Integrative and Comparative Biology
Integrative and Comparative Biology, volume 55, number 4, pp. 554–576
doi:10.1093/icb/icv088
Society for Integrative and Comparative Biology

SYMPOSIUM

Fishing for Effective Conservation: Context and Biotic Variation are Keys to Understanding the Survival of Pacific Salmon after Catch-and-Release

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From the symposium "Physiology in Changing Landscapes: An Integrative Perspective for Conservation Biology" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2015 at West Palm Beach, Florida.

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Synopsis Acute stressors are commonly experienced by wild animals but their effects on fitness rarely are studied in the natural environment. Billions of fish are captured and released annually around the globe across all fishing sectors (e.g., recreational, commercial, subsistence). Whatever the motivation, release often occurs under the assumption of post-release survival. Yet, capture by fisheries (hereafter "fisheries-capture") is likely the most severe acute stressor experienced in the animal's lifetime, which makes the problem of physiological recovery and survival of relevance to biology and conservation. Indeed, fisheries managers require accurate estimates of mortality to better account for total mortality from fishing, while fishers desire guidance on strategies for reducing mortality and maintaining the welfare of released fish, to maximize current and future opportunities for fishing. In partnership with stakeholders, our team has extensively studied the effects of catch-and-release on Pacific salmon in both marine and freshwater environments, using biotelemetry and physiological assessments in a combined laboratory-based and field-based approach. The emergent theme is that post-release rates of mortality are consistently context-specific and can be affected by a suite of interacting biotic and abiotic factors. The fishing gear used, location of a fishery, water temperature, and handling techniques employed by fishers each can dramatically affect survival of the salmon they release. Variation among individuals, co-migrating populations, and between sexes all seem to play a role in the response of fish to capture and in their subsequent survival, potentially driven by pre-capture pathogen-load, maturation states, and inter-individual variation in responsiveness to stress. Although some of these findings are fascinating from a biological perspective, they all create unresolved challenges for managers. We summarize our findings by highlighting the patterns that have emerged most consistently, and point to areas of uncertainty that require further research.

Introduction

How animals respond to stressors is a core interest in the study of ecology, evolution, and human medicine (Romero 2004; Dantzer et al. 2014; Ellis and Del Guidice 2014). The perception of, and experience imposed by, stressors elicits a complex suite of

Advanced Access publication July 21, 2015

changes known as the "stress response," which involves varied behavioral reactions, activation of the neuro-endocrine stress axis, and secondary physiological changes (for reviews, see Chrousos and Gold 1992; Wendelaar Bonga 1997; Sapolsky et al. 2000). The standard view is that the stress response results in tertiary changes to phenotype that are adaptive in the short term (i.e., resisting or escaping the stressor) but that may become maladaptive if sustained in the form of a chronic stress response (e.g., Barton 2002; Boonstra 2013). However, few attempts have been made to link responses to acute stressors, sometimes referred to as the activation of an "emergency life-history stage" (Wingfield et al. 1998), to tertiary responses and fitness-outcomes, especially in the study of wild animals (Breuner et al. 2008). Although acute stress responses are presumed to be adaptive, there can be substantial inter-individual variation in how animals respond to, and recover from, immediate (perceived) threats to survival (Breuner et al. 2008). Stress responses can differ depending on context (Wingfield et al. 1998; Barton 2002), and the magnitude of the response can affect fitness-related outcomes (Cook et al. 2014).

In their seminal review on the effects of glucocorticoids, Sapolsky et al. (2000) described the prototypical acute stressor as a predatory attack that occurs without warning, elicits injury, and includes 1 h of being stalked and chased—a challenge to survival that generates psychological stress and requires extended exercise, heightened cognitive functioning, and later, the process of repairing injury, and physiological recovery. Capture by fisheries can be as severe as the example described above, and for most animals it would likely be more severe than any acute stressor previously experienced in their lifetime (Davis 2002). Aquatic animals belonging to all major taxa are captured by fisheries. Regardless of the fishing gear used, capture elicits, to varying degrees, strenuous exercise, asphyxiation or exposure to hypoxia, injury, and a neuroendocrine stress response (see reviews by Chopin and Arimoto 1995; Davis 2002; Arlinghaus et al. 2007; Wilson et al. 2014). Individuals that are landed and survive the initial stress will be released if they have no value for the fisher or for conservation reasons—either mandatory or because of ethical considerations (Hall 1996; Arlinghaus et al. 2007).

Globally, billions of fish and other animals experience catch-and-release each year while an unknown number of others encounter, but escape, fishing gear (Cooke and Cowx 2004; Bartholomew and Bohnsack 2005; Kelleher 2005; Davies et al. 2009; Uhlmann and Broadhurst 2015). Despite the good intentions of releasing animals alive, post-release mortality (referred to as "discard mortality" in the bycatch literature) can occur hours or days after an encounter with fishing gear (Coggins et al. 2007), a phenomenon that has long been recognized (Huntsman 1938; Black 1958; Parker and Black 1959). Concerns about sustainability have been associated with high rates of post-release mortality (Coggins et al. 2007; Gilman et al. 2013), which is one of several forms of unaccounted fishing mortality (see Uhlmann and Broadhurst 2015 for a recent review). Correspondingly, a considerable literature has developed, particularly over the past 20 years, focused on estimating rates of post-release mortality in a variety of fisheries (Chopin and Arimoto 1995; Davis 2002; Donaldson et al. 2008), assessing sublethal effects of capture (Cooke et al. 2002; Wilson et al. 2014), and developing fishing methods that reduce bycatch (Kennelly and Broadhurst 2002) and post-release mortality (e.g., Olla et al. 1997; Farrell et al. 2001a; Parker et al. 2003; Broadhurst et al. 2008, 2009; Donaldson et al. 2013; Uhlmann and Broadhurst 2015).

Wild Pacific salmon (*Oncorhynchus* spp.) are useful models for examining the effects of catch-and-release on the physiology and fitness of wild fish. The remarkable characteristics of the spawning migrations of Pacific salmon have long fascinated biologists. Combined with their importance to the ecosystems, economies, and cultures of many countries bordering the Northern Pacific Ocean, this fascination has led to a wealth of knowledge that can be used to assist in interpretation of findings on the effects of acute stressors, such as fisheries-capture. In most studies of post-release mortality the animals are contained in tanks or pens for monitoring, which reduces the challenges of wild environments such as the risk of post-release predation (Raby et al. 2014a; Rogers et al. 2014) and can impose chronic stress from being confined; both processes complicate the interpretation of patterns of mortality (Donaldson et al. 2011; Raby et al. in press). Nevertheless, studies that use confinement to monitor survival are invaluable for detailed assessments of mechanisms leading to mortality (e.g., Wood et al. 1983; Jeffries et al. 2011; Raby et al. in press). Biotelemetry (the remote monitoring of animals released to the wild with transmitters), which has been proposed as the optimal alternative to confinement as a means of assessing mortality (Donaldson et al. 2008), has its own challenges, including (1) the poorly understood effects of the transmitter on the animal, (2) the need to surgically-implant or externally-attach transmitters that could add further stress and injury and bias mortality rates, (3) difficulties in assessing fate and survival based on data on the fish's movement, and (4) issues with insufficient area coverage by receivers or transmitter detection efficiency (Donaldson et al. 2014a). In the case of Pacific salmon, biotelemetry can be used to monitor post-release survival in ways that can minimize these limitations. Salmon cease feeding in the coastal ocean prior to their migration upstream through rivers and consequently their stomachs atrophy, which makes gastric insertion of telemetry transmitters an option for tracking individuals to their spawning areas (Ramstad and Woody 2003; Cooke et al. 2005). Gastric tagging is rapid, requires no anesthetic or dermal injury, and adds little or no hydrodynamic drag (unlike external attachment of transmitters). Moreover, Pacific salmon are semelparous (i.e., reproduce only once in their lifetime), which means that failure to reach their natal spawning area (spawning populations are identifiable using DNA from a small biopsy of tissue; Beacham et al. 2011) results in complete loss of fitness. With a primarily linear migration path, radio and acoustic telemetry receiver stations can be set up along the migration route, enabling straightforward assessment of the migration success of individuals implanted with uniquely-coded transmitters (Eiler 1995; English et al. 2005; Heupel et al. 2006).

In the coastal rivers and marine waters of British Columbia, Canada, there is multi-sector (i.e., commercial, aboriginal, and recreational), multi-species, multi-population fishing focused on anadromous Pacific salmon. Fish face a gauntlet of fishing gear as they attempt to migrate from oceanic feeding grounds to their natal spawning sites, and while millions of fish typically are harvested each year, a variable portion of all Pacific salmon species are released. For example, in fisheries targeting more abundant pink salmon *O. gorbuscha*, release of sockeye salmon *O. nerka* often is required in years of low abundance. Similarly, the endangered status of the interior Fraser River coho salmon (*O. kisutch*) population complex has necessitated a release policy in fisheries targeting pink, sockeye, chum (*O. keta*), or chinook salmon (*O. tshawytscha*) (Decker and Irvine 2013; Raby et al. 2014b). In British Columbia, there has been a shift of policy in fisheries management toward the philosophy of "selective fishing," defined as the goal of avoiding non-target animals and releasing them "alive and unharmed" if encountered (Fisheries and Oceans Canada 2001). Thus, there is a need among managers of these fisheries to gain further insight into post-release mortality. Indeed, management of Pacific salmon fisheries in British Columbia (the responsibility of Fisheries and Oceans Canada, referred to as DFO) takes steps to minimize incidental mortality of populations and species facing conservation issues. For example, fisheries are curtailed at key times and locations to avoid bycatch, or gears that elicit high bycatch mortality (e.g., gillnets) are restricted in favor of those that are thought to enable higher post-release survival (e.g., seines). Moreover, in efforts to meet management-set target numbers of fish that reach the spawning grounds, fisheries managers apply estimates of post-release mortality to fish that are released (Fisheries and Oceans Canada 2011). If post-release mortality causes total allowable fishing mortality for a particular non-target population or species to exceed set limits (based on pre-season management plans), the fishery generating that incidental mortality may be prematurely terminated. The issue is further complicated by the fact that fish may swim back and forth across the Canada–United States border while in marine waters; a binational Pacific Salmon Treaty and the Pacific Salmon Commission serve to address issues of co-management. This complex governance, including international treaty requirements, combined with the multi-sector nature of the fishery and the inherent biological complexity of a multi-species and multi-population fishery, results in a challenge to conservation and management. That some populations and species are in decline has led many stakeholders to have greater interest in catch-and-release as a conservation and management strategy.

For more than a decade, our team of scientists, in partnership with resource managers, fishers (from all sectors), and non-governmental organizations, has worked toward advancing our understanding of catch-and-release of Pacific salmon. We have taken a "conservation physiology" approach (Wikelski and Cooke 2006; Cooke et al. 2013a) by using physiological concepts and tools to study and understand the effects of fisheries-capture on fish, while attempting to develop solutions that mitigate post-release mortality. To maximize applicability, much of the work occurs in the field where we use biotelemetry (Cooke et al. 2008; Donaldson et al. 2008) to study the behavior and fate of fish after release. To help tackle the complexity of these model organisms and this study system, we have also integrated other approaches, including social science (see Nguyen et al. 2012; Young et al. 2013), laboratory experiments (e.g., Gale et al. 2011), and molecular methods (e.g., Donaldson et al. 2014b).

The objective of this article is to provide a synthesis of our work on Pacific salmon catch-and-release. In particular, we focus on two key messages that have emerged across many studies (1) the context of capture-and-release, particularly as it relates to environmental conditions (e.g., water temperature, location relative to freshwater–saltwater transitions) and the behavior of fishers (handling; choices of gear), dramatically influences the link between the acute stressor and the fitness outcomes, and (2) further complexity is provided by immense biotic variation, which includes variation among individuals (driven by disease, maturation, and energy states), populations (locally adapted to different environmental conditions) and species, as well as between sexes (females nearly always experience higher mortality). These two messages are conveyed through six themes relating to context and biotic variation that each has complicated the link between stressors and fitness outcomes, and impeded the conveyance of generic management prescriptions. How does one develop generalized management given limited time and resources to study all possible combinations of species, populations, and contexts, particularly for multi-sector mixed-species fisheries? Here we summarize the findings with the strongest weight of evidence and provide guidance on how further research can address uncertainties surrounding factors that modulate the link between capture-stressors and post-release survival.

A note on estimates of mortality

In British Columbia's salmon fisheries, resource managers apply different post-release mortality rates to different fishing gears in different locations. For example, a 40–60% mortality rate is applied to salmon released from commercial gillnets (marine environment and in-river), a 10–70% rate is assigned to purse seine bycatch depending on the location of capture (Fisheries and Oceans Canada 2013), and a 10% rate is used for salmon released from most recreational fisheries (marine and freshwater) (Fisheries and Oceans Canada 2013). In most cases, it is unclear how the numbers were generated; the annual salmon-management document that lists the mortality rates used (Fisheries and Oceans Canada 2013) does not provide citations for each mortality rate. The few cases where it is clear which study was used to generate the mortality rate involved short-term studies of confinement in net pens; such as the 24-h net-pen study used to generate a 3% mortality rate now used in sockeye salmon in-river recreational fisheries (Thomas and Cahusac 2012; Fisheries and Oceans Canada 2013). In the present paper, we occasionally cite estimates of mortality from our own studies (Table 1); these either come from telemetric studies (i.e., the percentage of fish released with transmitters that successfully migrate beyond our upstream-most receiver stations, usually located in terminal tributaries near, or on, spawning areas) (e.g., Donaldson et al. 2011, 2012) or from large-scale studies of laboratory-confinement of fish collected from the wild *en route* to spawning areas (e.g., Gale et al. 2011). Numbers from these studies (Table 1) are useful for analyses of trends and factors in post-release mortality, and can be used to provide scientific advice to management. Whenever mortality rates are mentioned below, we clarify the source of the numbers and how they were generated.

Capture and handling techniques

Every fish that is caught experiences some degree of injury, stress, and/or physical exhaustion; the severity of each of these components is largely driven by the type of fishing gear and the handling practices used to land and release fish (Cooke et al. 2013b; Uhlmann and Broadhurst 2015). Indeed, capture and handling techniques employed by fishers are the most widely recognized factors affecting post-release rates of mortality. This generality applies to fisheries science and management as a whole and has been reviewed and discussed elsewhere (e.g., Davis 2002; Arlinghaus et al. 2007), so our discussion here focuses on Pacific salmon.

The ultimate reason for using different mortality rates for different fisheries lies in the recognition that the severity of the stressor and the injuries incurred during capture are largely dictated by the type of fishing gear used. For example, fish can be entangled in gillnets for hours before being landed and released (in the case of the non-target species) (Buchanan et al. 2002), and salmon that are released, or that escape, can incur severe dermal injuries (Baker and Schindler 2009). In sockeye salmon from Bristol Bay (Alaska), gillnet injuries in escaped fish led to infection (e.g., by the freshwater mold *Saprolegnia* spp.) and were associated with a suppression of morphological and physiological changes involved in reproductive maturation, leading to failure of spawning in some cases (Baker and Schindler 2009; Baker et al. 2013).

The three main types of gear used to target Pacific salmon are (1) gillnets, which are used by commercial and aboriginal fisheries in marine and freshwater, (2) seines, either purse seines typically used by commercial fisheries in coastal marine waters, or beach seines used by aboriginal fisheries in freshwater, and (3) hook and line, used by recreational anglers in marine and freshwater fishing, and by

Table 1 A summary of the characteristics of Pacific salmon catch-and-release studies published by our research team to date

Citation	Relevant themes	Predictor variables			Response variables	Fisheries relevance
		Environmental	Biological	Fishing		
Donaldson et al. (2010b)	1, 3	~9.3°C, freshwater	Chehalis River hatchery coho salmon, early-mid state of maturation, sex comparison included	Standardized chase + air exposure simulation or corralling stressor. Location: Chehalis River hatchery	Sub-lethal: heart rate, indices of physiological disturbance in blood	Late-season (low temperature) lower river and terminal fisheries that cause minimal injury
Donaldson et al. (2011, 2013)	1	17.4–18.9°C, freshwater	Sockeye salmon from a mix of mid- and upper- watershed spawning areas, early state of maturation (silver), sex not identified	Capture via volunteer anglers using standard "bottom-bouncing" gear, "gentle" beach seine (64 × 7.5 m, 5 cm mesh) capture technique. Location: lower Fraser River	Sub-lethal: indices of physiological disturbance in blood. Lethal: post-release migration failure in fish telemetry-tracked to natal watersheds (~15–20 days monitoring period)	Directly applicable to lower Fraser River sockeye salmon recreational fisheries
Gale et al. (2011)	1, 2, 3	13, 19, and 21°C, freshwater	Summer-run sockeye salmon of mixed population origin, early state of maturation (silver), sex identified	Simulated catch-and-release treatments: brief handling, 3 min strenuous exercise chase, 3 min chase + 1 min air. Location: Cultus Lake laboratory	Sub-lethal: indices of physiological disturbance in blood, ventilation rate, righting reflex. Lethal: short-term (3-day) mortality in fish held in large outdoor aquaria	Lower-river fisheries targeting summer-run sockeye salmon that cause minimal injury
Clark et al. (2012)	3	7°C, freshwater	Chehalis River hatchery coho salmon, early- and mid- state of maturation, sex comparison included	Simulated catch-and-release treatment: 3 min strenuous exercise + 1 min exposure to air. Location: Chehalis River hatchery	Sub-lethal: indices of physiological disturbance in blood, reproductive hormones, metabolic rate	Late-season fisheries in cold water (<10°C) in terminal tributaries
Donaldson et al. (2012)	1, 4, 6	~17.2°C, freshwater	Sockeye salmon from two proximate but distinct populations, each at a different state of maturation, sex not identified	Captured by beach seine (90 × 7.5 m, 5 cm mesh) and released or exposed to capture simulations: gillnet (13.3 cm mesh), tangle net (8.9 cm mesh, monofilament), or prolonged crowding in the seine. Location: Harrison River. Location: Lower Fraser River	Sub-lethal: reflex impairment, indices of physiological disturbance in blood. Lethal: immediate and post-release mortality, monitored from release to spawning (up to ~2 months) using acoustic telemetry	Fisheries in terminal tributaries that catch-and-release sockeye salmon
Raby et al. (2013)	1, 4, 6	11.8–13.2°C, freshwater	Weaver Creek pink salmon and chum salmon, sexual maturation complete (spawning form), only females used	A range of catch-and-release simulations including gillnet entanglement (13.3 cm mesh size), angling with hook and line, and a standardized chase + air stressor. Location: Weaver Creek spawning channel	Sub-lethal: Reflex impairment, indices of physiological disturbance in blood. Lethal: longevity on spawning grounds and pre-spawn mortality	Fisheries in terminal tributaries that catch-and-release mature salmon adjacent to spawning grounds
Robinson et al. (2013)	1, 2, 3	16 and 21°C, freshwater	Summer-run sockeye salmon of mixed population origin, early state of maturation (silver), sex identified	Standard 3 min strenuous exercise + 1 min air catch-and-release simulation with or without a 1-min revival treatment. Location: Cultus Lake laboratory	Sub-lethal: indices of physiological disturbance in blood. Lethal: post-release mortality monitored in large outdoor tanks (for ~25 days)	Catch-and-release of summer run sockeye salmon in the lower Fraser River

(continued)

Table 1 Continued

Citation	Relevant themes	Predictor variables			Response variables	Fisheries relevance
		Environmental	Biological	Fishing		
Donaldson et al. (2014b)	3	11–12°C, freshwater	Weaver Creek sockeye salmon and pink salmon, fully mature, sex identified	Standard 3 min strenuous exercise + 1 min exposure to air. Location: Weaver Creek spawning channel	Sub-lethal: indices of physiological disturbance in blood, molecular indices of stress	Fisheries in terminal tributaries that catch-and-release mature salmon adjacent to spawning grounds
Gale et al. (2014)	1, 2, 3	13, 16, and 19°C, freshwater	Harrison River sockeye salmon, early to midway through their sexual maturation, sex identified	Standard 3 min strenuous exercise + air exposure catch-and-release simulation. Location: Cultus Lake laboratory	Sub-lethal: ventilation rate, righting reflex, indices of physiological disturbance in blood. Lethal: mortality monitored for 48 h post-release with fish confined in large outdoor aquaria	Lower river fisheries that catch-and-release late run sockeye salmon and cause minimal injury
Nguyen et al. (2014)	1	13.2–15.6°C, freshwater	Late run sockeye salmon (Adams-Shuswap), midway through sexual maturation, sex not identified	Capture by beach seine (90 × 7.5 m, 5 cm mesh), followed by release, brief gillnet entanglement (13.3 cm mesh), gillnet + 2 min air, or 2 min air without entanglement. Subset of fish revived in Fraser Box before release. Location: Lower Fraser River	Sub-lethal: indices of physiological disturbance in blood. Lethal: Post-release mortality monitored using radio telemetry to natal subwatershed (Adams-Shuswap area)	Lower river fisheries targeting late run sockeye salmon
Raby et al. (2014b)	1, 4	14.9–16.1°C, freshwater	Endangered Interior Fraser River coho salmon populations, early in sexual maturation (silver), sex not identified	Captured as bycatch in an aboriginal beach seine (90 × 9 m, 5 cm mesh) fishery. Location: Lower Fraser River	Sub-lethal: reflex impairment. Lethal: post-release mortality during migration to upper watersheds (~10–20 days) monitored using radio telemetry	Directly applicable to Fraser River beach seine fisheries
Raby et al. (2015a)	1, 2, 3	10 and 15°C, freshwater	Chilliwack River hatchery coho salmon, ranging from midway-through their maturation process to fully mature, sex identified	Simulated beach seine capture in large outdoor concrete ponds using fishery-standard beach seine mesh (5 cm mesh size). Location: Cultus Lake laboratory	Sub-lethal: heart rate, metabolic rate, indices of physiological disturbance in blood and white muscle. Lethal: immediate and short term (24 h) mortality monitored in large concrete ponds	Beach seine fisheries in freshwater
Raby et al. (2015b)	1	14–15°C, freshwater	Harrison River and Weaver Creek sockeye salmon, mid-way through sexual maturation, males only	Beach seine (90 × 9 m, 5 cm mesh) capture followed by 3 min exposure to air. Subsequently revived for up to 2 h using one of three revival treatments. Location: Harrison River	Sub-lethal: indices of physiological disturbance in blood, reflex impairment. Lethal: immediate mortality (<2 h) monitored during confinement in revival boxes and bags	Fisheries that catch-and-release sockeye salmon in terminal tributaries

(continued)

Table 1 Continued

Citation	Relevant themes	Predictor variables			Response variables	Fisheries relevance
		Environmental	Biological	Fishing		
Robinson et al. (2015)	1	13.2–19.0°C, freshwater	Sockeye salmon from a mix of populations, predominantly early in their sexual maturation, sex not identified	Fish exposed to standard chase + air exposure catch-and-release simulation or caught by volunteer anglers and released with radio transmitters after 1 min revival treatment (subset of fish). Locations: Harrison River and Fraser River	Sub-lethal: reflex impairment. Lethal: post-release mortality, monitored using radio telemetry—fish tracked to spawning sites (experiment 1) or to upper watersheds (experiment 2)	Catch-and-release angling of sockeye salmon in freshwater
Raby et al. (in press)	1, 4	8.5–9.8°C, saltwater	Wild and hatchery-origin coho salmon of mixed population origins, early in maturation schedule (silver), sex not identified	Captured by purse seine (549 × 55 m, 10 cm mesh) using standard commercial fishing gear and handling. Location: Juan de Fuca Strait	Sub-lethal: reflex impairment, injury, indices of physiological disturbance in blood. Lethal: post-release mortality monitored in fish held in a net pen (24 h), also in fish release overboard using acoustic telemetry (~10–20 days)	Purse seine fisheries that release coho salmon

Notes: The numbers listed under "relevant themes" correspond to the six themes discussed in this article: 1 = capture and handling techniques; 2 = water temperature; 3 = sex-specific effects; 4 = among-population differences; 6 = migration stage and maturation status. Experiments relating to theme #5 (pathogens) have yet to be published. This list is not exhaustive; only studies with a stated objective specific to catch-and-release fishing are listed. Relevant fisheries are listed but in nearly all cases, the results of these experiments (e.g., absolute rates of mortality) cannot be directly applied to management of the fisheries listed here, even though the factors examined and trends in the findings are relevant to understanding post-release mortality in those fisheries.

commercial troll fisheries in the marine environment. Among these gears, post-release mortality is generally highest for gillnets—as high as 70% in short-term confinement studies in the marine environment (Buchanan et al. 2002). Tangle nets offer an alternative to gillnets with higher potential for post-release survival, but are used for research and management more commonly than for harvest fisheries (e.g., Ashbrook et al. 2008; Donaldson et al. 2010a). Angled-and-released fish are likely to experience markedly lower post-release mortality than are gillnet-caught fish (e.g., exhibiting 40% post-release mortality in telemetry-tracked sockeye from release in the lower Fraser River to spawning areas, relative to ocean-tagged controls) (Donaldson et al. 2013). Capture by beach seines appears to offer the lowest post-release mortality among the main types of gear used in the Fraser River (12.5% in sockeye salmon [telemetry-tracked fish; Donaldson et al. 2013], 17–39% in coho salmon released from aboriginal beach seines; Raby et al. 2014b), particularly when using the more holistic approach of examining long-term mortality and success in reaching spawning areas, which is most relevant in a fitness context, rather than focusing solely on survival for 24–48 h. However, post-release mortality in angled fish can be exceptionally low in some contexts, such as if angling occurs in terminal tributaries (i.e., near the spawning area) and where water temperatures are low (e.g., <5% mortality among fish telemetry-tracked to spawning; Nelson et al. 2005).

Within a fishery, handling techniques and the condition of the fish that are released vary widely; estimates of mortality should (ideally) be based on a sample of fish representative of the normal range of handling conditions and of the resulting vitality of the fish. Nevertheless, understanding the effects of different capture-methods and handling techniques on stress and survival can highlight ways to reduce post-release mortality. For example, efforts to check gillnets more frequently (i.e., shorter soak times) can enable higher post-release survival (Buchanan et al. 2002). For recreational fisheries and small-scale in-river beach seines, the time between initiation of the stressor and the release of the fish generally is on the order of minutes (Donaldson et al. 2011; Raby et al. 2012), but small variations (e.g., 2 min versus 15 min of entanglement time) can cause significant differences in fish vitality (Raby et al. 2012) and physiological disturbance (Raby et al. 2015a). In a field experiment using telemetry, the addition of a brief gillnet entanglement reduced survival in sockeye salmon, whereas 2 min of exposure to air did not have a significant effect, suggesting injury and pre-removal stress may be more important than exposure to air (Nguyen et al. 2014). Similarly, in the Fraser River recreational fishery targeting sockeye salmon, the addition of 1 min of exposure to air after angling caused no change in the proportion of telemetry-tracked fish reaching spawning areas (30.8% versus 28.6%). However, adult Pacific salmon have relatively high requirements for oxygen and poor tolerance of anoxia (Brett and Groves 1979; Farrell 2009), such that even brief exposure to air can lead to near total impairment (i.e., loss of equilibrium and pattern of ventilation) (Raby et al. 2015b), so it seems highly likely that extending the duration of exposure to air beyond 1–2 min would increase post-release mortality in most contexts, particularly when the risk of predation is substantial (Cook et al. in press).

The role of water temperature

The effect of water temperature on Pacific salmon has generated considerable attention because of its critical role in physiological processes and survival (e.g., Brett 1952, 1956, 1971; Servizi and Jenson 1977; Jensen et al. 2004) and because climatic change is warming many rivers, with unknown future consequences for the sustainability of salmon (e.g., Richter and Kolmes 2005; Hague et al. 2011; reviewed by Martins et al. 2012a). High temperatures of rivers have been linked to migration and pre-spawn mortality (Macdonald et al. 2000, 2010; Martins et al. 2011), and can interact with other stressors like pathogens (Macdonald et al. 2000; reviewed by Miller et al. 2014) and fisheries-capture (Gale et al. 2013). Numerous field and laboratory studies from our research team have directly addressed the effects of water temperature on the physiology and survival of multiple species of wild adult Pacific salmon (i.e., pink, sockeye, Chinook, and coho salmon) at different levels of biological organization, including at the level of the cell (Jeffries et al. 2012a, 2014), tissue (Crossin et al. 2008; Clark et al. 2012; Jeffries et al. 2012b), whole organism (MacNutt et al. 2006; Farrell et al. 2008; Mathes et al. 2010; Clark et al. 2008, 2011; Eliason et al. 2013a), and population (Lee et al. 2003; Eliason et al. 2011, 2013b; Martins 2011, 2012b). These studies have helped characterize the “normal” physiological response to water temperature to compare with those experienced by fish exposed to a catch-and-release event. Because any experimental study on the effects of temperature on wild adult Pacific salmon requires that fish be captured, every study on the effects of temperature has, in effect, been a study of the combined effects of temperature and of stress caused by capture (e.g., transportation from the field and holding in the laboratory). In some experiments, fish were netted and handled multiple times to make repeated measurements (e.g., Jeffries et al. 2011, 2012b).

Although the potential effects of confinement stress in laboratory-based experiments prevent direct application to fisheries, comparisons among methods of capture and among water temperatures can reveal patterns and critical thresholds. Gale et al. (2014) simulated capture-and-release by manually chasing salmon in a circular tank and then exposing them to air, using fish that had been captured during migration upriver for transportation to a large outdoor facility where they were held at three fisheries-relevant temperatures: 13°, 16°, and 19°C. There was a strong effect of temperature and a weak effect of different methods of capture or handling; the increase in mortality from 13° to 16°C (~25% relative increase) was statistically non-significant, but a much larger increase in mortality occurred at 19°C, at which mortality was approximately double the rate observed at 13°C and also significantly higher than at 16°C. In a subsequent study using similar methods and the same species (*O. nerka*), 100% mortality occurred within 3 days after simulations of capture at 21°C, whereas mortality did not begin to occur until 4 days after the stressor in fish held at 16°C (Robinson et al. 2013). That mortality only began to occur after 4 days suggests that even modest stressors (in this case 3 min of exercise followed by 1 min of air), from which fish seemingly recover readily, may cause latent mortality through some loss of homeostasis, acceleration of senescence processes, or proliferation of pathogens. External and internal macroscopic examinations of dying fish in these laboratory-based experiments (Gale et al. 2011, 2014; Jeffries et al. 2011, 2012b; Robinson et al. 2013) largely motivated subsequent (ongoing) experiments more carefully aimed at understanding the role of pathogens in catch-and-release mortality (see "Interactions between capture stressors and pathogen loads" section, below). The occurrence of mortality several days or weeks after release is not unique to salmon or salmon fisheries (see Davis 2002).

In a study using hatchery-origin coho salmon that were exposed to long (15 min) or short (2 min) entanglements in nets in cool (10°C) or warm (15°C) water, the most severe stressor (15°C/15 min) was the only treatment to result in mortality (Raby et al. 2015a). That group also exhibited the highest physiological disturbance 1 and 4 h after release, with return to routine heart rate taking the longest of the variables measured (also see Clark et al. 2012). In general, ionic and metabolic measures have repeatedly indicated that greater physiological disturbances occur in fish captured in warmer water (Gale et al. 2011; Robinson et al. 2013) while the same fish more commonly experience loss of equilibrium (i.e., their righting reflex) and impaired ventilation (Gale et al. 2014).

Field-based studies of survival are more conducive to direct application to management as they give an indication of post-release survival under natural conditions of migration, but telemetry experiments are costly and have infrequently involved multi-year studies in which factors other than temperature remained the same. In one of the few such studies, in which survival of coho salmon released from a beach-seine fishery was assessed for three consecutive years, water temperature varied by <2°C (Raby et al. 2014b), partly because the fishery took place in the same week in September each year. The best alternative is to collate datasets from separate projects covering multiple years and a range of capture dates so that a mixture of temperatures and populations can be examined, as was done by Martins et al. (2011). Those analyses were based on fish captured by fish wheels and tangle nets; methods that were chosen to minimize stress and injury and that are not used by fisheries, so the absolute mortality rates generated are not directly applicable to management. Nevertheless, the study by Martins et al. (2011) found that post-release mortality increased with temperature across all populations, and corroborated the laboratory experiments (Gale et al. 2011, 2014; Robinson et al. 2013) by demonstrating that migration-success after capture and release in the wild decreases markedly in sockeye salmon when temperature increases from 14°–16°C to 19°C or higher. Similar to many of the other factors discussed in the present article, temperature has effects on post-release survival that are context-specific, including interactions with population and sex (see below).

Sex-specific effects of fisheries-capture

Mature, female Pacific salmon experience higher mortality than do males in most years in controlled laboratory experiments conducted under benign conditions (Patterson et al. 2004; Crossin et al. 2008), a trend that can be amplified by warm water (e.g., 19+°C; Jeffries et al. 2012b; Martins et al. 2012b) and catch-and-release stressors (Robinson et al. 2013; Gale et al. 2014). In the laboratory, Gale et al. (2014) found that following simulated catch-and-release, female sockeye salmon held at 19°C had higher mortality 24–48 h post-treatment compared to males held at 19°C and in comparison with both sexes at lower temperatures. Robinson et al. (2013) observed that females exhibited elevated mortality rates when held at 16°C, which approximates the average temperature experienced by Fraser River sockeye salmon during migration upriver (Patterson et al. 2007). With continued warming expected in the Fraser River (Morrison et al. 2002), there is growing concern that the increased mortality observed for females following catch-and-release at high temperatures could affect operational sex ratios at spawning grounds (McDaniels et al. 2010), which may become an important consideration for the management of fisheries when river temperatures are high. Indeed, telemetry-tracked sockeye salmon males survived to reach spawning areas at a rate 1.6× higher than did females when water temperatures exceeded 19°C (Martins et al. 2012b).

It has been postulated that female salmon have less capacity to cope with environmental stressors (Clark et al. 2011) because of physiological differences with males. Acute and chronically stressed female salmon typically have higher levels of plasma cortisol than do males (Fagerlund 1967; Pottinger et al. 1995, 1996). Even in unstressed pink salmon, coho salmon, and sockeye salmon, females can have a 2:1 or higher ratio of levels of cortisol in the plasma relative to males (Donaldson et al. 2010b, 2014b; Baker and Vynne 2014; Raby et al. 2015a). Sex-specific differences in corticosteroid modulations and high maternal investment in gonadal development, characteristic of Pacific salmon, likely contribute to enhanced susceptibility to disease in females relative to in males (Pickering and Christie 1980; MacDonald et al. 2000; Sandblom et al. 2009; Clark et al. 2010). Indeed, preliminary results show that female adult Pacific salmon carry greater loads of microbes than do males, although differences in mortality rates do not always match differences in microbe loads (A. Teffer, submitted for publication). In addition to hormonal differences, females can have higher heart rates, as well as elevated levels of lactate and glucose in blood plasma (Sandblom et al. 2009; Jeffries et al. 2012b). Mature male sockeye salmon also develop larger hearts than do females, measured as a proportion of body mass (Clark et al. 2009; Sandblom et al. 2009). Estradiol, which is an essential hormone for final maturation and senescence in Pacific salmon (Hruska et al. 2010; Jeffries et al. 2012b), was depressed during a stress response in a recent experiment (Donaldson et al. 2014b).

Several hypotheses have been proposed to explain why higher post-release mortality occurs in female salmon than in males. Potential mechanisms of mortality include physiological limitations, such as an impaired recovery of cortisol to routine levels following fisheries-capture during maturation, energetic constraints due to increased investment in gonadal development relative to males (Crossin et al. 2008), or differences in cardiorespiratory functioning at high temperatures (Clark et al. 2011; Eliason et al. 2013c). In a study of physiological recovery of coho salmon from simulated catch-and-release at two temperatures (10° and 15°C), cortisol was significantly higher at the higher temperature in both sexes 24 h after the stressor. However, in females, cortisol remained particularly high (i.e., ~300 ng mL^{-1}) relative to control values (~80-150 ng mL^{-1}; Donaldson et al. 2010a; Raby et al. 2015a), which provides support for the notion that impaired cortisol-recovery could be a mechanism for the observed sex-differences in warm water (Raby et al. 2015a). Further work is required to identify the mechanistic basis of the increased sensitivity of females to warm water and to fisheries-capture.

Among-population differences

Adult Pacific salmon return to their natal spawning grounds with high fidelity, particularly in the case of the highly philopatric sockeye salmon, which results in a discrete population structure. In the Fraser River watershed, there are more than 100 genetically distinct sockeye salmon populations (Beacham et al. 2005) that experience a broad range of environmental conditions, depending on when they enter the river and where they spawn. For example, the distance they migrate can vary from <100 km to >1000 km, gain in elevation can exceed 1100 m, river temperatures can vary from 6° to 22°C, and river-flow can reach up to 10,000 m^3s^{-1}. Consequently, a range of population-specific adaptations are postulated to have evolved in concert with the conditions under which migration takes place and the location of spawning (Lee et al. 2003; Crossin et al. 2004; Farrell et al. 2008). Body morphology, gross somatic energy, fecundity, and migratory behavior are population-specific and reflect apparent differences in the difficulty of migration (Crossin et al. 2004). Eliason et al. (2011) reported among-population differences in cardiorespiratory physiology for Fraser River sockeye salmon, whereby populations undergoing more challenging migratory conditions appear to be better adapted to those challenges by virtue of better performance in swimming tests, greater aerobic scope, greater cardiac scope, larger hearts, and a better coronary supply of oxygen to the heart (Lee et al. 2003; Eliason et al. 2011, 2013a). Populations were also able to maintain maximum aerobic performance in swimming tests across the range of temperatures typically encountered during their migration upriver; thermal-tolerance thresholds differed among populations (Eliason et al. 2011). Survival and migration rates can also be population-specific for sockeye salmon (Hinch and Rand 2000), with some populations likely being more vulnerable to elevated temperatures (Martins et al. 2011) and to catch-and-release (Donaldson et al. 2010a, 2012).

There is some evidence for population-specific effects of catch-and-release fisheries on adult sockeye salmon (Donaldson et al. 2010a, 2012), although evidence suggests otherwise for coho salmon (Raby et al. 2014b). Donaldson et al. (2012) investigated post-release survival in two sockeye populations that exit the marine environment at the same time, spawn in nearby locations, but one population (i.e., Harrison) spawns 1 month after the other (i.e., Weaver). Post-release survival was low overall, but the Harrison population had much lower survival than did the Weaver population, particularly following simulated capture by gill net or tangle net. Donaldson et al. (2012) found that Harrison fish exposed to the fisheries simulations were more likely to experience visible injuries, and impairment of reflexes predicted their short-term and long-term survival, but this was not the case for Weaver fish. Those results corroborated a prior study (Donaldson et al. 2010a), in which physiological condition at the time of capture-and-release was predictive of migratory fate for the Adams-Shuswap population-complex of Fraser River sockeye, but not for the Chilko population. Moreover, Adams-Shuswap salmon were slower migrators and less likely to reach natal subwatersheds relative to the Chilko fish (Donaldson et al. 2010a). Interestingly, both the Chilko and Weaver populations migrate directly to spawning areas (i.e., within days following capture-and-release), whereas the Adams-Shuswap and Harrison populations spend several weeks longer in freshwater prior to spawning. In both cases there were remarkably similar patterns, with nearly two-fold higher survival for the population that was closer (chronologically) to spawning (i.e., Chilko and Weaver). Such results suggest that population differences in maturation schedules relative to the time of capture may drive much of the observed differences in post-release survival (see sections below on pathogen loads and on the role of maturation status).

Interactions between capture stressors and pathogen loads

A common theme within studies of post-release mortality in Pacific salmon has been that among-treatment differences and explanatory variables (e.g., impairment of reflexes, fish length, blood parameters, methods of capture) sometimes fail to explain most of the variation in mortality that occurs (e.g., models of survival explained ~40% of the variation in survival in one study (Raby et al. 2014b), and 25–45% in another (Raby et al. in press)). Disease may be responsible for much of the unexplained variation, because of its influence on the magnitude and types of responses elicited by an individual (Cooke et al. 2013b). Whether disease induced by catch-and-release is a mechanism for post-release mortality is unknown (in any fish or fishery), although this phenomenon is often assumed to occur (Gilhousen 1990; Baker and Schindler 2009). Host–parasite relationships are presumed to be complex in anadromous fishes because individuals experience a broad range of environmental conditions (e.g., flow, temperature, salinity), undergo dramatic physiological changes (Hinch et al. 2006), and encounter diverse infectious agents (Miller et al. 2014). The spawning migration of adult Pacific salmon requires movement from the marine environment to freshwater, a physiologically taxing osmoregulatory transition that is layered onto the processes of maturation and senescence (see section below on the role of maturation status). Animals' migrations are intrinsically associated with, and influenced by, infectious diseases (Altizer et al. 2011) because the balance of host–parasite relationships is modified by changes in the environment (Wolinska and King 2009), which includes stressors such as catch-and-release.

We are currently exploring the role of infectious disease in catch-and-release survival by evaluating two hypotheses: (1) the status of infection at the time of capture affects post-release recovery and survival of the host, and (2) the infectivity, replication, and pathogenicity of microbes are altered by stress and injury sustained by the host during a capture event. Hypothesis-testing of this nature can be assessed using novel application of high-throughput quantitative polymerase-chain reaction (qPCR) coupled with holding the fish under controlled laboratory conditions, and in telemetry studies *in situ* (as first described by Miller et al. 2014).

The microbial assemblage carried by a fish at the time of capture may influence its ability to recover from the stressor. Microbes are accumulated throughout the Pacific salmon's lifecycle and can remain non-pathogenic or be maintained as sub-pathological infections. Carrier-state infections have the potential to become pathogenic and cause disease if the host's resilience is impaired (e.g., *Renibacterium salmoninarum*) (Bullock and Herman 1988; St-Hilaire et al. 2001). For wild fish, individual variability in microbe burden and host physiology are likely constrained by the ecological thresholds of infection, thereby influencing survival directly (i.e., disease) and indirectly (e.g., sub-lethal impairment leading to predation) (Miller et al. 2014). The potential therefore exists for loss of more impaired individuals in an advanced state of infection prior to entry into freshwater (Miller et al. 2011, 2014). This hypothesis is supported by data showing relative uniformity in microbe burden among returning adult salmon assessed shortly after they enter the river, with divergence among surviving individuals occurring later during residence in freshwater, and reflecting the severity of the stressor incurred (Miller et al. 2014; A. Teffer, submitted for publication). Physiological impairment is a typical characteristic of adult salmon after extended residence in freshwater, which can likely be attributed to the development of microbial infections and to senescence (Tierney and Farrell 2004; Wagner et al. 2005; Kocan et al. 2009). Thus, the period of residency in freshwater is an important co-factor in any study of disease in Pacific salmon.

Acute physiological stress caused by catch-and-release could affect immune function, especially if the host's resilience is compromised. In addition, direct injuries caused by hooking, netting, and handling are common and can range from mild (e.g., loss of mucus or scales) to severe (e.g., loss of skin; damage to gills and other organs) (see Cooke and Suski 2005; Baker and Schindler 2009; Cooke et al. 2013b). (Note: injuries that lead to significant loss of blood from the fish typically preclude release.) These injuries create sites for infection by opportunistic pathogens such as *Saprolegnia* spp (Baker and Schindler 2009) or *Aeromonas salmonicida,* which often replicate in the event of decreased effectiveness of the hosts' defenses (Kent 2011). Stress from capture likely accelerates the development of disease in more immunocompromised individuals who are unable to elicit an appropriate immune response to primary or secondary infections (Gilhousen 1990; Schreck et al. 2001; Miller et al. 2011; Jeffries et al. 2014). Conversely, in less impaired individuals, an acute stressor such as gill-net entanglement could augment immunity of the skin and gills to secondary infection via accelerated recruitment of leukocytes to affected areas and enhanced cytokine signaling (documented in mice; e.g., Dhabar 2002; Neeman et al. 2012). Indeed, premature mortality of adult salmon exposed to warm water and handling was associated with an insufficient stress and immune response observed in the gill transcriptome (Jeffries et al. 2014), implicating an interaction between temperature, handling, and disease.

Extended residency in freshwater prior to spawning can lengthen the duration of microbial infection, thereby increasing the infectious dose accumulated by migrating adults (e.g., Stocking et al. 2006). High temperature can further promote pathogenesis of certain microbes due to accelerated replication by the pathogen and/or to impaired resilience on the part of the host (Noe and Dickerson 1995; Wedemeyer 1996; Altizer et al. 2013; Miller et al. 2014). The type and intensity of transcriptomic responses of thermally stressed fish can also vary depending on the type of infectious agent (e.g., bacterial versus viral agents) (Hori et al. 2013). Years of elevated temperature in rivers are associated with high mortality rates of migrating adults both *en route* to, and after arrival on, spawning grounds (e.g., Fraser River: Crossin et al. 2008; Hinch and Martins 2011; Martins et al. 2011; Snake River: Keefer et al. 2008), with disease known to be a contributing factor (Wagner et al. 2005; Bradford et al. 2010; Miller et al. 2011; Hinch et al. 2012). In a changing climate, differences in the resiliency and thermal tolerance both of host and microbes will dictate the relative impact of various etiological agents and potentially shift historic regimes of disease as river temperatures rise (Wolinska and King 2009). If increasing temperatures alter the abundance, infectivity, and pathogenicity of infectious agents, estimates of bycatch-mortality may require adjustment.

Migration stage and maturation status

Given the profound physical and physiological transformations that salmon undergo during the spawning migration, and the fact that they can be captured in environments that range substantially in salinity and temperature, it is not surprising that migrants can vary in their vulnerability to catch-and-release at different stages of migration. For example, Raby et al. (2013) observed suprising resilience to acute and, in some cases, quite severe catch-and-release stressors in female pink and chum salmon that had arrived at spawning grounds (*ca.* 10% and 5% pre-spawn mortality, respectively, based on post-mortem inspection of egg retention; nearly identical to natural control levels), whereas sockeye salmon from the same watershed exposed to the same treatments two weeks earlier suffered 66% mortality (i.e., failure to reach the spawning area, based on acoustic telemetry tracking; Donaldson et al. 2012).

The biggest environmental transition experienced by adult salmon during the spawning migration is from saline marine to typically warmer freshwater environments, a remarkable physiological feat. In preparation for entry into freshwater, salmon restructure their ionoregulatory systems, transforming the epithelium of the gills from excreting ions in saltwater to absorbing ions in freshwater (Hoar et al. 1988). The capacity of returning migrants to ionoregulate in seawater begins to decline weeks before exposure to freshwater, and osmoregulatory function continues to change throughout migration (Shrimpton et al. 2005). Concurrently, increases in reproductive hormones further impair ionoregulatory ability in seawater (Lundqvist et al. 1989) and in turn these physiological alterations induce immunosuppression and increase basal levels of stress indicators (Maule et al. 1996; Miller et al. 2014).

Cortisol, the primary corticosteroid in fish (Barton 2002), naturally increases throughout the spawning migration (Hane and Robertson 1959; McBride et al. 1986; Hinch et al. 2006; Baker and Vynne 2014) and plays an integral role in activating key migratory processes (Carruth et al. 2002). It is also involved in ion uptake and in upregulation of gill Na-K-ATPase in salmonids (both in freshwater and saltwater isoforms) (McCormick 2011). However, variable basal concentrations of cortisol also have the potential to influence responsiveness to acute stress (Sapolsky et al. 2000). Therefore, the osmoregulatory status of a fish at a given time, combined with its osmotic environment, may affect recovery from catch-and-release. With a decreasing ability to tolerate saltwater (i.e., an increased need to excrete ions and a reduced ionoregulatory capacity to do so) and rising plasma cortisol levels, fish that choose to enter a holding pattern in saltwater and delay their entry into freshwater or those transitioning between environments of variable salinities may be more vulnerable to acute stress than is true of fish fully immersed in freshwater. However, little research has been conducted to properly test these hypotheses. Related evidence suggests that survival is lower for migrating fish that are held in saltwater in the laboratory, particularly if their maturation process is accelerated (Cooperman et al. 2010). Salmon similarly held in saltwater have higher resting and active metabolic rates (Wagner et al. 2006).

As Pacific salmon migrate upstream through freshwater, their skin thickens and their scales are absorbed as secondary sexual characteristics develop (Burgner et al. 1991), thereby reducing the potential for loss of scales, which is a normal effect of catch-and-release that can lead to mortality (Olsen et al. 2012; Raby et al. in press). Loss of scales is substantial when immature "silver" fish are captured in the ocean or early in the freshwater phase of their migration. Damage to the epithelial layer can further increase pathogenic infection in fish (Svendsen and Bogwald 1997; van West 2006), potentially leading to delayed mortality (Svendsen and Bogwald 1997; Howe and Stehly 1998; Davis 2002). Although loss of slime remains an issue even once scales are absorbed, decreased loss of scales should render fish more resilient to dermal injuries typical of those that occur during capture.

During the final phase of migration, as energy reserves become progressively depleted and condition deteriorates (Gilhousen 1990), fishes are unable to fight infection and are especially vulnerable to additional stressors and disease (Miller et al. 2014). The finding of Raby et al. (2013) that minimal mortality occurred following exposure to severe catch-and-release stressors on the spawning ground suggests, however, that despite starvation, disease, and depleted energy, once adult salmon have arrived at the cooler waters of their spawning area, they may resist the usual negative effects of prolonged stress. While exposure to stressors suppresses reproductive investment in many animals, thereby enhancing processes that enable survival, conserve energy, and maximize long-term fitness (i.e., activation of the "emergency life-history stage"; see Wingfield et al. 1998; Sapolsky et al. 2000), this strategy would be maladaptive in Pacific salmon with only one opportunity to breed (i.e., semelparity) (Wingfield and Sapolsky 2003). Indeed, concentrations of cortisol are at their highest on the spawning grounds (Baker and Vynne 2014) and although stress responsiveness (i.e., stressor-induced elevation of cortisol) is maintained (~51% increase from baseline in spawning pink salmon), elevations of cortisol are apparently constrained enough in most instances that reproduction is not impaired (Cook et al. 2011). In field studies assessing the link between stress responsiveness and spawning or migration success, there was evidence for selection against high-responding individuals—particularly earlier in the migration when the mean cortisol response was much larger than on spawning grounds (~300% increase versus a 50% increase) (Cook et al. 2011, 2014).

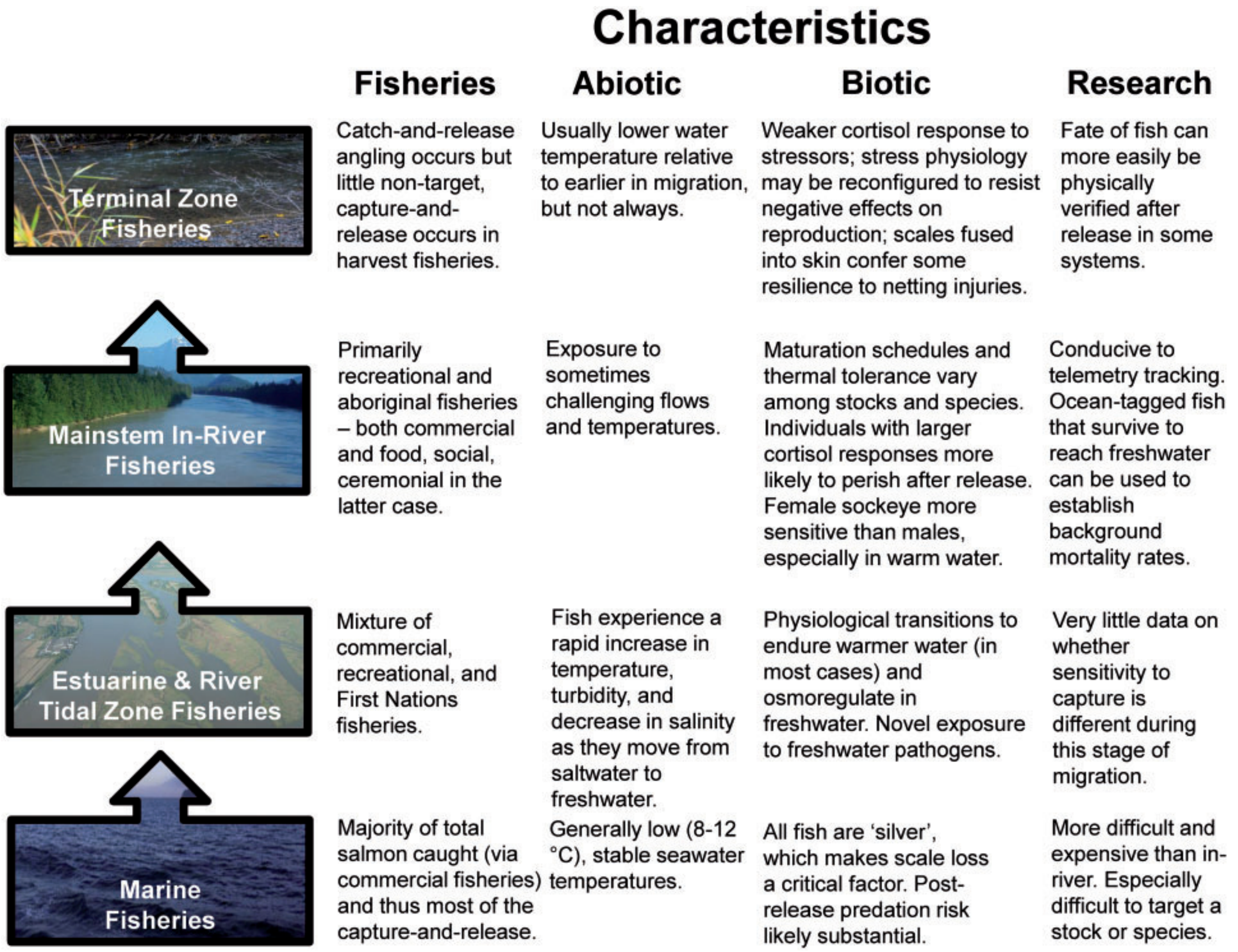
Spawning involves repeated agonistic interactions with other salmon (i.e., social stress; Gilmour et al. 2005), challenging environmental conditions, and a potentially heightened threat of predation because of conspicuous secondary sexual characteristics coupled with utilization of shallow streams (Quinn and Buck 2001). So it might be expected that successful spawners would be physiologically adapted to cope with acute stressors like catch-and-release (Wingfield and Sapolsky 2003). However, the mechanisms by which mature adult salmon resist the effects of elevated cortisol remain unclear. It seems likely that the HPI or HPG (hypothalamic-pituitary-gonadal) axes could be re-configured during spawning (e.g., via changes in glucocorticoid receptors) (Wingfield and Sapolsky 2003). Indeed, cortisol receptors (glucocorticoid receptors 1 and 2) are reduced in spawning fish, at least in gill tissue (Flores et al. 2012). Exposure to acute stress has been shown to accelerate development of disease in fish (e.g., Maule et al. 1987), which is a candidate mechanism for post-release mortality in migrating salmon (Miller et al. 2014). However, immune function progressively collapses in spawning salmon and therefore additional brief elevations in cortisol, for example, for 1–4 h (Donaldson et al. 2014b) may be relatively inconsequential for immune function at this stage. With respect to the stress of exhaustion typically accompanying catch-and-release, Raby et al. (2013) hypothesized that salmon become progressively more resilient due to a shift toward protein catabolism during spawning (Morash et al. 2013) and to more frequent use of anaerobic metabolism (Brett 1995).

It remains unknown if resilience to capture-stress changes in a systematic way across the spawning migration, or whether external factors can alter this trajectory. Salmon tend to experience cooler water as they approach spawning areas, although water temperatures also are low in marine fisheries (e.g., 9–10°C) where high post-release mortality can occur, for example, nearly 50% delayed mortality (Raby et al. in press). A minimum amount of time may be required following release for delayed mortality to become manifest, yet longevity was 8 and 15 days for chum and pink salmon, respectively (Raby et al. 2013)—a time frame in which substantial delayed mortality can occur in fish with transmitters released in the lower Fraser River (e.g., Donaldson et al. 2011, 2013; Raby et al. 2014b).

At present, there is a lack of understanding of how responses to capture-stress may change throughout the spawning migrations of Pacific salmon. With dramatic physiological and physical changes occurring during maturation, and stress hormones playing an integral role throughout the process (Baker and Vynne 2014), understanding these relationships is a challenge. Further population-specific field experiments are required throughout the spawning migration (both spatially and temporally) to determine if there are certain predictable temporal thresholds at which the normal physiological changes either induce a heightened response (e.g., while shifting from saltwater to freshwater) or confer resilience to acute stress (e.g., while on spawning grounds).

Application and future research

A conservation physiology approach has provided new insights into the ways in which context affects how salmon respond to and recover from fisheries-capture (Fig. 1). Although much of the work is of value to the biology of stress, an important goal of research on post-release survival is to generate management prescriptions that reduce unwanted collateral impacts of fisheries. Unfortunately, the complex nature of a multi-species, multi-population, multi-gear, multi-sector fishery that targets and releases fish that are dynamically changing during maturation and senescence is such that generic management prescriptions are difficult. Thus, management decisions are inherently subject to some degree of uncertainty and will usually need to rely on "imperfect" or incomplete scientific information. However, the level of uncertainty differs among the six themes described in this article. A considerable amount of work has focused on the effects of temperature on survival (Hinch et al. 2012), particularly in sockeye salmon, and some general trends are quite clear, one of which is that post-handling and post-release survival decrease substantially when water temperatures exceed 19°C (Gale et al. 2011, 2014; Martins et al. 2011; Robinson et al. 2013). Those trends have been observed both in the field and in the laboratory, and are supported by experimental data from multiple levels of biological organization (e.g., molecular, cell, whole-body; Eliason et al. 2011; Jeffries et al. 2011; Gale et al. 2014; Jeffries et al. 2014). Moreover, the general negative effect of warm water on stress and survival after catch-and-release is well established across fish species (Gale et al. 2013). Several recent telemetry-based studies of survival (e.g., Donaldson et al. 2011, 2012, 2013; Raby et al. 2014b, in press; Nguyen et al. 2014; Robinson et al. 2015) have yet to be integrated into a broader quantitative analysis of the effects of temperature, as previously carried out by Martins et al. (2011). This logical next step could enable management to dynamically adjust the estimates of mortality applied



	Characteristics			
	Fisheries	**Abiotic**	**Biotic**	**Research**
Terminal Zone Fisheries	Catch-and-release angling occurs but little non-target, capture-and-release occurs in harvest fisheries.	Usually lower water temperature relative to earlier in migration, but not always.	Weaker cortisol response to stressors; stress physiology may be reconfigured to resist negative effects on reproduction; scales fused into skin confer some resilience to netting injuries.	Fate of fish can more easily be physically verified after release in some systems.
Mainstem In-River Fisheries	Primarily recreational and aboriginal fisheries – both commercial and food, social, ceremonial in the latter case.	Exposure to sometimes challenging flows and temperatures.	Maturation schedules and thermal tolerance vary among stocks and species. Individuals with larger cortisol responses more likely to perish after release. Female sockeye more sensitive than males, especially in warm water.	Conducive to telemetry tracking. Ocean-tagged fish that survive to reach freshwater can be used to establish background mortality rates.
Estuarine & River Tidal Zone Fisheries	Mixture of commercial, recreational, and First Nations fisheries.	Fish experience a rapid increase in temperature, turbidity, and decrease in salinity as they move from saltwater to freshwater.	Physiological transitions to endure warmer water (in most cases) and osmoregulate in freshwater. Novel exposure to freshwater pathogens.	Very little data on whether sensitivity to capture is different during this stage of migration.
Marine Fisheries	Majority of total salmon caught (via commercial fisheries) and thus most of the capture-and-release.	Generally low (8-12 °C), stable seawater temperatures.	All fish are 'silver', which makes scale loss a critical factor. Post-release predation risk likely substantial.	More difficult and expensive than in-river. Especially difficult to target a stock or species.

Fig. 1 A schematic of how abiotic and biotic factors, fisheries, and research challenges can change across stages of the spawning migration of Pacific salmon in ways that are relevant to catch-and-release.

to released fish (e.g., apply a higher value when temperatures are 19+°C) based on water temperature data that are available in real-time from in-river monitoring stations and forecast models (Hague and Patterson 2014).

Unlike the ubiquitous effect of temperature, the trend of sex-specific patterns in stress and mortality seems relatively unique to salmon, but has emerged repeatedly (Gale et al. 2011; Clark et al. 2012; Jeffries et al. 2012b; Robinson et al. 2013; Raby et al. 2015a). Whether this trend can be used in management models remains unclear; managers of salmon fisheries currently have targets for the number of fish that reach spawning areas, but not sex-specific targets. Moreover, it remains unknown whether fisheries-induced sex-specific mortality can be detected in changes in sex ratios at spawning areas; empirically testing such a hypothesis would be a challenge. An alternative approach that emphasizes the reproductive value of females would be to apply a female-based mortality rate to all fish released by a fishery for which sex-specific estimates are available. Unfortunately, well-defined sex-specific rates of mortality are unavailable for most contexts because of difficulties in determining sex in the field. Most salmon fisheries target fish early in their reproductive maturation (in the ocean or shortly after freshwater entry) which usually precludes accurate identification of sex without the analysis of sex steroids because (external) secondary sexual characteristics are poorly developed at this stage of maturation. To allay the concern that drawing blood samples from fish (to assess sex steroids) could affect rates of mortality, we avoided doing so in field-studies focused on estimating mortality (e.g., Donaldson et al. 2011; 2013; Raby et al. 2014b; Robinson et al. 2015) despite some evidence that blood biopsies are relatively benign (Cooke et al. 2005; Raby et al. in press). Therefore, future recommendations on sex-specific mortality rates will need to rely on a combination of laboratory experiments and limited sex-specific field studies.

It is well-established in the fisheries literature that, all else being equal, greater levels of stress and physical injury lead to a greater likelihood of post-release mortality (Kaimmer and Trumble 1998; Benoit et al. 2010; Davis 2010), and that seems to hold true for Pacific salmon (Crossin et al. 2008; Baker and Schindler 2009; Donaldson et al. 2011; Raby et al. 2012, in press). Therefore, rapid and simple vitality assessments that quantify injury and reflex impairment (a useful proxy for fatigue and physiological disturbance; Davis 2010; Raby et al. 2013, in press; McArley and Hebert 2014) may provide an effective path toward a better understanding of the relative effects of different fishing gears, handling practices, and to some extent, temperature (Gale et al. 2011, 2013, 2014), across contexts and species. Vitality assessments can be used to provide rough approximations of post-release mortality risk (Benoît et al. 2010; Davis 2010), and as such could be used in fisheries observer programs to triage which fisheries require targeted research aimed at rigorously quantifying mortality and developing solutions (e.g., Donaldson et al. 2013; Raby et al. 2014b).

Substantial uncertainty remains surrounding the biological importance and management relevance of the latter three themes discussed: among-population differences, the role of pathogens, and the effect of maturation status. It seems clear that there are some morphological and physiological differences among populations of sockeye salmon (e.g., Crossin et al. 2004; Eliason et al. 2011), and that some populations may be more resilient to warm water (i.e., the Chilko Lake population of sockeye salmon; Eliason et al. 2011; Martins et al. 2011). However, it remains unclear whether there are significant among-population differences in resilience to the stress of capture (i.e., reactivity to stress, capacity for physiological recovery). Apparent among-population differences in post-release survival may actually stem from differences in maturation status (i.e., timing relative to spawning) at the time of capture for co-migrating populations (Donaldson et al. 2012; Raby et al. 2013). Some of our findings highlight that post-release mortality rates applied by management for fish caught in one locale may be inappropriate for the same fish caught at another time during their migration, and different stages of maturity may further complicate the issue. Fisheries managers already apply different post-release mortality rates to different locations, but their application is typically for different marine locales (i.e., not river entry vs near-spawning) and in many cases are driven by the different fishing methods and gears used in these fishing areas. In addition, there is a mix of wild and hatchery-origin populations (i.e., fish returning from the ocean after having been released from hatchery production facilities ~1–4 years earlier, depending on the species). Though we have mostly used wild populations for our research, in some cases hatchery-origin adults returning to their natal hatcheries have been used for logistical purposes (i.e., Donaldson et al. 2010b; Clark et al. 2012; Raby et al. 2015a). Surprisingly, little is known about whether stress reactions and/or survival differ between hatchery-origin and wild salmon after catch-and-release (but see Wydoski et al. 1976); such research would be informative to fisheries science and management.

Pre-capture pathogen abundance and post-release proliferation of pathogens could be linked both to differences among-populations and differences in timing relative to spawning. For example, among-population differences in early life or marine habitat pathogen exposures could affect pre-capture pathogen loads, and the differences in temperatures experienced in natal watersheds during the final stages of maturation would be expected to affect the rate of capture-induced disease development for some microbes. Likewise, fish that enter freshwater well ahead of spawning and experience catch-and-release may be more at risk of developing advanced pathogen infections prior to arrival on spawning grounds, especially without the use of thermal refugia (e.g., Mathes et al. 2010). Understanding and anticipating the effects of catch-and-release on survival and migration success in a complex ecological setting requires an equally comprehensive approach and state-of-the-art tools. High-throughput qPCR can be used to detect the presence and relative productivity of viruses, bacteria and other microparasites within host tissues (Michelet et al. 2014; Miller et al. 2014). Simultaneous monitoring of the physiology of the host over time with changes in microbe burdens can help to characterize the trajectory of disease development, which can be further complemented by histopathological assessments at death. Application of these techniques in ongoing research is two-tiered: laboratory experiments provide a setting for hypothesis testing in a controlled environment while field experiments using telemetric tracking of fish incorporate stochastic factors (e.g., river flow and associated metabolic costs of swimming). Characterization of the role of infectious disease in catch-and-release is among the most important research avenues aimed at identifying the proximate mechanisms of delayed mortality. This ongoing work at molecular and whole-animal levels will help clarify how catch-and-release can result in proliferation of pathogens in different species and populations exposed to stressors at different stages of maturation and under different thermal regimes (Miller et al. 2014).

Funding

Our work is supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), Ocean Tracking Network Canada, the Pacific Salmon Foundation, the Canadian Wildlife Federation, Fisheries and Oceans Canada, the University of British Columbia, and Carleton University. S.J.C. and A.P.F. were supported by the Canada Research Chairs program. G.D.R. was supported by an Ontario Graduate Scholarship.

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