to associations and not necessarily to a cause-effect resolution. Physiological intervention involves applying a treatment directly to the organism(s) of interest coupled with collecting pre- and post-treatment physiological samples followed by release. Tracking of the tagged organisms using biotelemetry then gives an understanding of how the treatment affects the animal, if the quality of the telemetry measurements is of sufficiently high quality. As such, it provides a powerful approach for testing hypotheses directly in the environment on the mechanisms underlying organismal behavior while avoiding the pitfalls which traditionally plague purely lab-based studies. Sensory impairment, endocrine manipulation, and exogenous treatment are three general classes of interventions that have been used as part of intervention-telemetry experiments, either alone or in combination with each other.

Sensory Impairment Interventions

Sensory impairment interventions involve blocking an organism's use of its visual, olfactory, and/or geomagnetic sensory apparatus. This approach can be used to explore how migrating salmon navigate. Despite extensive use of sensory impairment from the 1960s thru 1990s, sensory deprivation has only recently been coupled with positional telemetry. Ueda et al. (1998) used a combination of blinding, magnetic disruption, and telemetry to demonstrate that fish with sight swam in a straight line through Lake Toya (Japan) to their natal area while visually impaired fish swam in random directions. The authors concluded that Lake Toya sockeye relied on visual cues for the open-water phase of their migration and then switched to olfaction once in close proximity to their natal water. Geo-magnetic orientation and rheotaxis were ruled out as navigation tools used by these sockeye.

Endocrine Interventions

Endocrine manipulation interventions seek to selectively activate or suppress neurosensory or endocrine pathways believed to be involved in migration timing and behavior. One of the primary questions that these approaches have been used for is to explore how maturation state relates to migration timing, energy use, and swimming performance. Research has demonstrated that accelerated sexual development, initiated by injections of gonadotropin releasing hormone (GnRH), promoted more rapid arrival at spawning grounds, that male migration timing is associated with serum testosterone and 11-keteotestosterone concentrations, and that female migration timing is driven by high serum DHP levels and declining estradiol-17B levels (Van Der Kraak et al. 1984; Sato et al. 1997). Our research team used endocrine manipulations as a test of our sexual maturation hypothesis for the maladaptive shift to earlier freshwater entry timing of the Fraser River's late-run sockeye salmon. We intercepted migrating sockeye near the Queen Charlotte Islands (QCI; see Figure 1), approximately 700 km north of the Fraser mouth, and treated fish with GnRH, testosterone, or both hormones. Treated and control fish were fitted with acoustic transmitters, released back to the ocean and tracked to ultimate destination. Data analyses are underway and results are not yet available.

Exogenous Interventions

Exogenous treatment interventions implies subjecting test organisms to an altered environmental condition, such as warmer water temperatures or altered salinities, with the goal of eliciting a physiological and/or behavioral response which is then observed via positional telemetry. We examined the effect of high river temperature as an agent of migratory mortality in this fashion (Crossin et al. 2008). Specifically, adult late-run sockeye salmon were intercepted en route to spawning grounds and transported to large laboratory tanks where they were exposed to either a warm (18 °C) or a cool (10 °C) temperature treatment for ~3 weeks. The two holding temperatures simulated the effects of "early-timed" migrations which typically encounter warmer rivers and "normal-timed" migrations which encounter cooler rivers. At the end of the intervention, fish had accrued > 450 DD

Intramuscular injection of GnRH pellet into an adult sockeye salmon prior to releasing the fish and tracking it with the POST telemetry array.

in the warm treatment, and < 325 DD in the cool treatment, which led to high and low *Parvicapsula* disease expression, respectively (Wagner et al. 2005). Before being released back into the Fraser River to continue the migration, fish were non-lethally biopsied for blood plasma, gill Na^+K^+ ATPase activity, and somatic energy density. Migratory behavior and fate were then monitored in the two groups of fish as they swam through an acoustic receiver array leading to the spawning grounds. The results of temperature treatment on migratory behavior and fate were striking, as warm-treated fish suffered twice the level of mortality as cool-treated fish, both during the laboratory holding phase and during the completion of river migration. Females exhibited much higher mortality rates than males. These findings were consistent with the hypothesis that elevated water temperatures during the freshwater migration period probably contributes to higher levels of en route mortality in late-run sockeye salmon, and that disease may play a significant role.

In 2006, we combined endocrine and exogenous interventions into a single experiment to test the hypothesis that late-run sockeye which migrate into freshwater earlier than normal do so because they are reproductively more advanced and/or more prepared osmoregulatorily for freshwater than normal-timed migrants. We collected 300 migrating sockeye salmon from the Strait of Georgia (Figure 1), transported them to a lab, and held groups for 1 week in either 0 ppt (fresh), 14 ppt (iso-osmotic), or 28 ppt (coastal) salinity water crossed with and without GnRH injections. At the end of the holding period, we measured energy density, collected plasma, gill, muscle, and scale samples, implanted an acoustic transmitter to each fish, and returned fish to the Strait of Georgia for tracking and assessment of migratory behavior and fate. Data analyses are forthcoming.

Integration with Otolith Microchemistry and Stable Isotope Analysis

Stable isotopes provide the opportunity to evaluate nutritional status, feeding ecology, and trophic relationships, as well as inferring movement from the assimilation of site-specific isotopic signatures. Cunjak et al. (2005) suggested that isotopic studies could be strengthened by combining stable isotope analysis with telemetry techniques. Analyses conducted on radio-tagged downstream migrating Atlantic salmon smolts revealed different life-history strategies (Cunjak et al. 2005). Cunjak et al. (2005) also reported on remotely tracking fish with passive integrated transponders (PIT tags) and were able to distinguish between movements associated with foraging and seeking cool water refugia during high temperature periods. Stable isotope analysis can be conducted on scales, blood, or muscle tissue from non-lethal biopsies (see above) obtained from telemetered fish. Members of our team are currently analyzing scale samples collected from adult sockeye telemetered in the Pacific Ocean in an attempt to understand the influence of nutritional condition on migration behavior and fate.

An example of another recent synergy is the complimentary use of otolith microchemistry and radiotelemetry to examine life history variation in bull trout (*Salvelinus confluentus*) in the Hoh River, Washington (Brenkman et al. 2007). Data from tracking of radio-tagged individuals provided insight on the migratory behavior of the fish that helped to validate inferences drawn from variable strontium levels in otoliths. Obviously, otolith chemistry requires lethal sampling and is thus not possible on telemetered fish unless they are recaptured. However, coupling these two techniques, even in a complimentary manner, provided insight that would have not been possible had either of the two techniques been applied independently.

ON INTERDISCIPLINARITY

Our interdisciplinary research program arose out of necessity rather than a preconceived decision that we must adopt such an approach in an effort to understand the complex conservation crisis facing adult migratory Fraser River sockeye salmon (Cooke et al. 2004b). Interdisciplinary research is often motivated by a desire to tackle a complex problem, which demands knowledge and methods/tools from many disciplines (Rhoten and Parker 2004). Indeed, interdisciplinary research has been repeatedly identified as a promising strategy for addressing some of the most urgent environmental and conservation problems of today and tomorrow (Steele and Stier 2000; Sankar et al. 2007) and a perquisite for complicated policy decisions (Metzger and Zare 1999). Based on our experience with this project, we would concur that many of our discoveries would not have occurred and our collective understanding would be more rudimentary had we not engaged in collaborative interdisciplinary research. One problem that often occurs with interdisciplinary projects is scoping of the research problems. However, in fisheries science a conservation crisis (e.g., Cooke et al. 2004b) can often provide the necessary focus and scope for an interdisciplinary project.

Numerous challenges can obstruct interdisciplinary research. For example, it is impossible for a single person or laboratory to possess the range of skills needed to conduct truly interdisciplinary research on fish migration. Hence, researchers need to embrace collaboration with colleagues in other disciplines. We have seen recent unlikely marriages of disciplines, such as functional genomics and ecology (Feder and Mitchell-Olds 2003) and conservation and physiology (Wikelski and Cooke 2006). We anticipate that such synergies as have been outlined above will stimulate advances in other areas of migration science, similar to what we have been able to accomplish on Fraser River sockeye salmon. Such interdisciplinary programs are difficult to launch because stakeholders often lack shared experiences and shared concepts (Sankar et al. 2007). Indeed, working with colleagues who are outside of one's normal peer group can present challenges, particularly with respect to becoming fluent with the conceptual basis, language, and the scientific and technological limitations of the different disciplines. A mutual sense of trust and respect, as well as a high tolerance for different research cultures can be helpful. Obtaining funding for interdisciplinary research can also be challenging based on the organizational structure of granting/funding agencies as well as the institutional structure of a team that may undertake the research. For example, our team consists of academics from several institutions as well as several government agencies and industry. In our case, the conservation crisis and need for coordinated research yielded support from relevant natural resource agencies and flexibility in how funds could be disbursed to different team members. We are confident that the there is immense potential to make stunning discoveries about fish migration and enhance the management of fish populations, as well as to address other complex conservation or fisheries

science issues through interdisciplinary research.

CONCLUSION

We hope to encourage scientists studying migration to move beyond simply documenting localized movement and assessing survival whenever opportunities for adopting a more interdisciplinary approach are available and necessary. Even if movement and survival remain the central goal of a study, additional effort or additional infrastructure can yield far more mechanistic information. There is growing recognition that individual variability is real (and not experimental noise or error) and that it is relevant to population biology (Bennett 1987). Combining telemetry with non-lethal biopsy or physiological sensors enables the researcher to focus on individual differences in behavior or physiology and ideally to evaluate the relationship between behavior and physiology (Hinch et al. 2006). One of the challenges involves reconciling such individual variability with management and conservation goals. For example, most of the novel techniques which we discussed in this article focus on individuals, yet the fundamental fisheries management unit is the stock or population and management should ideally occur at the ecosystem level (Link 2002). Given the complexity of fish migrations, all of the tools and approaches covered in this article will be needed to advance migration science. Already, some of these techniques are being applied to understand the biology of Pacific salmon on the spawning grounds (Hruska et al. 2007), as well as during their migration to reach these sites. We hope that the fish migration studies that use telemetry will become more mechanistic and experimental (i.e., hypothesis driven) and, as a consequence, illuminate the mysteries of fish migration and inform the management and conservation of these important resources. Indeed, the understanding of mechanisms should also allow for predictions of impacts of natural variability and anthropogenic climate change on salmon and other fishes.

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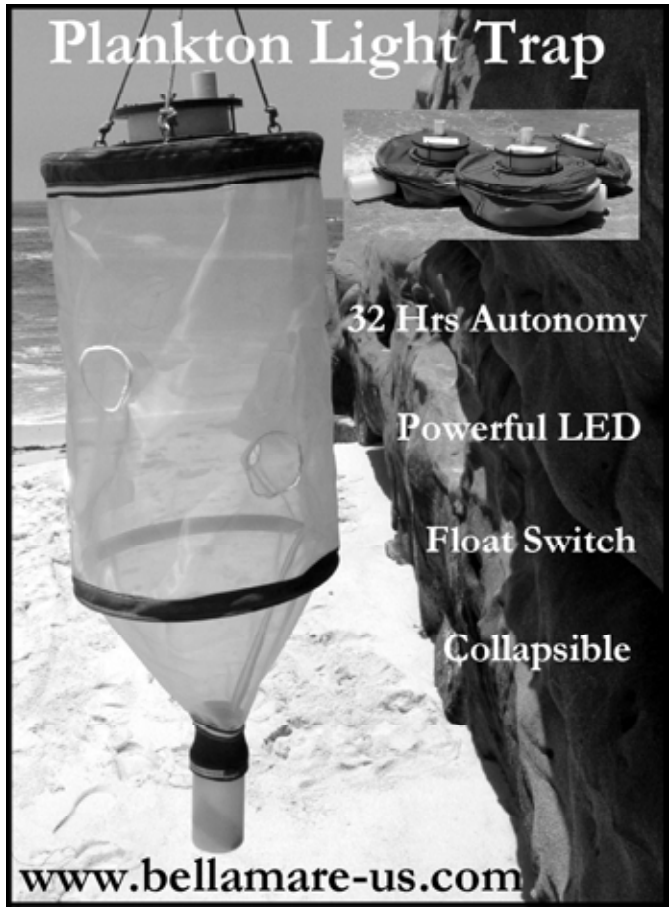

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