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Research

Conservation physiology in practice: how physiological knowledge has improved our ability to sustainably manage Pacific salmon during up-river migration

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Despite growing interest in conservation physiology, practical examples of how physiology has helped to understand or to solve conservation problems remain scarce. Over the past decade, an interdisciplinary research team has used a conservation physiology approach to address topical conservation concerns for Pacific salmon. Here, we review how novel applications of tools such as physiological telemetry, functional genomics and laboratory experiments on cardiorespiratory physiology have shed light on the effect of fisheries capture and release, disease and individual condition, and stock-specific consequences of warming river temperatures, respectively, and discuss how these findings have or have not benefited Pacific salmon management. Overall, physiological tools have provided remarkable insights into the effects of fisheries capture and have helped to enhance techniques for facilitating recovery from fisheries capture. Stock-specific cardiorespiratory thresholds for thermal tolerances have been identified for sockeye salmon and can be used by managers to better predict migration success, representing a rare example that links a physiological scope to fitness in the wild population. Functional genomics approaches have identified physiological signatures predictive of individual migration mortality. Although fisheries managers are primarily concerned with population-level processes, understanding the causes of en route mortality provides a mechanistic explanation and can be used to refine management models. We discuss the challenges that we have overcome, as well as those that we continue to face, in making conservation physiology relevant to managers of Pacific salmon.

Keywords: conservation physiology; fisheries management; genomics; field physiology; climate change

1. INTRODUCTION

There is a growing recognition that global biodiversity and ecosystem services are threatened by environmental change driven by humans [1], evidenced by declining populations and an increasing number of organisms being added to regional, national and international threat lists (i.e. the International Union for the Conservation of Nature red list [2,3]). Conservation scientists have taken up the cause of attempting to understand the factors responsible for population declines and trying to develop strategies to reverse such trends to sustain biodiversity and restore degraded habitats.

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One contribution of 13 to a Theme Issue ‘Conservation physiology: integrating physiological mechanisms with ecology and evolution to predict responses of organisms to environmental change’.

Conservation science is a crisis discipline, and due to the inherent complexity of environmental problems it often requires an interdisciplinary approach, bringing together disparate fields of study such as social science, biology, law and resource management [4]. A number of subdisciplines have emerged such as conservation social science and conservation genetics, which have helped to codify and rally research efforts aimed at addressing the biodiversity crisis and informing conservation actions. Conservation physiology, defined as 'the study of physiological responses of organisms to human alteration of the environment that might cause or contribute to population declines' [5], has been regarded as a new subdiscipline of conservation science. The premise is that physiological knowledge can be used not only to document problems, but also to generate management models for predicting how organisms will respond to change as well as developing and testing conservation strategies. Although conservation physiology is focused on anthropogenic stressors, rarely do stressors act alone so there is inherent need to cover other stressors such as disease that are often moderated by human activities [6].

Despite the recent publication of several syntheses [5,7–11], and convening of symposia [12–15] that document growing interest in applying physiology to conservation issues, it is important to question whether conservation physiology is informing policy and management. On the one hand, Cooke & O'Connor [16] suggest that conservation physiology has much to offer policy-makers because of the rigorous experimental approach and the focus on elucidating cause-and-effect relationships in individuals (also see [11]). However, they also suggest that some factors such as the relevance of biomarkers to population-level processes and the reliance of surrogate species rather than working on imperilled taxa create challenges for the acceptance of policies based on this approach. Despite apparent growing interest in conservation physiology, practical examples of how physiology has helped to understand or solve conservation problems remain scarce. If conservation physiology is to become a useful source of information for conservation practitioners and a relevant subdiscipline within conservation science, there is a need to highlight examples of both where and how that approach has succeeded and when and why it has failed [16].

Over the past decade, an interdisciplinary research team adopted a conservation physiology approach to address topical conservation concerns for Pacific salmon, including fisheries effects, disease and climate change, in the coastal waters and Fraser River of British Columbia, Canada (figure 1). The team did not form with the explicit goal of 'doing conservation physiology'. Instead, the focus was on understanding animal–environment and animal–human interactions, and on revealing the mechanisms associated with population declines. Initially by happenstance, those with the interest and skill sets to address those questions were a combination of physiologists and behavioural ecologists. Through time, it became more apparent that we were indeed 'doing conservation physiology' as did our collective interest in ensuring that our findings were of use to managers and policy-makers in the Fraser Basin.

The focus on Pacific salmon was logical for a number of reasons, including their economic, cultural, political and ecological importance to Canada. The five species of anadromous Pacific salmon (i.e. coho, chinook, sockeye, pink and chum) and steelhead represent some of Canada's last remaining large fisheries on wild fish. The commercial fishing industry in BC is one of the largest sectors of the provincial economy. Wholesale value of commercial salmon catch in BC is valued at $200 million annually (2003–2005, British Columbia Ministry of Environment 2006, unpublished data), with billions of additional dollars generated through subsidiary industries. Recreational salmon fishing in BC generates more than $1 billion annually in expenditures, supporting more than 10 000 jobs in communities throughout the province (Fisheries and Oceans Canada, unpublished data). About $40 million tax dollars are spent annually on salmon management and habitat conservation. Culturally, salmon are integral to the mythology, spiritual integrity and livelihoods of Pacific First Nations. Salmon provide important sources of protein for First Nations people throughout BC, and are public icons with abundant salmon returns confirming a healthy and productive environment. Ecologically, salmon are important to food chains in freshwater and marine areas [17]. Adult salmon carcasses are fundamental sources of nutrients for stream and riparian ecosystems in coastal Pacific watersheds. Notably, there have been a number of recent high-profile declines in the abundance of some iconic salmon populations (e.g. Interior Fraser coho, Cultus Lake sockeye), coupled with an overall decline in productivity for most Fraser River stocks. In some years, mass mortality events have been observed [18]. Peak summer water temperature of the Fraser River has increased by 2°C in the past 60 years, and climate forecasts predict a further increase of 2–4°C by 2100 [19,20]. Moreover, fishing gear interactions (e.g. either as bycatch or as released and escapees from fishing gear) have put additional pressure on some populations. Clearly, there is a need for science to support the sustainable management of Pacific salmon in the Fraser Basin and beyond. Indeed, an unprecedented low return of adult sockeye in 2009 coupled with years of declining productivity prompted the Prime Minister of Canada to order a judicial inquiry to investigate the situation.

Here, we introduce how novel applications of tools such as physiological telemetry, functional genomics and laboratory experiments on cardiorespiratory physiology have shed light on a number of conservation problems in the Fraser Basin. We adopt a case study approach where we discuss three issues: fisheries interactions, disease and health, and stock-specific consequences of warming river temperatures. For each issue, we present the problem, summarize research findings and then evaluate the extent to which we have succeeded or failed in informing management and policy. As our authorship team comprises scientists from academia and government as well as fisheries managers and science transfer and extension staff from government, we are able to provide a candid assessment of our collective experience as both scientists and managers. We provide a list of both the challenges that we

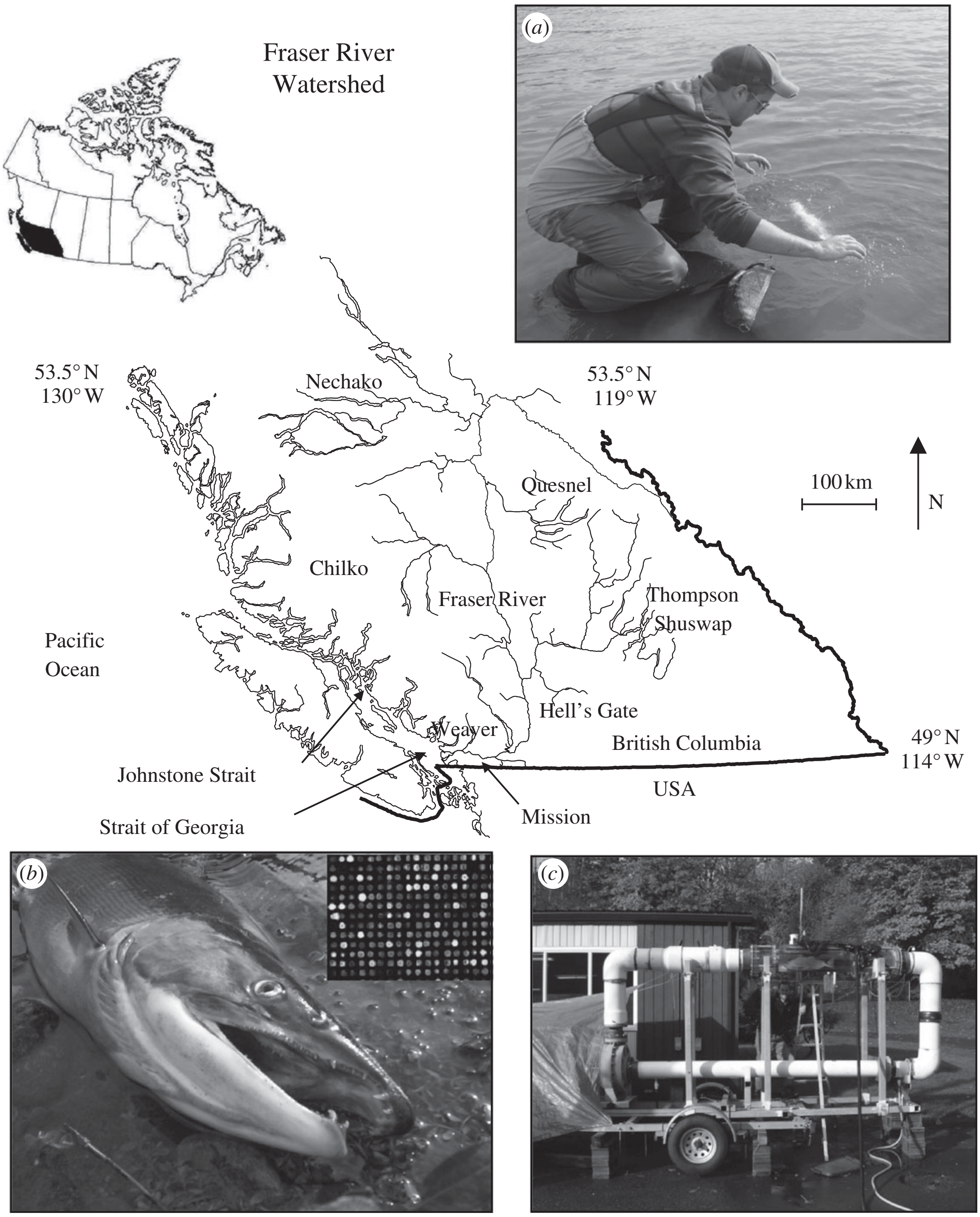

Figure 1. Map of the Fraser River Watershed, showing its position in Canada (black area on map of Canada) and (inset) illustrating key locations and sub-watershed mentioned in the text of the paper. Photos are representative of the three case studies presented in the paper: (*a*) salmon captured by recreational fisher and being evaluated for RAMP by member of research team (photo credit M. Donaldson); (*b*) a sockeye salmon that has died en route to spawning grounds along with inset of gene array used to study gene expression (photo credit S. Cooke); and (*c*) a sockeye salmon in a swim tunnel/respirometer (photo credit Glenn Wagner).

have faced and suggestions for others interested in using a conservation physiology approach to address conservation problems.

2. FISHERIES GEAR INTERACTIONS

(a) *Problem statement*

The anadromous migrations of Pacific salmon (*Oncorhynchus* genus) are cyclical and predictable in time and space, making these species vulnerable to fisheries capture [21]. Commercial, recreational and First Nations fisheries intercept salmon during their coastal approach (e.g. purse seine, gill net and trolling) or upon freshwater entry (e.g. gill net, beach seine, dip net and rod-and-reel). Regardless of gear type, fisheries capture typically results in physiological disturbances due to exercise stress from the capture event, periodic air exposure during removal from gear and handling stress (figure 2) [23–25]. Pacific salmon are commonly released either due to conservation ethic (in recreational fisheries) or fisheries regulations that require release for conservation purposes. Some fish also escape from fishing gear [23], which leads to stress and injury. Released fish may

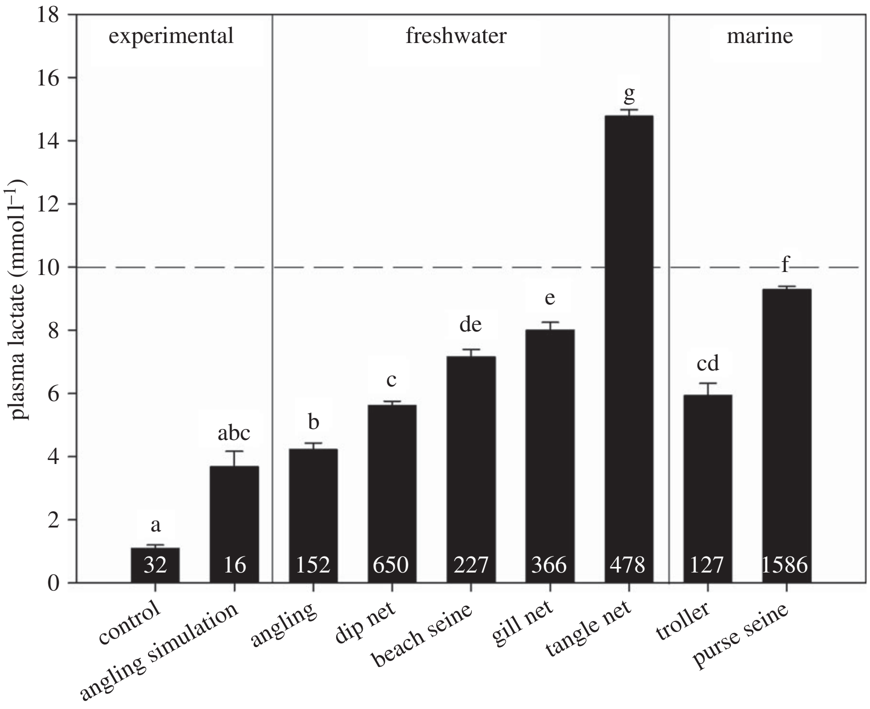

Figure 2. Plasma lactate measured in adult migrating sockeye salmon under control (i.e. sensory deprivation chamber for 24 h prior to sampling) and experimental simulations (i.e. chasing fish to exhaustion in freshwater or post-capture in freshwater and marine environments). The time between capture and sampling varied between capture types but biopsies were collected as soon as possible after fish were landed. Plasma lactate would increase following capture, typically peaking at 1–2 h (M. Donaldson, unpublished data), meaning that the values presented here illustrate the pre-release increase in lactate but not the peak lactate response that might ensue after release. The broken line indicates a threshold of 10 mmol l^{-1} that indicates a level of fatigue that has been previously suggested to prohibit short-term (i.e. 1 h) repeated swimming (Farrell *et al.* [22]). Dissimilar letters denote statistical differences between groups (one-way ANOVA and Tukey's post-hoc test) and sample sizes are noted on the bars.

resume their migrations and ultimately reach spawning areas, but the severe physiological stress can also result in immediate, short-term or delayed mortality [25–27]. While fisheries capture and release has been linked to migration failure for Pacific salmon, little is known about the physiological response to, and recovery from, fisheries interactions or how physiological condition influences post-release survival. Over the past decade, we have examined links between fish physiology and post-release survival to inform management and to develop tools to help manage and reduce mortality from release fisheries.

(b) *Research findings*

Our current research efforts on the development of tools to help promote post-release survival of fish in the Fraser River are based on earlier work by Farrell *et al.* [28] in the marine environment. Farrell *et al.* [28] found that non-target wild coho salmon (*Oncorhynchus kisutch*) captured by troll, seine and gill net showed signs of severe metabolic exhaustion at the time of capture, raising concerns over the likelihood of post-release survival. To address this concern, methods for facilitating and expediting physiological recovery were tested [28] and refined [29,30]. The idea of promoting recovery from fisheries capture stemmed from results of Milligan *et al.* [31], who provided evidence for accelerated metabolic recovery from exhaustive exercise in the laboratory of hatchery-reared rainbow trout (*Oncorhynchus mykiss*) when they were recovered in flowing water while swimming at constant velocity (i.e. 0.9 body lengths s^{-1}) relative to non-swimming individuals held in static water. This application of the results of the Milligan *et al.* [31] study was expanded to the commercial troll fishery where Farrell *et al.* [30] found that placing fish in a cage/net pen towed alongside the moving vessel resulted in rapid physiological recovery and no mortality during the 24 h assessment period. Facilitated recovery using a revival box, called the Fraser Box after the commercial fisher who constructed the first prototypes, successfully promoted physiological recovery, rapidly restoring swimming ability in 1–2 h, and resulted in high post-release survival, even for fish that appeared moribund at the time of gill net capture [29]. The survival benefit of the Fraser Box has resulted in these recovery boxes being implemented in marine commercial fisheries for releasing coho salmon.

Follow-up research by our team, involving biotelemetry and physiological sampling, is ongoing to assess whether recovery gears are as effective in freshwater for releasing salmon captured and released during up-river migration. However, the exact method and timing of facilitated recovery has proven critical, since long-term holding (i.e. 24 h) in in-river net pens resulted in a major stress response (fourfold increase in plasma cortisol and twofold increase in plasma glucose relative to levels measured at the time of capture) and high post-release mortality (97% mortality; [32]) rather than enabling sockeye salmon to recover from recreational fishing capture.

Another complicating factor is that different capture methods can result in different outcomes for survival, despite comparable physiological responses. Similar osmoregulatory and metabolic disturbances measured at the time of capture were found for sockeye salmon captured by either beach seine or angling [32] and for fisheries capture simulations [33]. Furthermore, biotelemetry to enable long-term tracking of individuals post-release revealed a greater than 95% survival 24 h after release from both beach seine and angling. Yet, when tracked to natal sub-watersheds, survival post-beach seine (52.2%) was higher than after angling (36.3%), suggesting a potentially important difference in survival between the two capture methods. Latent effects on survival of Pacific salmon and important stock-specific links between physiological condition and survival have also been documented [34], wherein the metabolic and osmoregulatory impairment from fisheries capture influenced the post-release behaviour and survival of one stock complex of sockeye salmon (i.e. Adams-Shuswap), but not another (i.e. Chilko).

Heart-rate biologgers are revealing that even seemingly benign capture and handling methods can result in prolonged recovery responses in Pacific salmon. Heart rate was seen to double (from 30 to 60 beats min^{-1}) following either a 10- or 30-min corralling treatment designed to simulate seine net capture [33]. Remarkably, it took 7.6 h for heart rate to recover to pre-corral levels after a 10-min corralling and no fish-handling, and 11.5 h for the 30-min corralling. When coho were exhaustively exercised and stressed (as reflected by increased plasma lactate, glucose, sodium, osmolality and cortisol (males only) and decreased mean corpuscular haemoglobin), to simulate capture by recreational angling, heart-rate recovery took nearly 16 h! Clearly, heart rate in coho is a very sensitive indicator of even modest stress events, with the possibility that a direct relationship exists between the intensity of the stressor and the duration of heart-rate recovery.

Research is also underway to develop and evaluate reflex action mortality predictors (RAMPs; [35]): a simple, field-based alternative to traditional physiological measurements (e.g. biopsy). RAMP involves assessing the presence/absence of reflexes normally present in fish with good condition and vigour. The reflexes tested include the ability of the captured fish to right itself when turned upside-down in the water column (see photo in figure 1*a*), and whether the fish exhibits a regular pattern of ventilation when held out of water. RAMP has been validated previously for monitoring fish condition in the marine environment and predicting delayed mortality following fisheries capture [35]. A more recent radio-tracking study has shown that endangered interior Fraser coho salmon released from a beach seine are more likely to reach their natal spawning areas with a better RAMP score (i.e. fewer impaired reflexes; [36]). Presumably by integrating underlying physiological systems, greater reflex impairment reflects a state further from homeostasis, from which a complete recovery is less likely and latent mortality is more likely. Given that in some cases traditional blood-based physiological measures have failed to predict mortality following fisheries encounter, RAMP shows promise as a tool that can be used by managers to evaluate the consequences of fisheries encounters on fish.

(c) *Application*

Through laboratory and field studies with Pacific salmon, our group has made progress in understanding the consequences of fisheries capture on wild fish and these results are being used to inform management. Donaldson *et al.* [33] illustrated the prolonged physiological recovery from capture stress, and while understanding the sublethal consequences of fisheries capture is of interest, managers often require survival as an endpoint to change management regimes. Donaldson *et al.* [32] provided telemetry-based mortality estimates for sockeye salmon released from two fisheries capture gears, addressing an important gap in knowledge previously filled by generalizing across sectors and locations (e.g. managers have applied mortality data from commercial troll fisheries in the marine environment to freshwater recreational fisheries). Identifying between-sector similarities is useful for developing general management principles that could simplify policy development and harvest allocations [37], but represents a research area that is challenging to address owing to inherent differences among capture methods, locations, environmental conditions and even among stocks [34]. The work by Farrell *et al.* [29,30] provides a robust technique for promoting physiological recovery and survival, and represents a relevant example of science being implemented into management regimes. Our work on coho bycatch in freshwater fills an important knowledge gap for a species of conservation concern, and tests a novel method for monitoring physiological impairment at the whole-animal level, through RAMP [36]. RAMP may become a simple tool for fishers to help decide whether an individual fish will benefit from facilitated recovery, and could be used by fisheries managers to rapidly generate inexpensive but informative mortality estimates. Indeed, stress responses typically revealed with blood physiology are not always clear mortality predictors in migratory wild adult salmon. Part of the difficulty lies with obtaining good baseline measures and the additional problem that plasma cortisol increases progressively with maturation and independently of stress [38]. Thus, RAMP may serve as an additional tool to enhance our ability to predict mortality. Taking a conservation physiology approach to understanding fisheries interactions with Pacific salmon remains a useful means of tackling a complex problem and transferring scientific knowledge to management.

3. DISEASE AND HEALTH

(a) *Problem statement*

Because Pacific salmon are semelparous, capital breeding animals, lifetime fitness depends on physiological condition and health during their spawning migration. Condition varies markedly among individuals, but there is also considerable variation within- and among-species as a product of local adaptation and selection for optimal life-history tactics [39,40]. An omnipresent challenge involves the suite of fungal (e.g. *Saprolegnia* spp.), bacterial (e.g. *Columnaris* spp., *Renibacterium* *salmoninarum*), myxozoan (e.g. *Parvicapsula* spp.) and protozoan (*Loma* spp., *Ichthyophthirius multifiliis*, *Cryptobia salmositica*), and viral agents to which salmon are exposed throughout their lifetime. Returning adult salmon have a fixed amount of somatic energy to accomplish a salt- to freshwater transition, an energetically demanding spawning migration, maturation and reproduction. To achieve any measure of lifetime fitness, a semelparous salmon must successfully complete all of these tasks, which in part depends on their relative susceptibilities to disease and the extent to which individual condition can buffer and defend against deleterious diseases. Furthermore, as an anadromous species, salmon are exposed to agents in freshwater during their early life history, in salt water where they grow and mature, and again in freshwater once adults have begun return migrations to spawning areas (see Rucker *et al.* [41] and references therein).

(b) *Research findings*

We have linked locational biotelemetry with plasma and tissue biopsy sampling to relate the physiological state or health condition of individual salmon as they traverse a broad spatio-temporal gradient extending from the ocean, to the mouths of natal rivers and onwards to spawning grounds [42,43]. Functional genomics offers a powerful discovery tool that can be used both to test hypotheses on specific physiological factors that may undermine performance as well as resolving factors not *a priori* hypothesized to be at play. We conducted functional genomic studies using cDNA microarrays on gill tissue that had been biopsied from adult sockeye salmon that were subsequently tracked by telemetry, and identified a mortality-related genomic signature (MRS) predictive of migration and spawning failure [44]. In fish tagged in the ocean 250 km from the mouth of the natal river, this signature was associated with a 13.5-fold increase in failure to reach the natal spawning area. The same signature was also associated with a 50 per cent increase in migration failure when salmon were biopsied just after entering the natal river and a 3.7-fold greater chance of dying before spawning while on spawning grounds. Functional analysis of the MRS was consistent with a response to viral infection present before fish entered the river [44]. Fish carrying the MRS also migrated more quickly into freshwater. Premature transcriptional shifts in osmoregulatory genes and plasma ionic imbalances associated with the MRS would have resulted in reduced tolerance of salt water, motivating rapid river entry and potentially affecting their fitness in the coastal marine environment. While research is ongoing to identify an infective agent associated with this signature, biomarkers for genes highly associated with the MRS have been developed to explore the relationship of this signature with survival in additional years. If this signature is shown to correlate with migration and spawning success across multiple years and stocks, these biomarkers could be applied to returning adult salmon to assess their disease state and general health before they enter the river and to inform management of how to adjust harvest rates to ensure adequate spawning ground escapement.

While molecular approaches offer a large amount of information on disease state, traditional histopathological analyses have been used to identify that a myxosporean parasite *Parvicapsula minibicornis* endemic to the Fraser River estuary is contracted by nearly all returning sockeye salmon. For most, the progression to kidney disease is slow and incomplete before they spawn and die naturally. However, histopathological analyses revealed that for autumn migrating (aka Late-run) Fraser River sockeye, parasite development is temperature-related and becomes a severe infection after migrants have accrued approximately 500° days during freshwater migration [45,46]. Normal-timed migrants accumulate less than 500° days prior to reaching spawning grounds whereas early migrants accumulate more than 700° days [46,47]. Thus, thermal progression may help explain why large numbers of Late-run Fraser River sockeye perish when they migrate early (i.e. 40–90% mortality; [18]), although the causes of the early migration remain unresolved ([15], but see [44]). High *P. minibicornis* loads impair ionic homeostasis [48]. Biotelemetry coupled with haematological sampling has also revealed that poor migration of early migrating Late-run sockeye was associated with impaired blood-clotting (i.e. haemophilia) [49]. At present, we do not know whether this is related to disease expression in Late-run sockeye, but when Pacific salmon become diseased, circulating thrombocytes tend to increase, which can then lengthen blood-clotting times [50].

Ultimately, Pacific salmon must arrive at spawning areas with sufficient reserve energy stores and in sufficient health to cope with pathogen burdens and maintain homeostasis long enough to complete spawning activities before their inevitable deaths. Moreover, the longer a female salmon remains alive on spawning grounds, the higher the proportion of her total egg complement will be deposited [51]. Salmon that die on spawning grounds prior to spawning show physiological and histopathological profiles indicative of gill and kidney diseases playing a significant role in mortality, in particular those caused by *P. minibicornis*, *Loma*, *Columnaris* and *Saprolegnia* [52].

In summary, our research has shown that the relative condition or health of salmon is a useful predictor of migration and spawning success. Our research programme has progressed from simply describing the multitude of health and physiological factors associated with migratory and spawning failure to using experimental approaches that can predict migratory failure. Another example has involved laboratory holding studies of adult sockeye salmon which revealed that loss of plasma chloride ion homeostasis (greater than 120 mmol l^{-1}) is predictive of imminent mortality (e.g. up to a week in advance; [53]). Ultimately, the survival of salmon during spawning migrations is subject to multiple endogenous and exogenous, as well as biotic and abiotic factors.

(c) *Application*

Annual population-specific estimates of in-river loss for Fraser sockeye have fluctuated from 0 to 90% over the past 16 years. Earlier, very poor information about the causes of mortality and limited capacity to predict variation forced managers to take a precautionary approach, restricting harvests in attempts to compensate for subsequent in-river mortality. Reduced harvests in years when fish were relatively healthy were then viewed as unnecessarily restrictive by some stakeholder groups. More recently, improved predictability and greater understanding of causal mechanisms have enabled fisheries managers to achieve a better balance between achieving spawning conservation goals and maintaining harvest opportunities. While predictive tools still remain somewhat empirical, by documenting a sound physiological basis for the variation in mortality, the conservation physiology research described herein has been a major driver for this shift in management approach. Future management tools may be more directly linked to physiological variables. For example, screening for biomarkers that predict in-river fate in marine test fisheries could be used to inform management of potential survival of a migrating population and adjustments to harvest could be applied proactively to marine and lower river fisheries; however, such 'real-time' management approaches have yet to be realized.

Research connecting fish health, river entry timing and in-river mortality using biotelemetry at a stock level, particularly for Late-run sockeye salmon for which we know that early migrants are in relatively poor health, has helped managers in making pre-season decisions to reduce harvest rates. In-river mortality is rarely observed (i.e. lack of physical evidence of dead fish), so reducing harvest to compensate for disease or health-related in-river mortality, and thereby maintain spawning ground escapement goals, has been a vexing and politically challenging area for fisheries management. Having an independent (e.g. biotelemetry studies conducted by non-government groups) and defensible explanation (e.g. demonstrated links between disease/health, river entry timing and survival) has helped managers to mollify the concerns among stakeholder groups regarding decisions to reduce harvest in the name of conservation.

4. WARMING RIVER TEMPERATURES

(a) *Problem statement*

Pacific salmon have a limited resistance to the impacts of climate change. Indeed, recent episodes of extreme summer river temperatures have been associated with massive en route mortality of hundreds of thousands of sockeye salmon [47,54]. With rising water temperatures, each new generation of adult salmon has a greater probability of encountering extremely high river temperatures during their once-in-a-lifetime migration from the Pacific Ocean to freshwater spawning grounds [55,56]. Yet the paucity of data upon which to base predictive relationships between warming river temperature and migration success has forced analysts to use empirical rather than mechanistic models in attempts to improve the sustainable management of salmon populations [57]. Even though the exact cause of the temperature-induced mortality is unknown, the aerobic challenge of up-river migration to spawn appears to be a significant bottleneck when river temperatures are warmer than normal. Therefore, we have focused one aspect of our research programme on the cardiorespiratory system and its capacity to transport sufficient oxygen from the water to the body tissues of salmon under conditions of high temperature.

(b) *Research findings*

During migration, wild adult salmon increase oxygen uptake and cardiac output to supply oxygen to locomotory muscles. The maximum they can increase oxygen delivery above routine is termed aerobic scope (figure 3) and cardiac scope, respectively, which are both temperature-dependent. To meet the increasing oxygen demand when warmed, salmon increase aerobic scope and cardiac scope with increasing temperature but once an optimal temperature (T_{opt}) is surpassed both variables decrease. Even so, T_{opt} for aerobic scope can vary considerably among adult Pacific salmon species. For example, it has a value of 8°C in a stock of coho salmon that migrates in late autumn/winter [58], ranges from 14.5°C to 17.2°C in summer/autumn migrating sockeye salmon stocks [59], and reaches 21°C in a summer/autumn migrating pink salmon stock [60]. Thus, this species variability in T_{opt} for aerobic scope may prove to be a useful physiological metric to help explain life-history strategies and predict resilience to climate change. Layered on top of genetic considerations are disease, physical damage and stress owing to fishing interactions (outlined above), which may impose limits on physiological capacity, which then restricts the optimal thermal window for aerobic performance (figure 3; [46,61,62]).

An accumulation of evidence suggests that high spawning site fidelity for sockeye salmon has resulted in intraspecific local adaptation. Populations with longer and more difficult spawning migrations appear to have morphologically and physiologically adapted to their specific up-river migration conditions quite differently than their short-migrating coastal conspecifics. Up-river populations have larger somatic energy stores at the onset of the up-river migration, smaller and more fusiform body shape, smaller overall gonadal investment, larger relative ventricle size with improved coronary supply, higher aerobic scope and more energetically efficient swimming [40,59,63]. Consequently, continued increases in summer river temperatures will likely result in population-specific responses of salmon [54,59]. In fact, based on differences in thermal tolerance and T_{opt} for aerobic scope, Weaver and Nechako sockeye salmon populations are predicted to be more susceptible to further river warming compared with the Chilko population [54,59]. By comparison, pink salmon may prove to be the most tolerant of all Pacific salmon to the current warming trend given their high T_{opt} and aerobic capacity [60]. Additionally, climate warming appears to select for individuals with smaller body size [64,65]. One physiological observation that might contribute to this selection is that large Chinook salmon cannot achieve the same level of oxygen uptake across the gills as their smaller conspecifics, a difference that becomes even more apparent at high temperatures [66].

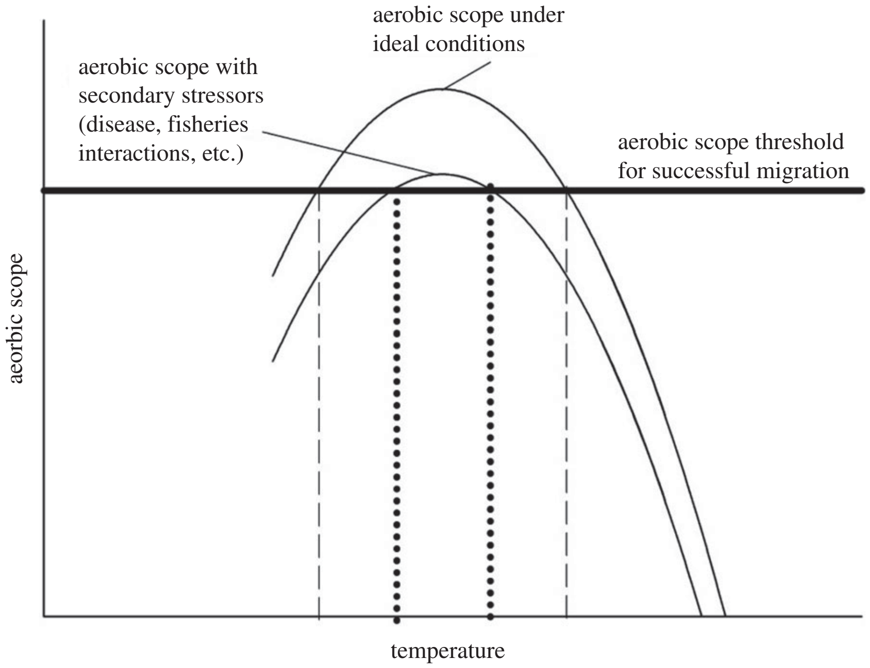

Figure 3. Aerobic scope curves under ideal conditions and under the influence of secondary stressors, as a function of temperature. For a given salmon population, there is a minimum aerobic scope threshold for successful migration to reach the spawning ground. This threshold will vary yearly depending on environmental conditions (e.g. may increase or decrease due to varying river flow, etc.). The optimal range of temperatures is restricted when fish are physiologically compromised due to secondary stressors (dotted lines) when compared with under ideal conditions (dashed lines).

Male and female sockeye salmon responded differently either when intentionally 'stressed' by holding them in tanks under different thermal or flow conditions [53,67,68], when stressed by encountering high temperatures [69], or when encountering migratory obstacles [70] during the up-river migration [69]. In each of these cases, females suffered significantly higher mortality than males. Correspondingly, females had significantly higher routine levels of plasma cortisol at all locations during the river migration [34,71,72] and a higher resting heart rate when confined [71], suggesting greater physiological stress in females than males. Sexually mature female Pacific salmon also possess an approximately 12 per cent smaller relative ventricle mass than males [60,71,73], which may explain why maximum cardiac output was lower in female compared with male pink salmon across a broad temperature range [60]. With such prominent sex-specific limitations in the cardiorespiratory exercise physiology of females, which perhaps reduces their capacity to cope with stressful conditions, a sex-specific approach to conservation and management of Pacific salmon is probably needed.

(c) *Application*

The management regime for Fraser River sockeye salmon includes a procedure for increasing the target number of spawners in response to expected mortality predicted from real-time forecasts of river temperatures and flows [57]. These models are not currently based on any mechanistic physiological relationships, but rather simply relate discrepancies between the abundance of salmon at lower and upper river sites in past years to historical river temperature and flows. In some years, hundreds of thousands of fish were removed from available harvest, leading to heated debates about the underlying causes of discrepancies and questions about why more carcasses are not being observed. Physiological research has provided the mechanistic basis for these discrepancies, diffusing debates and increasing the acceptance of reductions in harvest when adverse river migration conditions present themselves. Yet, these tools are based on rather large population groupings at a juncture when physiological research is increasingly demonstrating species, population/stock, sex and body size effects on temperature tolerance for Pacific salmon. While new knowledge is complicating current management practices, these factors are clearly unavoidable consequences of biological diversity. A marvellous example of applying this 'new' knowledge is to avoid trying to replace lost biodiversity in up-river watersheds by transplanting coastal populations of sockeye salmon, which we now know are poorer swimmers and cannot cope as well with expected increases in river temperatures in the future.

Species- and population-specific thermal tolerances suggest that some species and stocks will be less tolerant of climate warming than others. This information has been applied to model future climate scenarios and inform management of differential survival among populations [56]. For a given population/stock, the optimal range of temperatures depends on the aerobic scope threshold for successful migration and the condition of the fish (figure 3), which will vary among years depending on environmental conditions (e.g. a greater aerobic scope may be necessary when river flow is higher). While it is currently unknown exactly how much aerobic scope is necessary for successful migration [59], we have recommend that fisheries managers take into consideration that salmon (especially females) may be physiologically compromised and thus restricted to a narrow range of optimal temperatures. Currently, this knowledge provides a much needed rationale for fisheries managers to restrict fishing effort during periods where river temperatures exceed predefined values, in an effort to reduce the stress on migrating salmon and maximize the number of individuals successfully reaching spawning grounds [57].

5. CHALLENGES AND LESSONS LEARNED

(a) *Science perspective on conservation physiology*

From the perspective of scientists (i.e. those doing conservation physiology research), there are a number of challenges that we have faced in attempting to make our research relevant to practitioners. Perhaps foremost is the fact that managers tend to focus management on the population or stock, whereas physiology more often focuses on the individual [16]. A common theme in our work is that there is immense intra- and inter-specific variation in the physiology (including tolerances, capabilities to regulate), which extends further to sexual dichotomies. We consider one of our greatest contributions being the affirmation that populations and stocks do indeed differ in important respects, consistent with selective forces such as migration distance and temperature. Therefore, our work is relevant at the population level, helping explain patterns of mortality, particularly in the context of warming river environments, fisheries interactions and disease. The complexity associated with some of our findings (e.g. the fact that potentially sexes, populations/stocks and species differ) does not always lend itself to immediate conservation action, but it does help to document the level of biodiversity that exists among Pacific salmonids and the need for evolutionarily enlightened management strategies [74] which have the potential to embrace diversity at all levels. And, while some of our findings may not have direct management applications at this time, understanding the mechanisms leading to migration failure has become a fundamental feature of appropriate management action.

Also challenging at times is the fact that some of the detailed concepts and complex tools used by physiologists are foreign to fisheries managers who have relevant training in topics such as stock assessment and population modelling. This has been particularly the case for our genomic work where rapid advances in technology and data-generation capabilities have far outpaced the interpretation of such immense datasets, which still remains challenging. What is a fisheries manager to do with the knowledge of a genomic signature (hundreds of genes that are differentially regulated) or a plasma variable differing between those fish that make it to spawning grounds and those that fail to do so? While these discoveries can be of great potential benefit to management if validated over multiple years of sampling, our experience suggests that these data need to have a firm mechanistic basis before managers and scientists alike are willing to consider their application.

Additional work is clearly needed to better describe the ecological consequences of differential physiological profiles and to develop and validate simple biomarkers that have the potential to be incorporated into fisheries monitoring and management. Relatedly, a major impediment to conservation physiology is the difficulty of transferring findings of laboratory-based experiments to wild animals in the natural environment (see §4 on climate change for examples). While many physiological measurements remain restricted to controlled and confined conditions, advances in biologging and biotelemetry are progressively allowing conservation physiologists to study free-roaming animals [72,75,76]. These advances will be vital in investigating whether or not the physiology of Pacific salmon can, for example, adapt fast enough to match the unprecedented climate warming.

Although we concede that for some issues managers simply need to know how many fish live or die, the mechanistic approach provided by the inclusion of physiology data can not only provide mortality estimates but can also actually identify solutions or opportunities to refine practices. This has been most obvious for us in dealing with fisheries interactions where we are evaluating recovery gears and are able to identify a range of potential recovery environments. Managers can use such information to educate fishers on better handling practices using science-based information. Given that the backbone for much of our research is non-lethal biopsy and biotelemetry (as is the case in other conservation physiology studies; e.g. [76]), an additional challenge that we have faced is a general mistrust of our data by managers and stakeholders who question our assumption that our techniques do not alter the behaviour and survival of fish being studied. To increase the trust of managers in our tagging data, we have conducted validation studies comparing tagged and non-tagged conspecifics [77]. Also, rather than simply disseminating findings in peer-reviewed journals and scientific conferences, we have discovered that it is essential to hold workshops with stakeholders for the sole purpose of exchanging information. At such meetings, stakeholders not only have an opportunity to learn about and comment on what we have done, but they can also express their needs and concerns. Through such interactions, we have been able to better direct research activities towards management and conservation concerns in a collaborative manner (including joint grant applications with stakeholders as partners). In our experience, listening to stakeholders (managers, fishers and NGOs) and incorporating their knowledge and perspectives into research activity is the most productive strategy for ensuring that conservation physiology remains relevant to the end users of the information and truly informs conservation action. For example, prior to conducting a study examining the physiological condition and survival of fish caught and released by recreational anglers, our group held meetings with scientists and managers from Fisheries and Oceans Canada, collaborated with consulting firms for logistic support, and met with leaders of the recreational and First Nations fisheries communities to discuss research questions and experimental design. We also recognize that in the policy and management arena, change takes time and that given the uncertainty inherent in biology and resource management, decisions are usually based on a burden of evidence rather than a single study or finding. Knowledge of the realities and timelines associated with governance is essential so as to not become frustrated with the often slow process of uptake of what scientists see as seemingly relevant physiological data.

(b) *Management perspective on conservation physiology*

The management structure for Pacific salmon has provisions to adjust harvest to increase the probability of achieving spawning targets without unduly compromising harvest opportunities in an attempt to mitigate against environmental factors known to be associated with in-river mortalities, such as high river temperature, disease and captured fish release [57]. This provides a direct application for the results from the conservation physiology research outlined in this paper to aid Pacific salmon management. The science advice to management can describe factors that either are contributing to mortality or are used to predict this mortality. In the Fraser basin, conservation physiology research has already made tremendous contributions to describing how disease, water temperature and fisheries encounters have impacted in-river salmon mortality. These descriptions have greatly improved the acceptance of results from empirically based predictive models, despite the fact that the research has yet to yield physiologically based mechanistic models.

The main benefit to management derived from the three case studies presented herein is in evaluating the biological rationale for current management practices and in describing past mortality events. The fisheries release mortality research has refined our understanding of the inherent physiological stress associated with capture and delayed mortality, resulting in recognition that some of the current mortality estimates need to reassessed. More intriguing is the proactive approach of educating fishers on best practices for fish-handling based on conservation physiology. If proven effective, this should reduce release mortality estimates applied to a specific sector, and therefore directly benefit that sector with increased opportunities to capture fish. The work on disease and health has supported the sometimes unpopular management conservation measures enacted to protect late-run stocks by providing a mechanistic understanding of high in-river mortality. The work on thermal tolerance at the population level has provided justification for the current practice of limiting harvest during high-temperature events at a stock aggregate level [57], and is being used for examining future population-specific survival trends under warming conditions [56]. Current limitations to expanding the role of conservation physiology in shaping fisheries management include the dealing with cumulative impacts, management constraints and outcome uncertainty. More research can be applied to address the cumulative impact of disease, fish condition, high temperature and fisheries encounters on survival, whereas management constraints are more challenging. Pacific salmon destined for Fraser River spawning grounds are first captured in fisheries in the marine environment, followed by lower river fisheries, with a very limited number captured at or near spawning grounds. However, with a few exceptions, most of the conservation physiology research has been conducted in freshwater or in marine areas near river mouths. The ability to predict the fate of migrating fish requires an understanding and forecasting of survival probability well before they enter freshwater. The goal of developing more mechanistic models, while more appealing to conservation physiologists, may be impractical given the need for a relatively long time series of data. Such time series extend beyond the tenure commitment of typical research funding programmes (some of which come from fisheries management agencies). Fisheries management also has to contend with an outcome uncertainty that is very large when predicting the impact of disease or climate change on future salmon survival. The confidence in describing past events is very different to that in predicting future river mortality. Managers and conservation physiologists will most likely have to work together with quantitative experts in dealing with this uncertainty to better integrate conservation physiology results into management [78]. The complexity of Pacific salmon migrations requires this integrative research approach to improve management of vulnerable species and stocks.

6. CONCLUSION

Using three case studies to explore issues facing Pacific salmon, we described how our team has applied physiological tools and concepts to conduct research that has contributed to understanding of complex conservation and management problems. We also established synergistic exchanges with managers and stakeholders. Given that Pacific salmon management functions largely at the stock level, it is not surprising that some of our most significant conservation advances have been with understanding stock-specific responses of Pacific salmonids to different stressors (e.g. climate change, disease and fisheries). Other significant advances have been made towards addressing specific management questions such as those related to fate of fish released from fisheries and means of reducing post-release mortality. We believe that we have succeeded in making conservation physiology relevant to managers of Pacific salmon stocks, but challenges remain. It is our perspective that the most successful approach for realizing the benefits of conservation physiology is for researchers to engage managers (and vice versa) with open dialogue regarding the capabilities of physiological tools and how they can be used to address conservation and management problems. For conservation physiology to be truly effective, it must represent a meaningful collaboration of researchers and practitioners from defining the questions through to interpretation and application of the findings. Lastly, although this paper is focused on physiological tools, we also wish to emphasize the importance of interdisciplinary research. Inherent in many of our 'conservation physiology' research projects are aspects of animal behaviour (e.g. the telemetry component of almost all of our field studies; see [79]), oceanography, genetics and even social science. In other words, the best and only way to address complex conservation problems is through interdisciplinary research [80], of which conservation physiology is certainly becoming a recognized and important contributor.

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