

# On conducting management-relevant mechanistic science for upriver migrating adult Pacific salmon

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## ➔ Take-home message

Diverse physiological tools and approaches have revealed the mechanisms that underpin migration failure of Pacific salmon in the Fraser River of British Columbia, Canada, providing fisheries managers with predictive tools and management options for balancing fisheries opportunities with conservation of salmon populations.

### 3.1 Defining the conservation challenge—Pacific salmon in the Anthropocene

By any and all measures, Pacific salmon (*Oncorhynchus* genus) are among the most iconic of all migratory species. These anadromous species engage in impressive migrations that are cyclical and predictable in time and space (Groot and Margolis 1991). As adults, Pacific salmon have to migrate from open-ocean feeding grounds to spawning grounds. Except for steelhead (*Oncorhynchus mykiss*), Pacific salmon are exclusively semelparous whereby failure to reproduce

means zero lifetime fitness. Migration for salmon is not easy—along the way they experience dynamic and challenging environmental conditions (i.e. water velocity, turbulence, and temperature, as well as pathogens and predators). Pacific salmon are therefore especially vulnerable to environmental changes that make a difficult migration even more challenging (Crozier et al. 2008). Moreover, these predictable migrations make Pacific salmon particularly vulnerable to capture fisheries (commercial, recreational, and Indigenous) that use a diversity of gear types (ranging from hook-and-line to nets). While most fisheries are conducted to

harvest salmon, a component of the catch is released for conservation, either because of fishery regulations or the conservation ethic of fishers in the context of catch-and-release angling. Some individual salmon also encounter and escape from fishing gear (Patterson et al. 2017a, b) by engaging in high-intensity exercise, perhaps with injury, which introduces additional challenges for fish that need to reach spawning grounds to reproduce. Even catch-and-release fishing involves intense exercise, handling, and perhaps exposure to air.

Collectively, the natural and anthropogenic stressors encountered by Pacific salmon represent dramatic and important selective forces such that in some years and for some populations only a small proportion of individuals survive to reach spawning grounds (Cooke et al. 2004). Indeed, many Pacific salmon populations are in decline as a result of multiple stressors that are experienced by fish at various times during their life history (Lichatowich et al. 1999; Portley et al. 2014; also see International Union for Conservation of Nature [IUCN] Red List for individual stocks that are listed). As such, there is a dire need for science-based tools that consider the mechanistic basis behind mortality or fitness impairments to identify opportunities for mitigating threats and informing management options.

Historically research on Pacific salmon focused on characterizing trends and patterns in population size (e.g. Shea and Mangel 2001) and vital rates (e.g. Bradford 1995)—*how many* fish are there—*how many* fish were harvested—*how many* fish died—*when* did they die—and *where* did they die? While these are essential aspects of stock assessment, much less effort was devoted to understanding *why* fish died. This is not surprising given the stock assessment and research tools available, which tended to involve use of external markers at best and typically considered the fate of individuals. Today we have modern electronic tagging (see Figure 3.1) and genomics tools combined with laboratory cardio-respiratory assessments and other multi-disciplinary approaches to understand how salmon interact with each other, their environment, and humans. Our team has used a diversity of approaches, tools, and endpoints that span the lab and field to understand how Pacific salmon

complete (or attempt to complete) their complicated life history. Indeed, among all animal taxa, some of the most impressive and clear stories (see Madliger et al. 2016) related to conservation physiology exist among Pacific salmon (e.g., Cooke et al. 2012). Therefore, we are much closer to understanding when, where, and why a Pacific salmon dies during its river migration.

Here we use a case study approach to explore how our collective work on Pacific salmon migration biology has advanced our understanding of Pacific salmon biology and in doing so generated policy- and management-relevant science. Our approach involves providing an overview of how eight specific scientific impacts of environmental/ anthropogenic stress have been informed by multiple measures of physiology to generate new knowledge that has been used by practitioners and policy makers for conservation gains. Our story is unique in that it is long term and we have previously synthesized some of our findings (e.g. Cooke et al. 2012; Hinch et al. 2012; Patterson et al. 2016). Rather than focusing solely on the biological science, we have included both social scientists and practitioners on our team. We consider how the diverse contemporary tools available to the practising conservation physiologist can be applied more broadly to other taxa. The tools that underpin the examples presented here both serve to advance the field and constrain what is possible. This juxtaposition represents the frontier of animal biology and is where major investments are needed.

## 3.2 Elevated temperatures can kill salmon

### 3.2.1 The science

For over half a century, researchers have explored the role of water temperature on the biology of adult Pacific salmon (e.g. seminal work by Rolly Brett). Early work focused on swimming performance and respiratory aspects of energetics (Brett 1971, 1973). Over the decades that work has expanded to include extensive lab and field studies that range from understanding the effects of water temperature (especially warming temperatures) on



**Figure 3.1** Research focused on wild Pacific salmon engaged in upstream migration inherently requires consideration of behaviour and physiology while combining research from the lab and the field. A core component of such work is biotelemetry (1A), which for upstream migrating Pacific salmon often means the gastric implantation of a telemetry transmitter to enable the tracking of behaviour and fate. Photo credit: S. Cooke. Another key tool is non-lethal biopsy (1B) of various tissues (e.g. gill, muscle, blood), which can be done on fish that are tagged with telemetry transmitters. Photo credit: S. Cooke.

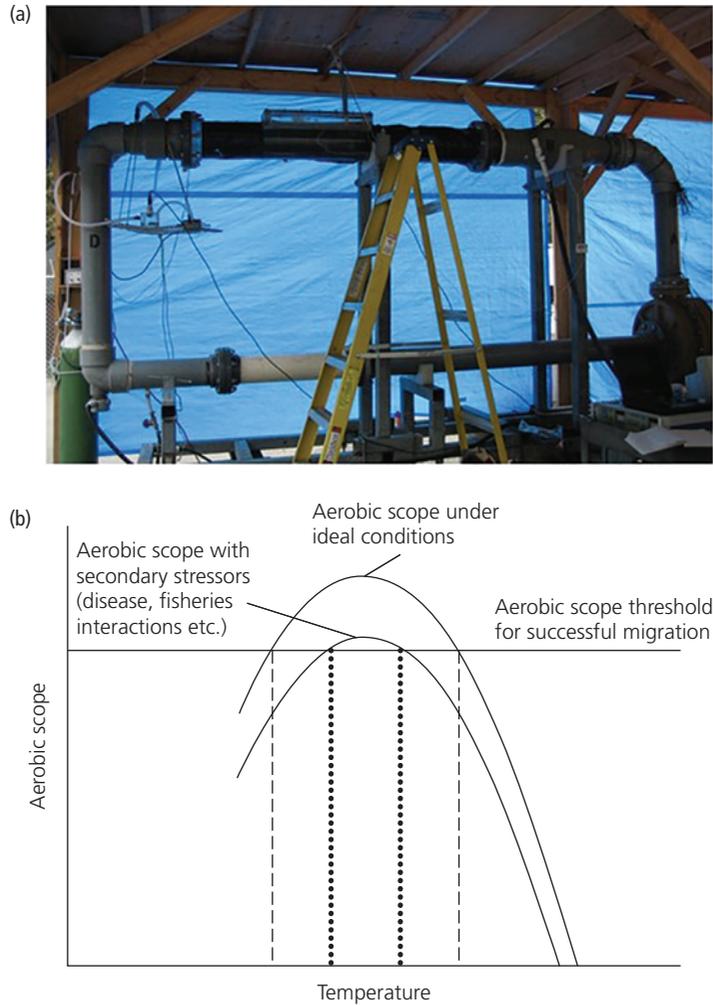
gene expression (Jeffries et al. 2012a, b, 2014a, b; Akbarzadeh et al. 2018), field energetics (Rand et al. 2006), and fate (i.e. whether it survives to spawn or dies prematurely; Farrell et al. 2008; Martins et al. 2012a, b).

One of the core messages with that collective body of work is that elevated water temperatures can kill salmon. Furthermore, that acute (*sensu* Hinch et al. 2012) warm water can lead to exceptionally high levels of salmon mortality when they are faced with challenges of upstream migration even at temperatures well below the upper lethal limits for the species (Servizi and Jensen 1977). Yet, the mechanisms by which hot water kills salmon are diverse. For example, detailed swimming per-

formance studies have suggested that aerobic scope (see Figure 3.2) collapses at high temperatures (which are stock specific; Farrell et al. 2008; Eliason et al. 2011), presumably underpinned by constraints on cardiac function (Eliason et al. 2013a, b). Indeed, maximum heart rate in non-salmonid fish is typically reached below the upper acute lethal limits (Farrell 2016). These laboratory studies (e.g. Eliason et al. 2011, 2013a, b) align well with field-observed patterns of mortality using telemetry across a range of upriver migration temperatures (e.g. Farrell et al. 2008).

Another mechanism associated with mortality can be additional energy depletion at elevated water temperatures. In warm years, it is possible for fish, which have ceased feeding before entering the river, to run out of energy due to enhanced costs of swimming, brought about by an increase in standard metabolic rate amplifying the overall cost of swimming, rather than an increase in net cost of swimming (Brett 1995). Consequently, a migration delay in warmer water as fish hold waiting for preferable migration conditions (Cooke et al. 2004) will burn up valuable energy stores at a faster rate without the fish moving upstream. Hinch et al. (2005) proposed that sockeye salmon need an energy density of at least 4 MJ/kg when they reach the spawning area to successfully spawn. With rising water temperatures in the Fraser basin, it is anticipated that fish will deplete energy resources more quickly and thus we anticipate seeing more instances of condition-dependent pre-spawn mortality (Martins et al. 2012a).

What is particularly valuable about this overall body of work is that it spans lab, field, and modelling realms, and combines observational (including comparative physiology and genomics) and experimental approaches. In particular, the experimental approaches have helped to establish causation. For example, Crossin et al. (2008) captured upriver migrating sockeye, held them in the lab at two temperatures (an optimal temperature and a super-optimal temperature) for several weeks; then released them back into the wild to complete their migration. Such studies linked laboratory findings to field-relevant patterns of mortality and definitively show that hot water kills upriver migrating salmon.



**Figure 3.2** To simulate strenuous swimming conditions experienced during migration, laboratory swim flume studies (2A) can be used to assess swimming performance and cardio-respiratory physiology. Photo credit: S. Cooke. Aerobic scope curves (2B) 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) compared with under ideal conditions (dashed lines).

### 3.2.2 The conservation implications

In the Fraser River, peak summer water temperatures have been steadily rising by an average  $\sim 0.5^{\circ}\text{C}$  over the past half of each century (Morrison et al. 2002). Because Pacific salmon are locally adapted, even slight increases in water temperature can push

fish from their optimal temperatures to those where aerobic scope is constrained, which could alter migration success (Hague et al. 2011; Farrell 2016), not to mention alterations in pathogen exposure and pathogenicity (Miller et al. 2014). Because of the manifold effects of water temperature on fish along with these specific examples for upriver migrating

Pacific salmon, managers have accepted that hot water kills salmon (although admittedly it took some time; Cooke et al. 2012). This knowledge has translated to changes in the management adjustment model—a model that is used by fisheries managers to determine the levels of catch that can be permitted in the face of predicted en route loss associated with adverse environmental conditions to achieve the desired level of spawning escapements (i.e. the number of fish that reach spawning grounds; Macdonald et al. 2010; Patterson et al. 2016).

### 3.3 Intraspecific variation is the norm

#### 3.3.1 The science

Pacific salmon, and especially sockeye salmon, return faithfully to their natal areas to reproduce, resulting in hundreds of reproductively isolated populations across a diverse range of environments (Groot and Margolis 1991). Morphological, physiological, behavioural, and life history traits vary extensively among populations and much of this diversity is a result of local adaptation (Taylor 1991; Crossin et al. 2004; Fraser et al. 2011; Eliason et al. 2013a, b). For example, considerable research has focused on the adult upriver spawning migration, where populations can encounter highly variable migratory conditions depending on when and where they spawn (e.g. varying in temperature, flow, distance travelled, elevation). Fraser River sockeye salmon populations with more difficult migrations (e.g. longer distances, greater elevation gains) start their migration with more somatic energy, have a more streamlined body shape, fewer eggs, larger hearts with more compact myocardium and its associated coronary circulation, and greater cardiac sarco(endo)plasmic reticulum  $\text{Ca}^{2+}$ -ATPase activity (which means  $\text{Ca}^{2+}$  can cycle faster to increase heart rate). They also have higher aerobic capacity, greater cardiac performance, and enhanced swimming performance compared with populations with shorter, easier migrations (Lee et al. 2003a, b; Crossin et al. 2004; Eliason et al. 2011; Eliason et al. 2013; Anttila et al. 2019). Taken together, variation in how challenging the upriver migration is has

selected for specific morphological and physiological traits that enable an energetically conservative yet high-performance athletic phenotype.

Thermal biology also varies across populations. The optimal range of temperatures for aerobic scope (thermal dependence curve) generally corresponds to the typical range of temperatures encountered for adult Fraser River sockeye salmon (Lee et al. 2003a, b; Farrell et al. 2008; Eliason et al. 2011). Similarly, a warm-temperature migrating population of chum salmon (*Oncorhynchus keta*) in Japan had a thermal dependence curve for aerobic scope shifted 3°C higher compared with a cool-temperature migrating population (Abe et al., 2019). In contrast, the thermal performance (i.e. swimming) of two coastal populations of adult autumn-migrating Coho salmon (*Oncorhynchus kisutch*) displayed divergent patterns, matching historical conditions in one case (Lee et al. 2003a, b) and extending above historical temperatures in another case (Raby et al. 2016). Thermal tolerance also varies across populations at other life stages. Egg thermal tolerance differed substantially for nine Fraser River sockeye salmon populations reared in a common garden experiment at three temperatures (Whitney et al. 2013). The emergent juveniles showed population-specific differences in their upper acute lethal limits, but this difference may have been a result of thermal plasticity or the juveniles emerging at different body size (caused presumably by differences in egg size among populations) because these population differences disappeared when test were performed at a common body mass of ~1 g (Chen et al. 2013). Importantly, these studies reveal that thermal tolerance is a flexible trait and is constrained at different life stages.

Finally, over the past decade or so, our team has identified an alarming trend where adult female salmon have elevated mortality compared with males, especially when exposed to secondary stressors (e.g. Roscoe et al. 2011; Jeffries et al. 2012a, b; Martins et al. 2012a, b). This trend is consistent across both field studies (e.g. tagging studies and passage studies through dammed watersheds; Roscoe et al. 2011; Martins et al. 2012a, b) and lab studies (e.g. experimental holding studies while exposing fish to various temperature regimes; Jeffries et al. 2012a, b). However, the physiological

mechanisms driving these sex-specific differences in mortality are currently unknown.

### 3.3.2 The conservation implications

Managers and stakeholders cannot assume Pacific salmon species, populations, or sexes will respond similarly to environmental stressors. Pacific salmon display huge variability in traits, largely as a result of local adaptation (Taylor 1991; Fraser et al. 2011). This trait variability makes fish differentially susceptible to natural and anthropogenic perturbations (Martins et al. 2011, 2012a, b; Eliason et al. 2011; Donaldson et al. 2014). Greater population diversity has been shown to buffer against the impact of climate variability and change (Anderson et al. 2015), so preserving genetic diversity and a broad range of thermal tolerances is critical to support a robust metapopulation. Given that female salmon govern the fecundity of a reproducing population, a differential elevation in adult female mortality is a serious concern. Despite recent work in this area, the underlying mechanisms of this phenomenon still need identifying so effective mitigation can occur.

## 3.4 Stressors rarely act alone

### 3.4.1 The science

Bringing wild large-bodied fish into a laboratory to conduct controlled studies is challenging. Yet, this approach already has extensively characterized the responses of Pacific salmon to relevant environmental stressors (e.g. Wagner et al. 2005; Crossin et al. 2008; Clark et al. 2011; Eliason et al. 2011; Jeffries et al. 2012a). Like most lab studies they typically study one specific stressor at a time, whereas the reality in nature is that fish face multiple, simultaneous environmental stressors (Figure 3.3). Therefore, interactions among stressors can make interpretations of performance (e.g. migration success, fitness) difficult (Johnson et al. 2012). For example, an adult salmon moving from the saltwater to freshwater in summer face dramatic and simultaneous changes in their water temperature and salinity. In addition, fish become exposed

to freshwater-specific pathogens (e.g. Tierney and Farrell 2004; Wagner et al. 2005; Bradford et al. 2010). Furthermore, pre-existing pathogen infections can potentially influence the response to traumatic handling stress related to fisheries (Teffer et al. 2018). Therefore, the cumulative impact on wild fish populations of pathogens and abiotic stressors is likely pervasive but poorly understood.

One possible way to tease apart the types of stressors that a salmon is responding to is to develop molecular biomarkers (i.e. gene expression) of a response to a certain type of stressor (Akbarzadeh et al. 2018; Houde et al. 2018a, b; Miller et al. 2017), including an immune response to a range of pathogens (Miller et al. 2014; Jeffries et al. 2014b). This approach is challenged, however, by the fact that individual genes often respond to multiple stressors (e.g. certain heat shock proteins) as part of a generalized stress response (Feder and Hofmann 1999; Kultz 2005). As a result, directly linking a shift in expression of a single biomarker to a specific stress response and/or to a performance- or fitness-level consequence may not always be possible. A new approach to stressor prediction developed by our team relies on the resolution of panels of biomarkers that, when co-expressed, are indicative of individual stressors. For example, temperature holding studies that utilized transcriptome-wide screening approaches across multiple salmon



**Figure 3.3** Visualization of the multiple stressors that often act together to influence the fate of migratory Pacific salmon. Photo credit: S. Cooke.

species (Jeffries et al. 2012b, 2014a; Tomalty et al. 2015) were mined for the development of biomarkers for thermal stress response in Pacific salmon (Akbarzadeh et al. 2018). The activity and specificity of this, and other panels of biomarkers activated in gill tissue, were then validated in a multi-stressor challenge study (Houde et al. 2018a), which not only resolved the most robust panels of biomarkers capable of identifying individual stressors, but also revealed biomarkers within those panels that were predictive of ensuing mortality. Simultaneous assessments of multiple biomarker panels are enabled through use of high-throughput microfluidics quantitative (q)PCR techniques. Host biomarker panels can be combined with assays for a range of pathogens (e.g. Miller et al. 2014; Jeffries et al. 2014b) to characterize the interplay between stress and infectious disease development. Overall, we anticipate that this approach will bridge the gap in our understanding of cumulative stressor/disease impacts from the laboratory to the field.

### 3.4.2 The conservation implications

Establishing approaches to tease apart responses to multiple stressors will aid in our ability to prioritize efforts to minimize the effects of certain stressors on Pacific salmon. Some stressors may be beyond our control (i.e. natural pathogen communities; but for an example of experimental surface flushing flows where extra water is released to reduce *Ceratonova shasta* concentrations in the river and address disease concerns, see Voss et al., 2018), however regulating activities that can exacerbate the effects of other stressors (i.e. fisheries encounters, industrialization) is one potential strategy. Additionally, the lower reaches and estuaries of major salmon-producing rivers (e.g. Fraser River, Columbia River, Sacramento River) often have an accumulation of municipal, industrial, and agricultural contaminants that can interact with other abiotic stressors affecting fish in a system. Contaminants in aquatic systems generally occur in mixtures and the direct and indirect effects on anadromous fishes are often complex (Laetz et al. 2008; Tierney et al. 2008). Understanding how adaptive responses to natural stressors and homing during migrations are impacted

by chemical contaminants will be a challenge for salmon researchers in the future (Ross et al. 2013).

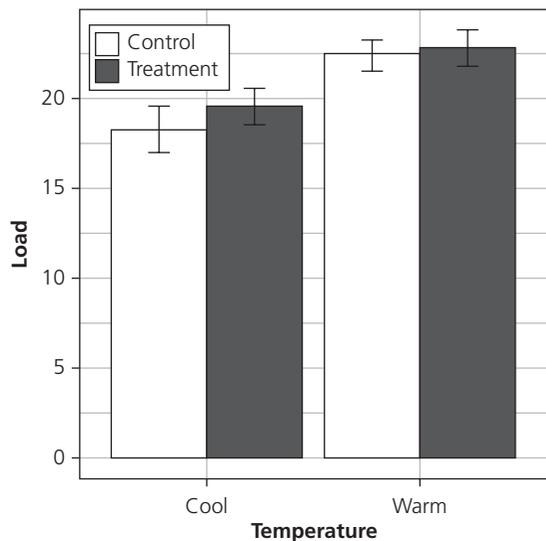
## 3.5 A range of indices associated with compromised health can predict migration fate

### 3.5.1 The science

Stress and health biomarkers can be linked to migration failure of Pacific salmon at both the outbound juvenile (Olivier 2002; Tucker et al. 2016) and the inbound adult life stages (Young et al. 2006; Miller et al. 2011; Cooke et al. 2012; Hinch et al. 2012). These indices can be measured at molecular, cellular, sub-organismal, and whole-animal levels. Evaluations that comprise responses at multiple levels (e.g. genomic, metabolic, behavioural, disease-associated) provide a comprehensive assessment of the mechanisms of migration failure. Our understanding of how fish health impacts migration capacity has benefited from the use of physiological indices, such as hormone and metabolite levels in blood (Barton 2002; Cook et al. 2014), and molecular biomarkers described in previous sections (e.g. thermal and osmotic stress), as well as those relating to host immunity (Miller et al. 2017) and pathogen presence (Miller et al. 2014, 2017). Genomic tools for assessing wild salmon health are quickly becoming an invaluable method for detecting and describing infectious agents in wild salmon populations (Miller et al. 2014; Bass et al. 2017; Figure 3.4) because of the advent of high-throughput methods. Molecular approaches have also been used to evaluate pathogen impacts on health, longevity, and migration success of wild salmon, often within the context of environmental or fisheries stressors (Jeffries et al. 2014a, b; Teffer et al. 2017, 2018; Bass et al. 2019).

Infectious disease processes are increasingly being investigated as mechanisms of migration failure and mortality of wild salmon at both juvenile (Jeffries et al. 2014a, b; Miller et al. 2014) and adult life stages (Miller et al. 2011; Teffer et al. 2018; Bass et al. 2019). For juvenile salmon, indices that identify abnormal physiological processes involved in smoltification (i.e. osmoregulatory and immunological shifts from fresh- to saltwater) or starvation

in the marine environment can be used to predict migration failure as fish fail to meet the energetic demands of seaward migration (Maule et al. 1987; Groot and Margolis 1991; Houde et al. 2019). Physiological or disease-associated impairment during this critical life stage may also enhance predation risk, which is a major factor influencing juvenile survival and population productivity (Miller et al. 2014; Furey 2016; Tucker et al. 2016). During the adult spawning migration, tremendous physiological and metabolic changes comprise osmoregulatory, reproductive, and immunological components (Shrimpton et al. 2005; Miller et al. 2009; Dolan et al. 2016). Deviations from these trajectories may not only impact migratory fate, but also reproductive potential and survival (Cooperman et al. 2010; Evans et al. 2011; Jeffries et al. 2011; Miller et al. 2011; Teffer et al. 2017). Molecular and metabolic indices that identify physiological impairment due to injury, osmotic imbalance, or aerobic collapse



**Figure 3.4** Loads of *Parvicapsula minibicornis* in the gills of adult Coho salmon from the Chilliwack River, British Columbia, Canada. Samples were taken after fish were held for 1 week at cool (10°C) or warm (15°C) temperature and a subset of fish from each temperature group received a simulated bycatch release treatment (gill net entanglement and air exposure). Loads were derived using qPCR and then subtracting the quantification cycle from 40 (maximum). Data from Teffer et al. (2019).

are predictive of migration failure and often found in association with migratory stressors like high temperature or fishery interactions (Eliason et al. 2013a, b; Donaldson et al. 2014; Raby et al., 2014, 2015a, b; Bass et al. 2018). Like all organisms, Pacific salmon respond to their environment and exhibit an array of indices that can predict migration fate.

### 3.5.2 The conservation implications

As we learn more about genomic and physiological responses of wild salmon to environmental stressors and become better equipped to measure molecular biomarkers in large numbers of fish in the wild, we can combine this information with environmental parameters to inform management decisions that regulate human activities (e.g. land use, fisheries). If wild migrating fish are found to be exhibiting a particular response (e.g. thermal or osmotic stress), management actions can be taken towards short-term (e.g. reduce additional stressors like fisheries) and long-term solutions (e.g. improve habitat quality, river temperature regulation at dams). Great strides have been made in comprehending the molecular signatures of thermal stress (Akbarzadeh et al. 2018), osmotic impairment (Houde et al. 2018b), and viral disease development (Miller et al. 2017), which can be used to derive physiological and disease-associated biomarkers for reduced survival and reproductive success of wild salmon. Incorporating molecular biomarker data and other indices of unhealthy fish from in-season sampling into population dynamics models may improve the precision of productivity estimates under different ecological conditions.

## 3.6 Simple reflex indicators can be used to refine fishing practices

### 3.6.1 The science

RAMP (Reflex Action Mortality Predictors), first pioneered in the laboratory (Davis 2005, 2007; Davis and Ottmar 2006), is a simple technique for assessing

the vitality of a captured fish (Davis 2010). A RAMP assessment typically incorporates five or more reflexes consistently exhibited when a fish is vigorous and healthy. These reflexes, however, progressively disappear in fish that are exhausted, in poor condition, or moribund (Davis 2010; Raby et al. 2012). RAMP assessments are rapid, taking just 10–20 s per fish; the RAMP score is the proportion of reflexes that were absent (impaired; Davis 2007) and so higher RAMP scores indicate low vitality and a higher probability of delayed mortality. Although aspects reflexes are behavioural, the mechanisms underpinning reflexes are entirely physiological. The original promise of RAMP for field application was an objective, inexpensive, and rapid predictor of mortality.

We adapted RAMP for Pacific salmon assessment in the wild (Raby et al. 2012). Our motivation for doing so was to evaluate whether RAMP could be applied across Pacific salmon fisheries, many of which release non-target salmon species, to rapidly generate estimates of post-release mortality in fish discards (bycatch released overboard; Davis 2010). Five reflexes were scored, such as whether the fish responded to having its caudal fin held ('tail grab') and whether it righted itself when turned upside-down in the water ('orientation'). Given the ease of performing RAMP assessments, they were used in many studies examining post-release mortality in simulated adult salmon fisheries (Donaldson et al. 2012; Raby et al. 2012, 2013, 2014, 2015a, b; Robinson et al. 2013; Gale et al. 2014; Nguyen et al. 2014; Cook et al. 2018, 2019). Collectively, our work showed that RAMP responds well to variation in the severity of stressors like handling and air exposure that cause exhaustion (e.g. Raby et al. 2013; Nguyen et al. 2014) and therefore is a useful indicator of adult salmon vitality (Figure 3.5). RAMP is a powerful assessment tool because it conceivably integrates individual fish stress, independent of a prior condition or a stress imposed during the actual fishery encounter (e.g. its position within a crowded net; Raby et al. 2014, or its unique responsiveness to stress; Cook et al. 2014).

In some situations, RAMP predicted a fish's likelihood of surviving after release (Raby et al. 2014), but not all situations had clear relationships between stressor severity and rates of mortality (Donaldson et al. 2012; Raby et al. 2013; Robinson et al. 2013),

especially ones where injury was a major contributor to survival probability (Donaldson et al. 2012; Nguyen et al. 2014). Therefore, in fisheries where visible injuries are common, injury metrics should be integrated with RAMP into vitality assessments (Raby et al. 2015a; Uhlmann et al. 2016; Meeremans et al. 2017; Cook et al. 2018, 2019). Importantly, in addition to repeatedly showing that RAMP is sensitive to differences in fishing techniques, RAMP is effective at reflecting underlying physiological disturbances based on established, but much harder to determine, indices of exhaustion based on blood samples (e.g. lactate build-up, disturbance to ion concentrations; Raby et al. 2013, 2015a; Cook et al. 2019, and see McArley and Herbert 2014).

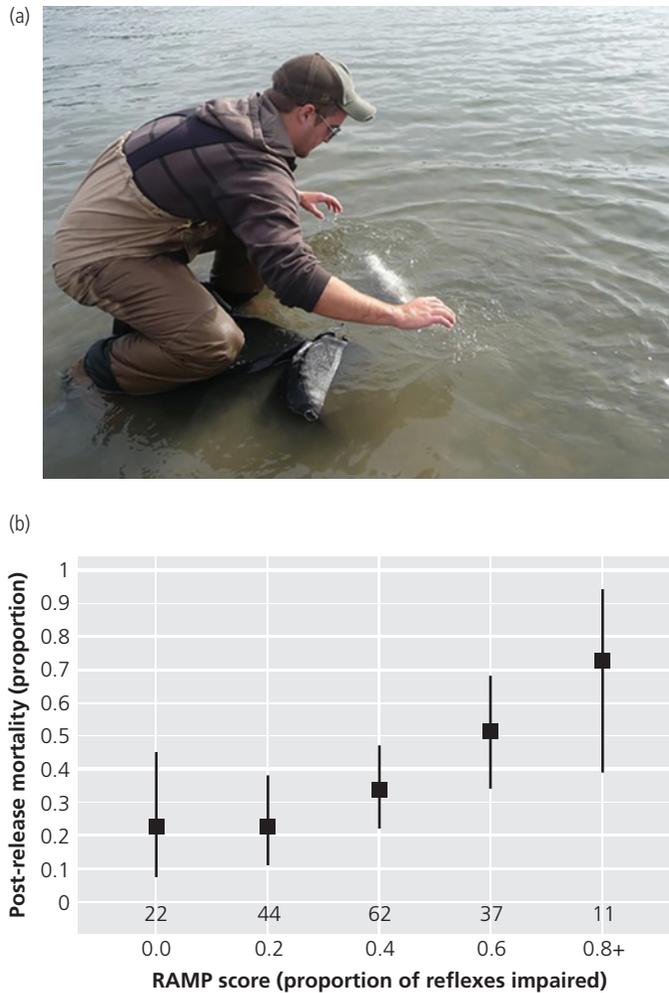
### 3.6.2 The conservation implications

Some of our recommendations for fish handling have passed on to the fishers by fisheries managers (Raby et al. 2014) with the intention of RAMP becoming an integral part of a 'rapid assessment' of the survival probability whenever a salmon was released from a specific fishery (Patterson et al. 2017a, b). In British Columbia alone, there are over 100 such fisheries with different combinations of fishing gear, species, location, and environmental conditions. Some existing fisheries observer programmes are already using vitality assessments on discarded bycatch (e.g. Benoît et al. 2012) and were incorporated (more crudely as a ranking scale) in earlier Pacific salmon bycatch research (e.g. Farrell et al. 2001a, b). Clearly, using RAMP moves these types of vitality evaluations to a new and more objective level and provides the research community with a cheap and simple biomarker of complex underlying processes that are often difficult to measure. Although more RAMP work has been done on Pacific salmon than any other fish species, the technique is being employed across a diverse range of freshwater and marine fish and even other taxa (e.g. turtles).

## 3.7 Facilitated recovery of exhausted salmon is context-dependent

### 3.7.1 The science

When Pacific salmon encounter various fishing gears (rod and reel, seine net, gill net) a component



**Figure 3.5** Reflex Action Mortality Predictors (RAMP) are obtained from fish to assess vitality. One of the more important and responsive indicators is the righting response (5A) where fish are turned upside-down to determine if they can right themselves within 3 s. Photo credit: V. Nguyen. (5B) Post-release mortality increases with increasing levels of reflex impairment (RAMP score) for adult Coho salmon released from a beach seine fishery in the Fraser River. Sample sizes for each level of RAMP score are given along the bottom of the figure. Symbols represent observed level of mortality (failure of telemetry tagged fish to reach terminal radio telemetry receivers near spawning areas), while error bars indicate 95 per cent confidence intervals calculated using the Clopper–Pearson Exact Method. The RAMP assessment upon which was the score (x-axis) was based is described in detail by Raby et al. (2012). Figure created using data for Raby et al. (2014), which are publicly archived alongside the paper.

of the catch is often released to comply with regulations or because of voluntary conservation ethic. The condition of live fish following capture varies greatly from extremely vigorous to moribund. Because fishing and associated handling (including air exposure) induce physiological disturbances (e.g. depletion of tissue energy stores, elevation

of metabolic rate, accumulation of metabolic by-products), fish that are to be released may be exhausted. This state of exhaustion can lead directly to mortality or do so indirectly whereby exhausted fish are susceptible to post-release predation, displacement (e.g. being washed downstream), or simply holding until suitably recovered to continue the

migration. We have conducted experiments in the lab and field using tools such as blood and muscle physiology, RAMP (as described above), biotelemetry, and even swimming studies to determine if it is possible to facilitate recovery of exhausted fish.

Early work in the marine environment revealed that it was possible to take adult Coho salmon that were fully exhausted (i.e. unable to maintain equilibrium) after capture by gill net or trolling; by holding them in a 'fish-sized' compartment with a jet that forced water towards the mouth of the fish, most individuals would be vigorous within 15 min after recovering their physiological status (as assessed by blood and muscle biochemistry; Farrell et al. 2001a, b). Even fish classed as 'moribund' were revived and, after an overnight recovery in a net pen, performed a swim test just as well as fish classed as 'vigorous' at the time of capture. Indeed, the short-term mortality rate on incidentally caught Coho salmon could be reduced to as little as 6 per cent with the use of the recovery box, modified gear, short net soak times, and careful handling of fish on removal from the gill net, compared with the more typical Coho mortality rate of 35–70 per cent associated with gillnetting (Buchanan et al. 2002).

Because of the apparent success of this method of facilitated recovery in the marine migration phase (assessed using blood and muscle biochemistry; Farrell et al. 2001a, b), we have also tested the value of using a recovery box during the upriver migration phase, while recognizing the impracticality of using such a box designed for a large vessel with shore-based fishers or small vessels. The recovery of migratory adult fish was certainly facilitated with the recovery box, but it did not translate to higher levels of post-release survival assessed with biotelemetry, likely because dermal injuries enable opportunistic pathogens to take hold in freshwater more so than seawater (Nguyen et al. 2013). Further tests with portable and inexpensive fish holding bags that were more suited to river fishing came to a similar conclusion (Donaldson et al. 2013; Raby et al. 2014); short-term holding suppressed the cortisol stress response, but unless the salmon was completely exhausted, there was little benefit in terms of post-release survival (Donaldson et al. 2013). Lastly, efforts to facilitate recovery by hand

(just by holding fish into the flow) also seemed to generate minimal benefits except for the most exhausted individuals (Robinson et al. 2013, 2015).

### 3.7.2 The conservation implications

We concluded that it is best to immediately release a salmon if it is not completely exhausted, able to maintain equilibrium, and not severely injured; facilitated recovery benefited salmon in the very worst condition, that is, unable to maintain equilibrium. Of course, RAMP is a type of vitality assessment that can distinguish whether a salmon is fully exhausted. This simple tool can be used by fishers to triage captured fish that must be released to comply with harvest regulations.

## 3.8 The smell has to be the right one to get home

### 3.8.1 The science

Pacific salmon rely on their highly developed sense of smell (olfaction) to locate their natal streams during the spawning migration. Early research found that salmon imprint on the odour of their natal water as juveniles and are progressively guided by those imprinted cues as adults get closer to the natal stream using their sensory physiology apparatus (Hasler and Scholz 1983). Yet, water resource developments such as dams can alter the odour cues if they involve altering the relative contribution of different water sources to flow. Imprinting occurs during the juvenile parr-smolt transformation stage (Dittman and Quinn 1996), although recent studies indicate it may even occur prior to this life stage (Bett et al. 2016; Havey et al. 2017). Regardless of the timing, successful migration is nonetheless reliant on detection of imprinted cues, which can be difficult for returning salmon to detect if the natural movement or composition of water in their natal system is disrupted. For example, recent work in a regulated watershed in British Columbia, Canada found that an altered water flow pattern and composition associated with a power-generating station caused confusion and a migration delay in adult sockeye salmon (Middleton et al. 2018). In this sys-

tem, natal water is partially diverted from the migratory route for power generation, and the remaining natal water is diluted with make-up water from another watershed. In these systems we have used biotelemetry and controlled behavioural choice experiments to show that normal hydro-operational procedures that would reduce the amount of dilution appeared to enhance migration speed and migration success through the area (Bett et al. 2018; Drenner et al. 2018).

Olfactory toxicity, or a reduction in olfactory sensitivity following exposure to pollutants, is another concern for salmon homing. Electrophysiological and behavioural studies indicate that chemicals such as pesticides or heavy metals impair a salmonid's ability to detect and respond to olfactory cues (Tierney et al. 2008; Sovová et al. 2014). Urban areas release these and other pollutants into rivers, potentially affecting adult salmon navigation to natal spawning areas. In addition, because the olfactory abilities of juvenile Pacific salmon are adversely affected by the projected increases in freshwater CO<sub>2</sub> (Ou et al. 2015), a similarly negative effect may occur in returning adults. Whether or not pollutants or elevated CO<sub>2</sub> levels encountered along the migratory route also affect pheromone detection is unknown. Pheromones have long been considered to play a role in salmon homing and are now believed to be particularly important directional cues when salmon stray to seek alternate, non-natal spawning habitat (Bett and Hinch 2015).

### 3.8.2 The conservation implications

Navigation problems could be compounded by issues related to dam passage, making careful management of regulated systems a significant concern for salmon populations. Hydroelectric development that best emulates the natural flow patterns along migration routes will limit the negative consequences to salmon navigation. Increased urbanization and rising CO<sub>2</sub> levels could also negatively affect navigation, although restrictions on industrial effluents, agricultural runoff, or other sources of pollution could mitigate these effects. More research that integrates field observations (via telemetry) with behavioural and physiological

experiments will be needed to determine the extent to which these factors can affect olfactory ability, and as a consequence navigation and migration success.

## 3.9 Not too much, not too little

### 3.9.1 The science

Burst swimming (i.e. when fish swim at near maximal speeds using white muscle fibres that are fuelled by anaerobic metabolism) is used by fish to negotiate and pass through areas of high water flow. Swimming anaerobically cannot be sustained indefinitely and requires oxygen uptake elevated for a substantial period post-exercise (known as excess post-exercise oxygen consumption, or EPOC; Lee et al. 2003a, b). If a fish has fatigued, the time to recovery from EPOC is up to 4 h (Brett 1973; Milligan 1996). But if a fish is exhausted and no longer able to maintain a righting reflex, recovery is much longer (12–15 h to recovery from EPOC; Zhang et al. 2018) to re-establish metabolic homeostasis. Thus, anaerobic swimming, if excessive, has the potential to influence subsequent behaviour, survival, and spawning success of salmon.

Salmon are often exposed to high water flows in dam tailraces (i.e. area downstream of dams). Yet, the potential for carryover effects (i.e. when an individual's previous history and experience explain their current performance; O'Connor et al. 2014) associated with dam passage is generally underappreciated and overlooked by researchers and natural resource managers because few studies have made a direct link between an individual's experience during dam passage and their ability to fulfil other life history requirements. Recent research on sockeye salmon passage at Seton Dam in British Columbia, Canada found reduced survival to spawning grounds following dam passage (Roscoe et al. 2011). Burnett et al. (2014) aimed to understand the mechanism(s) underlying poor post-passage survival, with a focus on characterizing high-flow-induced burst swimming. Using acoustic accelerometer transmitters to estimate swimming speed and oxygen consumption, Burnett et al. (2014) identified a trade-off where sockeye salmon required burst swimming to successfully

pass through fishway attraction flows, but this behaviour had significant consequences for survival to spawning grounds. Individuals that spent more time swimming anaerobically were less likely to reach spawning grounds, perhaps because they became fatigued or, worse still, exhausted, which resulted in a greater and more prolonged EPOC (Lee et al. 2003a, b; Zhang et al. 2018). With an understanding of the physiological mechanism of reduced survival, Burnett et al. (2017) conducted a large-scale management experiment of fishway attraction flows to maximize dam passage and survival to spawning grounds. Fish tagged with acoustic accelerometer transmitters and Passive Integrated Transponder (PIT) tags were released and tracked to spawning grounds under two flow conditions: (1) a baseline condition that has been used by managers since the 1950s; and (2) an alternative condition that attempted to reduce the exposure of fish to high flows during their approach to the fishway entrance. Fish exposed to alternative flow conditions required significantly more time to pass Seton Dam but showed improved survival to spawning grounds—a finding that scaled up from individual tagged fish to the population level. Ultimately, the benefits of reducing high flows to improve survival to spawning grounds outweighed the costs associated with increased passage time.

### 3.9.2 The conservation implications

Taken together, this research has pointed to a less impactful, cost-effective flow management strategy that maximizes the survival of sockeye salmon to spawning grounds without impacting power production and downstream flow requirements. Fishway attraction flows at Seton Dam are operated in a manner consistent with facilities worldwide, where attraction flows are released directly adjacent to the fishway entrance. Dams are ideal model systems for testing management options in the field (Memmott et al. 2010) through large-scale experiments (Walters and Holling 1990), highlighting that there are opportunities elsewhere to understand and minimize the effects of dams and dam operations on aquatic animals. Research of this nature highlights the value of integrating applied ecological research and adaptive management to

provide natural resource managers and conservation practitioners with the information required to make responsible environmental management decisions.

### 3.10 Reflections on physiology in practice

The above examples of applied conservation physiology research have improved our scientific understanding of how environmental stressors mechanistically impact salmonid performance and fitness. As a result, the incorporation of physiology has helped to reduce uncertainty in the scientific advice presented to managers on a broad range of topics related to Pacific salmon migration. However, researchers simply presenting a better mechanistic understanding of salmon physiology in relation to individual fish survival does not automatically translate into management actions directed primarily at the population level. Working with managers for over 20 years has afforded our group with the opportunity to reflect on both reasons for success and failure in management effectively using science information in their decision-making processes (Hinch et al. 2012; Patterson et al. 2016). The main reasons for failing to adopt scientific advice include scientific uncertainty, science management integration, and institutional resistance of management agencies.

The lack of adoption of science information by management can result from uncertainty in scientific results, especially results that either appear contradictory or challenge current beliefs. For example, the lack of universal benefit to facilitated recovery has likely delayed clear management responses. Results that challenge the current management paradigm and/or have a high cost to implement make the adoption of the advice more difficult and increase the scrutiny of the uncertainty in the results. One of the key successes of the research at Seton Dam was that the changes in flow regime were cost-neutral. In contrast, the initial attempts to reduce salmon harvest levels based on forecasts of salmon exposure to prolonged high water temperatures were met with scepticism and resistance, even though there was good physiological research on temperature impacts and robust

correlational models between high temperature, freshwater residence, and in-river mortality (Macdonald et al. 2010). One of the main advantages of using physiologically based mechanisms to predict survival is the ability to generate consistent results over time (Horodysky et al. 2015), unlike many other studies that simply link environmental covariates to fish survival, which break down over time (Myers 1998). More recently, management has accepted the results from the environment-based correlation models, in large part due to the model not breaking down since it was first proposed 20 years ago! In the interim, we continued to add physiological research support of a problem we believed in. Challenges still remain in communicating uncertainty, especially for the challenging multiple stressor work, but these can be overcome with better integration with management.

Science working in isolation of management, as well as being detached from the groups that are potentially affected by the results, can create impediments to use of science information. For example, our work to research and understand sex-specific differences in adult survival was done in isolation from management. This isolation was primarily because initially we did not expect sex-specific differences, but began to notice the difference when we tried to match the numbers of males and females in our experimental designs. Neither did management expect the differences that emerged. As such, there is no current mechanism within the management structure to use the unexpected information; spawning objectives would have to be changed to explicitly consider sex-specific targets. Similarly, failure to integrate/communicate at the beginning of the fisheries interaction work did lead to suspicions and active attempts to discredit the work before results had been generated by some user groups that could be impacted by changes to post-release mortality rates. We have now learnt to share study designs and preliminary results with managers and interested parties during our regular workshops to build awareness, answer questions, communicate uncertainty, and build trust in the work. For example, the innovative work on biomarkers is being shared with relevant branches within Fisheries and Oceans Canada (DFO) to maximize the potential utility of these powerful tools.

Institutional resistance within management organizations is often overlooked when examining the failure to adopt science advice. Resistance can result from the relatively low importance of science in the organization's existing decision-making framework and the lack of organizational support (expertise, workload, and funding) to integrate science. Science, of course, is only one of many factors considered by decision makers, and so science inevitably competes with social factors that also influence the decision process (Rice et al. 2011). Therefore, the best hope to affect positive change is to increase the scientific expertise within the organization. We have been particularly fortunate to work with fisheries management staff who have science backgrounds. Indeed, many of our former graduate students now work for the regulatory agencies. However, while many managers may have the necessary science literacy, a common refrain is that they may not have time to properly evaluate the research due to workload issues; as such the information becomes tabled.

Many funding opportunities in Canada aimed at improving management decisions through better science actually restrict any money going back to the regulator (i.e. government agency). This then restricts participation of both the managers that are responsible for understanding and processing the science information being generated by the funds, and government scientists who can help with interpretation and implementation of the work. Where possible we have tried to include funding for management to deal with extra work associated with working with scientists; this includes funds to help organize and/or reanalyse their own data and participate in workshops. In addition, we have social scientists within our research groups to help understand the successes and failures of science from the perspective of management and different groups affected by the work.

### 3.11 Insights from social science

In parallel to the physiological work, and in order to better understand the potential applications of this research, we have also collaborated with social scientists to develop an interdisciplinary research programme focusing on the socio-ecological dimen-

sion of fisheries governance in the Fraser River. The social-ecological approach sees environmental conditions (biological, physical, and ecosystem) and human actions (perceptions, decisions, and relationships) as intertwined, with each factor deeply affecting the other (Ostrom 2009). Human beings impact the natural environment via their individual and collective actions, and the environment affects humans by providing natural resources and imposing material constraints, as well as by providing cultural symbols and shaping lived experiences (Berkes et al. 2003). Therefore, our social science research programme included in-depth interviews with the fishers (Indigenous and non-Indigenous), the leaders of stakeholder and rights-holder groups, the participants in fisheries co-management, the scientists (inside and outside of government), the regulators, and the policy makers (see Nguyen et al. 2016; Young et al., 2016a, b; 2018).

Findings from the social science research reinforced the often-heard argument that salmon have deep economic and cultural significance in British Columbia (Scarce 2000). The cultural importance of salmon to the province's Indigenous (First Nations) people cannot be overstated: salmon movements and physiology play a key role in the cosmology of many groups and communities in both coastal and inland regions (Harris 2001). Salmon also have deep cultural significance to non-Indigenous stakeholders, and to fisheries managers in government, who are personally committed to the animals and their proper management. The economic and cultural prominence of salmon can, however, complicate the integration of new science—including physiological science—into fisheries governance. The social science research found that stakeholders and government employees alike are reluctant to take risks in salmon management, and modifying the evidence base for decision making is perceived as risky (Young et al. 2013). The high profile of salmon issues in the province means that all participants in fisheries governance feel under the microscope, and believe that a broad consensus on the validity of new knowledge is required prior to adjusting policy. Participants from all backgrounds reported that the complexity of the issue made it difficult to evaluate the veracity of new knowledge

and evidence (Young et al. 2016a, b, 2018). Government employees stressed the importance of having new knowledge vetted by the DFO, in the form of a Canadian Science Advice Secretariat report, before being comfortable using that knowledge. Stakeholders, on the other hand, expressed scepticism about the reductionist or decontextualized knowledge that can result from such reviews. Instead, they often stressed the importance of researchers' personal knowledge and understanding of the Fraser River as key markers of valid knowledge, because researchers who understand the social-ecology of human-salmon interactions are more likely to make responsible recommendations and less likely to be careless in their thinking. This gulf in preferences about the form and format of new knowledge and evidence is a hidden but significant barrier to the uptake of new science into practice.

### 3.12 Conclusions and future directions

Starting in the mid-1990s, a team of academic and government scientists engaged in mission-oriented research focused on understanding the factors that influence migration success in Pacific salmon. Along the way we incorporated diverse expertise, disciplines, and techniques that told us about animal-environment and animal-human interactions. Extensive interaction and collaboration with resource managers through a co-production model ensured that the research was relevant to knowledge users. Nonetheless, challenges remain with respect to incorporation of findings into management. Through collaboration with social scientists and ongoing reflection, we identified barriers to knowledge mobilization and worked actively to overcome them. What is clear is that there was no magic bullet—rather all of the advances in management that occurred as a result of this collective body of research were because of application of multiple tools and approaches (spanning the lab and field and including modelling, observation, and experimentation) in a co-production framework. We adeptly and vigorously incorporated emerging tools and technologies (e.g. genomics, telemetry) into our research programme and more innovations

are certainly on the horizon. Yet, it is not a single tool or study that matters—it is about how the individual tools combine and how the individual studies compound to generate nuanced, comprehensive, and evidence-based knowledge. The single most important advice that we have for others engaged in conservation physiology is to engage in frequent and meaningful collaboration with knowledge users—that is the formula for success in conservation physiology. Specific to Pacific salmon, most of the research on migration biology thus far has focused on sockeye salmon, so there is need for similar research on other species to understand the extent to which the observations presented here represent general phenomena. In addition, there is need for mechanistic research on migration that extends across all life stages—not just the adult migration phase. That type of work is ongoing but it is too early to attempt synthesis.

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