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Life-history strategies in salmonids: the role of physiology and its consequences

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ABSTRACT

Salmonids are some of the most widely studied species of fish worldwide. They span freshwater rivers and lakes to fjords and oceans; they include short- and long-distance anadromous migrants, as well as partially migratory and non-migratory populations; and exhibit both semelparous and iteroparous reproduction. Salmonid life-history strategies represent some of the most diverse on the planet. For this reason, salmonids provide an especially interesting model to study the drivers of these different life-history pathways. Over the past few decades, numerous studies and reviews have been published, although most have focused on ultimate considerations where expected reproductive success of different developmental or life-history strategies are compared. Those that considered proximate causes generally focused on genetics or the environment, with less consideration of physiology. Our objective was therefore to review the existing literature on the role of physiology as a proximate driver for life-history strategies in salmonids. This link is necessary to explore since physiology is at the core of biological processes influencing energy acquisition and allocation. Energy acquisition and allocation processes, in turn, can affect life histories. We find that life-history strategies are driven by a range of physiological processes, ranging from metabolism and nutritional status to endocrinology. Our review revealed that the role of these physiological processes can vary across species and individuals depending on the life-history decision(s) to be made. In addition, while findings sometimes vary by species, results appear to be consistent in species with similar life cycles. We conclude that despite much work having been conducted on the topic, the study of physiology and its role in determining life-history strategies in salmonids remains somewhat unexplored, particularly for char and trout (excluding brown trout) species. Understanding these mechanistic links is necessary if we are to understand adequately how changing environments will impact salmonid populations.

Key words: energetic status, lipids, maturation, metabolic rate, migration, partial migration, Salmonidae, spawning, stress

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I. INTRODUCTION

Life-history theory is based on the premise that there are trade-offs between reproduction, energetic costs and the risk of mortality. Life-history strategies are therefore the means by which organisms achieve successful reproduction in various environments or given a certain set of constraints (i.e. behavioural or physiological; Stearns, 1992). In vertebrates, the diversity of life-history strategies can be organized along a fast–slow continuum. At one end, fast life histories are typified by rapid growth, early maturation, high reproductive rates and short lifespans. At the other end, slow life histories are characterized by slow growth, delayed maturity, low reproductive rates and long lifespans during which opportunities to reproduce are repeated (Promislow & Harvey, 1990; Stearns, 1992). Although these different life-history strategies have been well studied and are now widely recognized, they are perhaps best known among the salmonid fishes. Salmonids hatch in fresh water, where they spend a few months to several years growing depending on the species and location (Groot & Margolis, 1991; Klemetsen *et al.*, 2003). As juveniles, they may migrate to sea (anadromy) or remain in fresh water their whole life (residency), although not all species display partial migration. All mature individuals spawn in fresh water (or estuaries in the case of pink salmon, *Oncorhynchus gorbuscha*), after which some individuals may die (semelparity) while others may survive (iteroparity), again depending on the individual and species. As such, salmonids can deviate from the fast–slow continuum in several ways; for example larger, slower-maturing individuals (anadromous) do not necessarily have longer lifespans or repeated opportunities for reproduction (semelparous).

It is these deviations from the fast–slow continuum, or the resulting diversity of life-history patterns among salmonids, that have piqued the curiosity of salmonid researchers for decades. This has stimulated a plethora of studies on various life-history tactics such as age and size at maturity (Bohlin, Dellefors & Faremo, 1996; Barson *et al.*, 2015), alternative reproductive tactics (Gross, 1985; Fleming & Reynolds, 2004; Dodson *et al.*, 2013), and alternative migratory tactics (Bond, Miller & Quinn, 2015; Quinn, McGinnity & Reed, 2015; Ferguson *et al.*, 2019). Most studies have used ultimate considerations to make predictions about the expected fitness (i.e. reproductive success) resulting from different life-history pathways. While valuable, this approach does not attempt to define the mechanisms or drivers (proximate considerations) of life-history strategies.

Interest in understanding the drivers of life-history strategies, particularly on an individual basis (i.e. why does individual A follow strategy X, while individual B follows strategy Y?), has grown in recent years. Differences in life-history strategies can have both environmental and genetic underpinnings (Pulido, 2011), although the degree to which these contribute to resulting strategies can vary widely (Ferguson *et al.*, 2019). The conditional strategy concept proposes that if the fitness gained from alternative life histories depends primarily on individual phenotype (e.g. age, sex, energetic state, etc.), then different strategies regulated by the same genotype may be maintained within populations (Repka & Gross, 1995; Gross & Repka, 1998). For example, phenotypic expression related to aspects of lipid synthesis and metabolism differs markedly between migratory and resident brown trout (*Salmo trutta*) living sympatrically (Wysujack *et al.*, 2009). In the realm of salmonid research, much attention has been given to the environment (e.g. Nevoux *et al.*, 2019) and genetics (e.g. Ferguson *et al.*, 2019) as proximate causes for life-history strategies, but much less has been given to physiology (Birnie-Gauvin *et al.*, 2019; Ferguson *et al.*, 2019). By mediating the links between individuals and their environment, physiological processes related to metabolism, nutrition, stress and thermal relationships (Ricklefs & Wikelski, 2002) are increasingly being recognized as necessary to understand and explain animal variation in life histories adequately (Hinch *et al.*, 2005).

There is a fundamental need to obtain and/or have sufficient energetic resources necessary for maintenance, growth and reproduction, which drives a wide range of behavioural processes (Stearns, 1989). Energetic resources are inherently linked to physiological processes, including metabolic rate, energy storage and stress (e.g. diseases). It would therefore be valuable to investigate physiology as a proximate cause of life-history tactics. To date, there is no literature reviewing physiology as a driver of life-history strategies in salmonids. Our aim was therefore to provide such a review, focusing on major life-history 'decisions' found broadly in many/most salmonids: (*i*) anadromy *versus* residency; (*ii*) timing of juvenile outmigration; (*iii*) timing of sexual maturation and age at maturity; (*iv*) timing of return migrations; (*v*) reproductive investment; and (*vi*) repeat spawning and associated behaviours. We further discuss how these may be impacted by environmental change, the related implications, and provide a research agenda to guide researchers in their quest to understand the physiological drivers of life-history strategies.

II. PHYSIOLOGICAL ASPECTS AND THEIR ROLE IN DETERMINING LIFE-HISTORY STRATEGIES

(1) Anadromy *versus* residency

Many species of salmonids are known as partial migrants, where some individuals migrate to sea while others remain in freshwater their whole life. Brown trout, rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*) and Arctic charr (*Salvelinus alpinus*) are well-known partially migratory species. There is also evidence suggesting that migratory strategies are not as dichotomous as first thought but are better described as a 'migration continuum' (Cucherousset *et al.*, 2005; Boel *et al.*, 2014). However, for the purpose of this section, we will strictly focus on the physiology that underlies the decision to migrate to sea (anadromy) or reside in rivers.

Generally, the expression of anadromy or residency is shaped by factors affecting energy acquisition and allocation (e.g. Forseth *et al.*, 1999; Morinville & Rasmussen, 2003; Boel *et al.*, 2014; Sloat & Reeves, 2014), and is influenced by environmental factors and presumably underpinned by genetically determined norms or thresholds (Pulido, 2011). The threshold model has been used widely to describe whether an individual will migrate or reside (Bohlin *et al.*, 1996). The model initially relied on the idea that if size or growth performance surpassed a certain threshold at a decision window (thought to be in late summer/early autumn), migration will take place the following spring (Metcalfe, 1998; Thorpe *et al.*, 1998). The model has since been extended to describe the role of various status traits; for example, if lipid stores surpass a certain threshold at a decision window, residency and/or maturation will occur (Thorpe *et al.*, 1998; Boel *et al.*, 2014). The 'threshold' is thought to be, at least in part, genetically determined, and influenced by factors such as sex and the environment. Consequently, most research to date has focused on the role of genetics and the environment (Ferguson *et al.*, 2019), with less work on physiology despite evidence for its role in determining anadromy or residency at the proximate level.

Metabolic rate, and its consequences on energy acquisition and allocation processes, appears to play a critical role in the decision to migrate or not. However, metabolic rate can be confounded with factors such as food consumption and growth (Rosenfeld *et al.*, 2015), so the link between metabolic rate and migration is dependent on other factors such as food availability (Metcalfe, Van Leeuwen & Killen, 2016). In brook trout for example, migrants tended to have higher metabolic costs, such that future migrants had consumption rates 1.4 times higher than those of future residents, but had significantly lower growth efficiencies (Morinville & Rasmussen, 2003). Increased metabolic costs can result from higher standard metabolic rates (SMRs) and/or higher activity costs, and appear to encourage migration to sea, where food opportunities are greater and thus high metabolic demands can be sustained. Individuals with a high SMR could, however, be slow growers because their energy intake is allocated to metabolic costs instead of growth or if food is limiting (Metcalfe *et al.*, 2016), and may explain why slow-growing sockeye salmon (*Oncorhynchus nerka*) migrated while fast-growing individuals matured in fresh water (Ricker, 1938). Similar results have been observed in migratory steelhead and resident rainbow trout, where individuals with the highest growth performance did not migrate, although this was not related to SMR as individuals with a high SMR were more likely to migrate (Sloat & Reeves, 2014). However, studies have generally shown that individuals with a high SMR have higher growth rates (e.g. Yamamoto, Ueda & Higashi, 1998; Finstad *et al.*, 2007; Millidine, Armstrong & Metcalfe, 2009; Norin & Malte, 2011; Reid, Armstrong & Metcalfe, 2012), although this is context specific, with other factors such as food availability or temperature affecting this pattern.

There is much evidence supporting the idea that migrants tend to have a higher SMR than residents, at least within the same cohort [Atlantic salmon *Salmo salar* (Seppänen, Piironen & Huuskonen, 2010); brown trout (Forseth *et al.*, 1999; Cucherousset *et al.*, 2005); rainbow trout (Sloat & Reeves, 2014)], but again, these trends are likely to vary depending on the environment to which these individuals are exposed. For example, studies have demonstrated a negative correlation between migration and food availability, suggesting that even fish with higher SMRs may be less inclined to migrate when food is more abundant (Wysujack *et al.*, 2009; Archer *et al.*, 2019), further supporting the idea that migratory and resident counterparts have different energy budgets and constraints (Morinville & Rasmussen, 2003; Kendall *et al.*, 2015). It is likely that a difference in plasma growth hormone (GH) which is an important regulator of growth and metabolism in teleost fishes (Wood, Duan & Bern, 2005) will influence the SMR in individual fish. High levels of GH would increase linear growth (i.e. growth in length) relative to mass growth (lower condition factor) and potentially make the freshwater environment less suitable for some individuals (McCormick, 2012). These fish may then decide to migrate rather than remain in sub-optimum growth conditions. For instance, in landlocked (non-migratory) Atlantic salmon there is no increase in plasma GH at a time when it is elevated in migratory conspecifics (Nilsen *et al.*, 2008).

Nutritional and lipid status have been posited as candidate indicators for future life-history strategies in salmonids, generally indicating that smolts have lower lipid energy reserves than immature resident counterparts of the same age. For example, Jonsson & Jonsson (2005) found that smolts of both Atlantic salmon and brown trout had reduced lipid reserves at the smolt stage compared to the parr stage, which is supported by the finding that the process of smoltification is characterized by a period of lipid depletion and changes in lipid metabolism in steelhead trout (Sheridan, Allen & Kerstetter, 1983, 1985). Similarly, Boel *et al.* (2014) found that migrants tended to have lower plasma triacylglycerides and cholesterol levels than residents. In fact, many vertebrates that undergo physiological and morphological changes in response to a life-history decision experience a period of lipid storage followed by a period of lipid depletion (Sheridan & Kao, 1998). However, these studies, and most studies on this topic, have generally focused on internal differences after the decision to migrate or reside has already been made rather than exploring energetic status as a driver of the decision. Because migration requires a suite of physiological, morphological and behavioural changes (Tanguy *et al.*, 1994; McCormick, 2012), differences observed between migrants and residents after the decision window do not necessarily reflect the key proximate drivers at play. For example, Birnie-Gauvin *et al.* (2017) found that migrants had significantly higher antioxidant levels than residents in the autumn prior to spring migration, but this finding could still be a response to the initial decision to migrate thought to be made in late summer. Future research should aim to take physiological measurements and samples prior to the first 'decision window' to gain a better understanding of the proximate drivers at play in this context (e.g., Birnie-Gauvin, Larsen & Aarestrup, *in press)*. For instance, plasma cortisol levels may be an early indicator of whether a fish is likely to migrate or remain a resident. Cortisol is important in seawater adaptation in salmonids and studies have shown that exogenous treatment with cortisol stimulates salinity tolerance and many of the underlying mechanisms involved in saltwater osmoregulation in the gill and gut (McCormick, 2001). The relationship between a 'stressful' freshwater environment (e.g. low food, high levels of antagonistic behaviour with conspecifics) would result in elevated cortisol levels. These levels may then initiate the smolting process in fish that will later migrate to sea. Interestingly, plasma cortisol concentrations do not increase as extensively in a landlocked strain of Atlantic salmon that do not migrate during their life cycle (Nilsen *et al.*, 2008).

Experimental approaches on juvenile salmonids have shed some light on the potential impacts of stressors, including climate change, on the anadromy–residency decision, although effects can vary depending on the trait or level of organization considered. At a physiological level, increased temperature may increase metabolic rate and could lead to increased anadromy, but it may also increase feeding rate and thus balance out the effects of increased metabolic rate or even cause desmoltification. A recent study by Archer *et al.* (2020) investigated the effects of rearing brown trout under food restriction and warming (by 1.8°C) during an 18-month period, and found antagonistic effects of temperature and food restriction. Because stressors do not occur in isolation in nature, the authors highlighted the need to consider the effects of multiple stressors simultaneously, particularly given that the responses to these stressors may be contrasting (Archer *et al.*, 2020). At a population level, warming may reduce the survival of individuals which could impact the ratio of anadromy to residency. For example, Chinook salmon (*Oncorhynchus tshawytscha*) are being threatened throughout their life cycle as a result of climate change (Crozier *et al.*, 2021). If survival at the early life stages is threatened, then ratios of anadromy to residency are likely to change as these tend also to be affected by density-dependent processes.

(2) Timing of juvenile outmigration

The timing of juvenile outmigration is an important aspect of migration in anadromous species because it is an important determinant of survival at sea (McCormick *et al.*, 1998). Timing varies across populations, and individuals, so that sea entry coincides with optimal conditions, both in terms of food availability and environmental conditions (Thorstad *et al.*, 2012). Individual growth and condition, as well as other related physiological processes such as ability to acquire and utilize food, are also important factors affecting the timing of migration (Metcalfe, 1998; Forseth *et al.*, 1999; Acolas *et al.*, 2012). For example, in Atlantic salmon, individuals with higher SMRs migrated sooner than those with lower SMRs (Metcalfe & Thorpe, 1992; Metcalfe, Taylor & Thorpe, 1995), perhaps because these individuals have more to gain from reaching the sea earlier (in terms of feeding opportunities and meeting energetic demands), or because of better swimming capabilities.

Smoltification is a process by which salmonids prepare for life in sea water, which encompasses changes in morphology, behaviour and physiology, such as changes in osmoregulatory and energy allocation processes (McCormick & Saunders, 1987). For example, thyroid hormones (e.g. thyroxine) have often been linked to smoltification and imprinting in salmonids. Analyses of 27 groups of hatchery-reared coho salmon (*Oncorhynchus kisutch*) found that thyroxine peaked with the new moon, providing a mechanism by which thyroid-dependent developmental changes are synchronized in salmonid stocks (Grau *et al.*, 1981). Further, these results may suggest that thyroid hormones are involved, to a certain extent, in determining the timing of outmigration, as well as olfactory imprinting during outmigration (Ueda *et al.*, 2016). The progress of smoltification can be monitored by measuring Na^+, K^+-ATPase levels in the gills which is correlated with seawater tolerance (Nielsen, Madsen & Björnsson, 1999) and readiness to migrate (Aarestrup, Nielsen & Madsen, 2000). Accordingly, we may expect that individuals that are more advanced in the smoltification process, or that complete smoltification sooner, will migrate earlier. However a study by Nielsen, Aarestrup & Madsen (2006) showed that gill Na^+, K^+-ATPase levels in brown trout were low in migrants that migrated early in March (beginning of smolt migration), increased in late March and April, and finally decreased again in early May and continued to be low for the remaining migrants. Levels of Na^+, K^+-ATPase in the gills were nonetheless correlated with visual appearance (silvering) such that fish described as smolts had higher activity levels of the ATPase than fish described as pre-smolts (Nielsen *et al.*, 2006). Given that both smolts and presmolts were captured throughout the entire study period, it appears that completing smoltification may not be a requirement for migration, particularly given that some salmonids can tolerate salt water at 34 ppt with little changes in plasma chloride levels (Ugedal *et al.*, 1998), and can move directly into salt water with no 'adjustment period' (Moore *et al.*, 1998). Taken together, these results may suggest that other intrinsic processes, such as those related to metabolism and energy allocation, may be more important in determining migration timing than smoltification. In another study, Lee & Ueda (2012) found that during the smoltification period, masu salmon (*Oncorhynchus masou*) that lost an aggressive interaction to another individual exerted strong influence on downstream movement and olfactory function. Specifically, less-aggressive individuals had higher olfactory sensitivity (measured by an electro-olfactogram) and migrated earlier than more-aggressive individuals. Thus, previous encounters with conspecifics – especially aggressive interactions – can influence migration timing *and* associated physiological processes.

A range of studies have been conducted on how different experimentally applied stressors may affect the timing of migration in salmonids. These studies are particularly enlightening because they provide a link between proximate physiological causes and ultimate ecological consequences (Birnie-Gauvin *et al.*, 2020). For example, Midwood *et al.* (2016) explored the roles of energetic state and activation of the glucocorticoid stress response on migration in juvenile brown trout by food-depriving one group for 2 weeks, and elevating plasma cortisol levels through intracoelomic injections in another. The results showed that while control and cortisol-treated fish migrated at the same time, food-deprived fish were delayed by approximately 1 week, perhaps as they attempt to compensate for lost growth (Nicieza & Metcalfe, 1997). Juvenile brown trout feed extensively while still in fresh water to prepare for migration, and thus small reductions in food consumption can have important consequences (Jonsson & Jonsson, 1998). This was observed in a study by Davidsen *et al.* (2014) where juveniles with reduced feeding 6 months prior to migration were more likely to migrate before their fed conspecifics. A study by Larsson, Serrano & Eriksson (2012) found similar results, and demonstrated that hatchery smolts with lower energetic status (measured as lipid content) and wild smolts were more likely to migrate than hatchery smolts of higher energetic status. In a different study, Peiman *et al.* (2017) exposed fish to high temperatures, exogenous cortisol manipulation (i.e. increased cortisol), food deprivation and chase to exhaustion, and found that increased cortisol, high temperature and food deprivation all led to earlier migrations in low-growth individuals. These results further demonstrate that stressors, in combination with pre-existing differences in organism state (i.e. condition, growth rate), can affect when individuals migrate, and highlights the role of intra-specific differences in important life-history decisions.

Many populations of salmonids are showing earlier migration, which has been attributed to increasing river temperatures. In the North Atlantic, an analysis of Atlantic salmon smolt migration in 67 rivers over the last five decades revealed that smolt seaward migration has occurred 2.5 days earlier per decade (Otero *et al.*, 2014). The authors suggest that this shift in phenology is a response to current changes in global climate, but the effects of this shift on intrinsic physiological processes remain unclear. For example, do earlier migrations mean that fish are less prepared to enter the marine environment? Are earlier migrations contingent on earlier acquisition of adequate resources to survive migration? Do fish that leave earlier, presumably when water temperature at sea is cooler, have a lower thermal tolerance? These questions have yet to be answered, but are important for our understanding of the consequences of changing climate on the drivers of migration.

(3) Timing of sexual maturation and age at maturity

Mating systems often include alternative reproductive phenotypes, typically resulting in distinct morphologies and behaviours (Emlen & Oring, 1977). Alternative tactics are particularly well described in males of all salmonines (*Salmo*, *Onchorhynchus* and *Salvelinus* spp.), where both age and size of males at maturity are known to vary greatly (Fleming & Reynolds, 2004). Large anadromous males typically develop a large kype (hooked jaw) and rely on aggressive behaviour to compete for females during spawning, while smaller resident males 'sneak' up to females to fertilize their eggs (Gross, 1991). The advantage of early maturation (also known as precocious maturation) in males is thought to be linked to reduced pre-reproduction mortality in comparison to later maturation (Gross & Repka, 1998). Precocious mature male parr may mature again, or subsequently smoltify and migrate to sea (Berglund, 1992; Fleming, 1996). The proximate causes producing these two distinct reproductive strategies are not yet fully understood, but genetics, the environment and their resulting physiology are thought to be potential drivers (Morinville & Rasmussen, 2003; Thériault, Bernatchez & Dodson, 2007; Ferguson *et al.*, 2019). Part of these differences are a direct result of a prior life-history decision – that of anadromy *versus* residency. Anadromous and resident counterparts invest differentially in reproduction because anadromous individuals are typically older and larger, and thus have a greater age at maturity (Quinn & Myers, 2004). To avoid overlap with the previous sections, this section focuses on the physiological drivers of precocious maturity, although relevant points are made about the influence of physiology on age at maturity more broadly.

Sexual maturation begins at fertilization, at the embryo stage, when investment in gonadal growth begins and germinal tissue starts to differentiate (Adams & Thorpe, 1989). Maturation is regulated through inhibition and is continuously repressed until the 'decision' to sexually mature is made (Thorpe, 1994). Lipid content and size in early life are thought to be particularly important in determining individual maturation schedule, and have been the focus of most research on precocious maturity (e.g. Thorpe *et al.*, 1998; Shearer *et al.*, 2006; McMillan *et al.*, 2012). For example, a study on wild rainbow trout found a positive relationship between early maturity, growth and whole-body lipids 6 months to 1 year prior to spawning (McMillan *et al.*, 2012). Similar findings have been observed in brown trout (Jonsson & Jonsson, 2005), Atlantic salmon (Jonsson & Jonsson, 2005) and Chinook salmon (Shearer *et al.*, 2006). Similar determinants are likely at play in other salmonid species.

Because maturation and smoltification are considered competing processes, maturation is also affected by factors related to energy acquisition and partitioning (Dellefors & Faremo, 1988). Evidence to date suggests that individuals able to acquire energetic resources and allocate them into lipid storage efficiently are more likely to mature early, and that this early maturation strategy is far more common in males than females (Jonsson & Jonsson, 2011). In this context, a key intrinsic trait shaping energetic processes is SMR, a measure of the rate at which an animal partitions energy to maintain basic physiological functions. In salmonids, SMR is known to vary extensively among individuals (Enders & Scruton, 2005; Tyler & Bolduc, 2008). Atlantic salmon with higher SMR had greater total energy expenditure when digesting a meal than individuals with lower SMR, but the duration of increased metabolism after eating was shorter (Millidine *et al.*, 2009). Thus, even though higher SMR can be associated with greater access to food and/or greater food consumption, it may come at the cost of lower energy assimilation efficiency, and is therefore likely to have an important proximate influence on the timing of sexual maturation (Millidine *et al.*, 2009; Sloat & Reeves, 2014). In one study, female rainbow trout with low SMR were more likely to mature early (Sloat & Reeves, 2014). Taken together, these results suggest that females with low SMR had more surplus energy available due to lower metabolic demands, thus enabling early maturation. Sloat & Reeves (2014) also found no effect of SMR on maturation in males, which may be a result of the lower cost of maturation in males compared to females (Fleming & Reynolds, 2004). This is further supported by the fact that precocious maturity in females is rather rare. In another experiment, where Atlantic salmon were reared under either low or high swimming speeds, and low or high dissolved oxygen levels, precocious sexual maturation in males was associated with low swimming speed, but not dissolved oxygen levels (Waldrop *et al.*, 2018). Again, this likely is a result of low swimming speed being associated with lower energy expenditure, and thus the energetic surplus in these individuals could be allocated to maturation (Palstra & Planas, 2011). Energetic budgets and physiological processes are thus at the core of the *when* to sexually mature.

Age at maturity is an important fitness trait, for which selection usually favours earlier maturation in males than in females (Schaffer, 2004). In salmonids, this may be viewed in the context of precocious maturation in fresh water, or as shorter periods spent at sea in anadromous individuals (one *versus* two sea winters). A study by Barson *et al.* (2015) on Atlantic salmon found that the vestigial-like family member 3 gene (*VGLL3*) promoted earlier maturation in males and later maturation in females. The gene is known as an adiposity regulator in humans, thus the timing of sexual maturation in salmonids appears to be linked to physiological processes due to (at least in part) genetic influence. Similar studies on other salmonid species have not (yet) found such a significant influence of genetics, even in the closely related brown trout [see Ferguson *et al.*, 2019 and references therein].

Growth and development in fishes are strongly influenced by water temperature through its effects on physiological processes (Railsback & Rose, 1999; Farrell *et al.*, 2009). However, it is difficult to make predictions about how increasing water temperatures may affect the timing of sexual maturation because the 'decision' to mature early or late is complex, and likely differs depending on location. For example, increasing temperatures may result in faster growth rate, under the assumption that adequate food availability is present, and thus lead to early sexual maturation. However, increasing water temperatures may also lead to increased SMRs, and may result in faster energy utilisation, reduced lipid content, and thus later sexual maturation (Tocher, 2003; McMillan *et al.*, 2012). Within this context, changing climate is likely to impact the timing of sexual maturation, with potentially important consequences on population dynamics. This is an important concept to explore, especially given that our understanding of the proximate drivers for sexual maturation is incomplete, but also because sexual maturation could have important effects on the sustainability of salmonid populations.

(4) Timing of return migration

As fish begin to mature, it is necessary for them to start their journey back to fresh water to reach their inland spawning grounds. In reality, the time salmonids spend at sea (a few months to several years) is very much cyclical as they explore the rich ocean feeding ground (Groot & Margolis, 1991; Klemetsen *et al.*, 2003; Jensen *et al.*, 2020). That is, even as they are maturing they may already be moving closer to their spawning ground. As such, discussions about the timing of return migration are complex in that we know little about the exact transition between the time when fish are feeding and maturing in the ocean to when they begin active homeward migration (and any potential overlap between these stages). Very little physiological research has occurred in the high seas, so most of our knowledge about the timing of migration arises from work in the coastal approach, estuaries, or the initiation of upriver migration. Thus most of the discussion here focuses on these latter phases rather than those pertinent to when salmonids make decisions to mature and begin their homeward journey [but see Bett & Hinch, 2016 and Ueda, 2019 for reviews on homing].

From an ecological perspective, the timing of reproductive migration (referred to as the return migration in the context of salmonids) is extremely important. Timing needs to coincide with (*i*) when animals have secured sufficient energy to migrate and mature, (*ii*) conditions that match their physiological tolerances and capacities, (*iii*) when conspecifics from the same population are themselves about to undertake their journey back to fresh water, and (*iv*) when conditions are adequate for egg survival and development as well as early juvenile development. For these reasons, and because return migrants also need to arrive at the spawning grounds during favourable environmental conditions for reproduction and egg development, the timing of return is a highly heritable trait (e.g. Hansen & Jonsson, 1991; Smoker, Gharrett & Stekoll, 1998; Quinn, Unwin & Kinnison, 2000). Therefore, poor decisions with respect to the timing of return migration will have important consequences for individual fitness and population-level processes.

The high level of predictability in timing reflects population-specific (and individual) adaptations to historic conditions experienced during the freshwater stage of migration such as temperature, flow and other abiotic factors (Hodgson *et al.*, 2006; Jonsson & Jonsson, 2009). Indeed, research has revealed that body shape (Crossin *et al.*, 2004), energetics (Hendry & Berg, 1999), and even cardiorespiratory performance (Eliason *et al.*, 2011) are associated with migration difficulty and historic environmental conditions emphasizing the role of local adaptation. Water temperature is inherently linked to physiology in that it influences all biological processes in fish. However, even sea surface temperatures can influence migratory timing (Hodgson *et al.*, 2006; Drenner *et al.*, 2015). Specifically, there is evidence that variations in salmonid distributions at sea among years reflect temperature conditions with the timing of homeward migration initiation being a population-specific trait and largely independent of the actual location of the fish (Jonsson & Jonsson, 2011). In reality, all environmental conditions presumably interact with organismal state and life history in complex ways to influence migration timing for a given individual and population (Robards & Quinn, 2002; Dahl *et al.*, 2004).

Because salmonids transition from salt water to fresh water in order to begin their upriver migration, timing also depends on individual fish making necessary physiological adjustments related to osmoregulation (Høgåsen, 1998). In fact, salinity in the coastal approach and estuaries may play an important role in river entry timing. Thomson & Hourston (2011) revealed that lower estuarine salinities encountered by returning sockeye salmon were associated with earlier river entry. Yet, several studies of gill Na^+, K^+-ATPase have failed to identify strong relationships between osmoregulatory preparedness and upriver migration (Shrimpton *et al.*, 2005), perhaps because the surface to volume ratio is smaller in larger fish, and thus the effects of changes in salinity are likely also smaller in large fish. Crossin *et al.* (2009*a*) found some evidence that fish that entered early had higher levels of gill ATPase than those that remained in the estuary. It appears that these mechanisms are most important in the phase associated with river entry, with little evidence that preparation occurs in the high seas.

Much of what we have learned in recent years about the direct link between physiological status and spawning migration initiation comes from a series of studies that combine telemetry with non-lethal tissue biopsy (e.g. for physiological assays or genomic analysis). In a study of sockeye salmon destined for the Fraser River of British Columba, fish were intercepted ~200 km from the estuary, implanted with radio tags, and non-lethal biopsy (e.g. blood sample, gill tissue, energy assessment) was conducted before the fish were released to continue their journey (Cooke *et al.*, 2008). Some of the tagged fish stayed in the estuary (which is normal) while others entered the river immediately. Fish that entered the river immediately were in a more advanced state of reproductive maturation based on hormones and energy measures. Although only correlative, this study provided evidence that triggers for early migration into fresh water may be related to a relatively advanced reproductive development and higher energetic status relative to 'normal-timed' migrants. A similar study (Crossin *et al.*, 2007) using acoustic telemetry and the same non-lethal sampling protocol in other sockeye salmon stocks revealed a correlation between levels of circulating testosterone and river entry timing for females but not males. Plasma K^+, Cl^-, glucose, lactate and osmolality were also correlated with entry timing in both sexes emphasizing that a number of physiological systems are implicated in the timing. Unfortunately, there has been much more research combining telemetry and physiological samples to study return/spawning migrations in semelparous species than iteroparous species, calling for more focus on the latter in future studies.

Crossin *et al.* (2009*b*) tested the pleiotropic effect of reproductive hormones on migratory behaviour using an experimental approach. Sockeye salmon bound for the Fraser River were intercepted while they were transiting the Gulf of Alaska and then gonadotropin-releasing hormone (GnRH) and/or testosterone were experimentally elevated and fish were implanted with acoustic telemetry tags to assess behaviour. The study found little evidence that exogenous hormone treatment influenced migration speed and timing but pre-treatment levels of testosterone (measured in non-lethal blood samples) correlated negatively with travel times across all treatments. However, other studies that involve exogenous application of GnRH revealed that it does trigger the hypothalamic–pituitary–gonadal (HPG) axis, thus accelerating maturation and presumably the timing of river entry (e.g. Sato *et al.*, 1997; Fukaya *et al.*, 1998; Mylonas & Zohar, 2001). There is therefore evidence that GnRH and HPG activation are involved in initiating spawning migrations although the exact time at which these mechanisms come into play is unknown.

The development of the olfactory system in maturing salmonids may also be a physiological mechanism controlling the final stage in the spawning migration (Moore *et al.*, 2012). The sense of smell is known to play an important role in the homing of salmon to the spawning grounds (Nordeng, 1977; Hasler & Scholz, 1983; Nevitt *et al.*, 1994; Dittman & Quinn, 1996; Dittman, Quinn & Nevitt, 1996) although identifying the olfactory cues involved has been problematic. It has been posited that olfactory cues from natal rivers flowing into the sea may trigger upriver migration in Atlantic salmon (Hasler & Scholz, 1983). Spawning female Atlantic salmon are known to release olfactory cues that attract males (Moore & Scott, 1991), that prime the reproductive status of the males, and thus ensure synchronized spawning between the male and female (Moore & Waring, 1996; Moore *et al.*, 2002). However, the olfactory sensitivity of the male salmon to female reproductive pheromones only occurs during a brief window when the fish is sexually mature during October/November (Moore & Scott, 1991; Moore & Waring, 1996). The seasonal olfactory sensitivity of salmon to reproductive cues may be a possible explanation as to why some fish may reside for long periods in fresh water during significant flow events but subsequently undertake the final migration to the spawning grounds later in the year.

If marine environments offer better growth opportunities for anadromous salmonids, they should stay at sea as long as possible to maximize fecundity. However, 'premature migration', where fish return long in advance of reproduction, has been observed in all major genera of salmonids (reviewed in Quinn *et al.*, 2015; Reed *et al.*, 2017). While the causes for premature return migrations remain elusive, Quinn *et al.* (2015) have proposed two (non-mutually exclusive) hypotheses. First, the 'best of a bad situation' suggests that if freshwater return migrations are particularly challenging, such that fish could not ascend shortly before spawning, they may return in advance, but pay an energetic cost from lost feeding opportunities at sea and fasting in fresh water (Healey, 2001). However, this hypothesis cannot explain premature migrations in locations without challenging freshwater conditions. The second 'risk of mortality' hypothesis posits that fish may be balancing the costs of early departure from sea (lost feeding opportunities) against the costs of remaining at sea (i.e. increased mortality due to predation risks and parasitism). This hypothesis may explain why larger, older Atlantic salmon are often observed as the first to arrive in spring, even though spawning only occurs in the autumn (Shearer, 1990) or why premature return migrations are observed in sea trout infected with salmon lice (Halttunen *et al.*, 2018) or why the availability of habitat in lakes and rivers affects the occurrence of premature migrations (Reed *et al.*, 2017). Within this context, migration timing thus reflects energetic trade-offs. Smaller fish might benefit more from staying at sea longer as they would grow more in proportion to their size than larger fish, because larger fish already have a size advantage for competition. Smaller fish also exhaust finite energy stores more quickly than larger fish because they have higher mass-specific metabolic rates (Lennox *et al.*, 2018). Because growth is regulated by intrinsic physiological processes, physiology is a key factor regulating the timing of return migrations due to its impact on the trade-off between gained energetic benefits and increased mortality of staying at sea. While the topic has been investigated in Pacific salmon species, it remains a rare focus of research in many any other salmonid species, providing us with an interesting avenue for future research.

The timing of reproduction migrations in migratory animals is changing as a result of climate change (e.g. Cotton, 2003; Wilcove & Wikelski, 2008). Although climate change can act on wild salmonids in many ways (e.g. prey mismatches, thermal tolerances), almost all of the predicted changes have a physiological link given the manifold effects of water temperature on fish. There is already evidence of earlier migrations occurring across populations of Atlantic salmon (Juanes, Gephard & Beland, 2004) with dates of upriver migration shifting by 0.5 days per year (on average). More recent work by Dempson *et al.* (2017) found similar evidence of advances in migration timing with warming climate while in Europe there is evidence that climate change is delaying migration (e.g. Aprahamian, Davidson & Cove, 2008). Other work on Chinook salmon has revealed roles for both broader environmental conditions (e.g. ocean conditions and indices) as well as in river conditions for influencing migration timing (Keefer, Peery & Caudill, 2008*a*), emphasizing the potential for climate change to influence conditions both on the high seas and at river mouths. Other studies have revealed that climate-related changes in CO_2 and ocean acidification affect olfaction in pink and coho salmon, with likely effects on homing (Ou *et al.*, 2015; Williams *et al.*, 2019). Overall, there is a need to understand better how climate change will influence the mechanisms (e.g. environmental, genetic, physiological) associated with individual and population differences in migration timing. This should include physiological research with an emphasis on physiological genomics and the incorporation of an experimental approach (Birnie-Gauvin *et al.*, 2020) rather than relying solely on associations.

(5) **Reproductive investment**

Reproductive investment can be divided into three components: (*i*) the production of gametes, (*ii*) intra-sexual competition, and (*iii*) parental care (Williams, 1966). The study of these components is of interest to explore how individuals adapt to their environment and simultaneously maximize their reproductive output, but remains challenging as partitioning reproductive investment between these components is difficult. To date, studies investigating reproductive investment in salmonids have generally used loss of mass as a proxy for energy expenditure during reproduction, although this approach combines mass loss as a result of both gamete release and breeding behaviours (e.g. Jonsson, Jonsson & Hansen, 1997; Fleming & Reynolds, 2004). However, Gauthey *et al.* (2015) investigated the energy expenditure associated with brown trout reproductive investment using both variation in mass and variation in plasma metabolites, as well as estimating overall reproductive success through the genetic assignment of offspring. Interestingly, the study showed that plasma triglycerides and fatty acid concentrations decreased throughout reproduction, while amino acids and glucose concentrations did not change. The authors found that the decrease in lipids was not related to initial concentrations nor to variation in mass, and suggested that metabolite variation during spawning likely reflected energy investment (Masello & Quillfeldt, 2004). Gauthey *et al.* (2015) additionally found that females generally had higher concentrations of triglycerides and fatty acids than males at the onset of reproduction. Furthermore, the relative variation in metabolites and mass during reproduction was correlated with the number of offspring produced, indicating that gametic and behavioural reproductive investments contribute greatly to reproductive success, at least in brown trout.

Breeding systems of sexually reproducing organisms are classified as semelparous (single life-time reproductive event) or iteroparous (repeated reproductive events) as strategies to maximize lifetime fitness (Cole, 1954; Murphy, 1968). Among salmonid species, there is wide variation in reproductive strategies, where some species are almost exclusively semelparous while other species show various degrees of iteroparity. In the context of a life-history trade-off between current and future reproduction, energy investment in each spawning event (for spawning migrations, gamete production, development of secondary sexual traits, as well as competitive and spawning activities) is negatively associated with the probability of future (repeated) spawning in salmonids (Fleming, 1998; Fleming & Reynolds, 2004). More specifically, species investing 71–85% of their total energy reserves into current reproduction are semelparous, while Atlantic salmon and steelhead trout, which invest up to 65% of their total energy in reproduction, generally show relatively low levels (10–11%) of iteroparity (Fleming, 1998; Fleming & Reynolds, 2004). In comparison, brown trout, Arctic char, brook trout, and Dolly Varden char (*Salvelinus malma*), which generally invest less in each spawning event (46–52% energy investment), tend to show a higher repeat spawning probability (21–40%) of iteroparity (Fleming, 1998; Fleming & Reynolds, 2004). This continuum in spawning investment and iteroparity can also be observed within populations of the same species, as illustrated for Atlantic salmon by Jonsson *et al.* (1997) who found that the level of energy expenditure for reproduction was negatively correlated with the post-spawning survival rate within populations.

Unfortunately, the role of physiological mechanisms has seldom been assessed in the context of identifying potential proximate drivers of variability in reproductive investment in salmonids (with a few exceptions, such as those presented above). This is an important area of focus for future research, with important implications for individual fitness, selection and associated population-level processes.

(6) Repeat spawning and associated behaviours

Despite limited knowledge on the factors underlying individual variability in the migratory decisions and success of the post-spawning life-history stage of iteroparous salmonids (i.e. kelts) (Drenner *et al.*, 2012; Lennox *et al.*, 2019), a growing number of studies have documented that post-spawning nutritional state can affect subsequent migratory behaviour and survival of wild salmonids. Within populations, Atlantic salmon kelts in poor post-spawning body condition and low blood plasma triglyceride levels (the principal energy substrate in fish; Sargent, Tocher & Bell, 2002) have been observed to initiate seaward migration earlier than individuals in better nutritional condition (Halttunen *et al.*, 2013; Bordeleau *et al.*, 2019). Earlier marine entry of post-spawned individuals has also been linked to low levels of blood plasma triglycerides in brown trout (Eldøy *et al.*, 2021). Furthermore, Birnie-Gauvin *et al.* (2019) observed that early-descending post-spawned kelts of both Atlantic salmon and brown trout had elevated levels of baseline plasma cortisol and suggested that the early timing of decent was a behavioural stress response to depleted energy stores. Early-descending Atlantic salmon kelts in poor post-spawning nutritional state (low body condition and plasma triglyceride levels) or elevated stress levels (high plasma cortisol and glucose) and potentially immune altered (high prostaglandins E2 concentration), have a reduced probability of survival to repeated spawning (Bordeleau *et al.*, 2018*b*, 2019). Similarly, Keefer *et al.* (2008*b*) documented that post-spawned steelhead kelts in Colombia River in good external condition (based on the degree of visible external damage) were more likely to return from the following marine feeding migration compared to individuals in poorer body condition.

Once in the marine environment, brown trout individuals in low body condition have been found to migrate further out in fjord systems in Norway, to potentially riskier habitats, compared with individuals in better nutritional condition (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018*a*). In addition, brown trout in poor nutritional state (i.e. low plasma triglyceride) also tended to spend longer periods at sea to recondition (Bordeleau *et al.*, 2018*a*; Eldøy *et al.*, 2021), with prolonged exposure to marine threats. Collectively, these studies provide evidence of condition-dependent risk-taking (McNamara & Houston, 1987, 1994; Heithaus *et al.*, 2007; Anholt & Werner, 2009) in some salmonids, where energy-depleted kelts have lower survival prospects, likely due to a combination of limited resources to sustain basal metabolic processes and the necessity to migrate to a risker habitat in order to regain nutritional balance (Bordeleau, 2019). Similarly, Haraldstad *et al.* (2018) showed that brown trout with poor post-spawning body condition were more likely to skip the following spawning season, possibly due to insufficient reconditioning. However, this study did not attempt to recapture fish nor did it account for straying, so these results should be interpreted carefully. While little scientific evidence exists on the drivers of consecutive and alternate repeat-spawning strategies, findings from Reid & Chaput (2012) point towards energy limitation acting as an important factor, with consecutive Atlantic salmon spawners showing lower egg quality than alternate spawners who had more time to recondition.

These findings suggest that the post-spawning nutritional state of salmonid kelts, as determined by pre-spawning energy stores and the level of energy investment into spawning, are at least partly responsible for subsequent individual variability in spatiotemporal aspects of their habitat use, as mediated by environmental conditions and anthropogenic stressors. While many factors are at play, the interaction between spawning investment, post-spawning physiological state, subsequent behavioural responses and the effect on future repeat spawning potential of iteroparous species should be of particular focus to understand the related trade-offs better. Such studies also offer a promising avenue for predicting the consequences of anthropogenic impacts and climate change on the population dynamics of iteroparous salmonids. For example, warming rivers due to climate change, delay at barriers, light pollution and other anthropogenic changes are expected to increase the energy use of salmonids while in fresh water (Lennox *et al.*, 2018; Nevoux *et al.*, 2019). Given the available information about how post-spawning nutritional state influences subsequent migratory behaviour and survival, this should merit further investigations as it may compromise the ability of some individuals to reproduce more than once. Studies have revealed that larger body size in Atlantic salmon resulted in less relative energy depletion and greater resilience to increases in pre-spawning temperature, which could confer a benefit to larger, repeat spawners (Lennox *et al.*, 2018). Other studies have identified similar patterns, such as a higher thermal tolerance and lower vulnerability to thermally induced reproductive inhibition in repeat spawners than in maiden spawners [cultured Tasmanian Atlantic salmon (Pankhurst *et al.*, 2011; Anderson *et al.*, 2012)], suggesting greater tolerance to environmental disturbances in repeat spawners. Furthermore, the eggs of repeat spawners were also found to have greater tolerance to hypoxic conditions (cultured Tasmanian Atlantic salmon; Polymeropoulos, Elliott & Frappell, 2016). In that context, rising water temperatures may affect an individual's ability to reproduce more than once.

While iteroparity is a bet-hedging strategy allowing the risk of reproductive failure to be spread over multiple spawning seasons (Slatkin, 1974), with quantified benefits to population-level processes, increased post-spawning mortality due to anthropogenic activities (e.g. hydropower production, open net-pen aquaculture, fishing activity, or captive reproductive programs) could potentially lead to the disappearance of iteroparity in some regions (Bordeleau *et al.*, 2020), with important repercussions on population recovery and resilience.

III. IMPLICATIONS AND FUTURE WORK

Understanding both the proximate and ultimate drivers of migration is necessary if we are to predict the fate of migratory species as they face changing environmental conditions (Wilcove & Wikelski, 2008; Shaw, 2016). Most studies to date have focused on genetics and the environment as proximate causes of life-history strategies in salmonids, with limited attention to the influence of physiology. These are important considerations to address important knowledge gaps in our

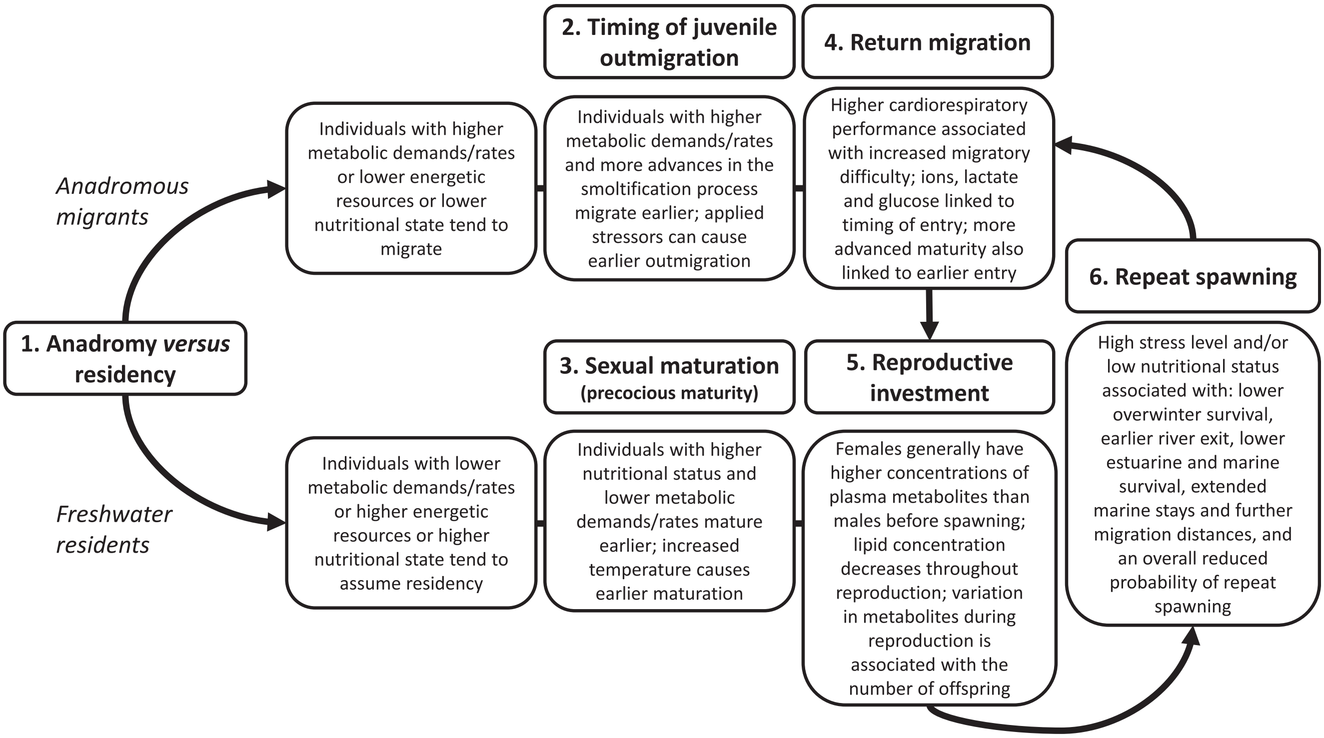

Fig 1. Summary of findings indicating the role of physiology in determining life-history strategies in salmonids. Note that this summary is not exhaustive, but rather summarizes the most common findings found across species.

understanding of the mechanistic links between internal state and behaviour (Lennox *et al.*, 2019). Along with abiotic factors, biotic factors such as genetics, morphology and physiology regulate an individual's internal state, and facilitate the maintenance of homeostasis (Uusi-Heikkilä *et al.*, 2008). As demonstrated in this review, an individual's internal state can directly influence behaviour, and behaviour can feed back to influence an individual's internal state in return, without the need for these phenotypic traits to be determined genetically. Physiological processes are at the very core of an individual's life cycle, and should be considered more broadly when studying the drivers of life-history 'decisions' (Fig. 1).

Despite being one of the best-studied families of fish, some aspects of salmonid biology remain elusive and not fully understood, particularly in terms of physiology, and more so for some salmonid species than others (Table 1). There has been relatively little physiological work done in the wild to answer some of the questions discussed herein, perhaps due to regulatory (legal) considerations associated with animal welfare legislation that impede some forms of research (Cooke *et al.*, 2016). In many instances, these regulations can be difficult to conform to in laboratory and hatchery settings, but can be a great deal more difficult to achieve when studying animals in the wild (see Sikes & Bryan, 2016). However, carefully thought out animal care protocols and that consider the 3Rs of animal experimentation (Replacement, Reduction and Refinement) can facilitate physiological samplings in the wild. Where possible and relevant, studies on wild fish may be replaced by modelling studies, but basic physiological information is still needed if scientists are to input appropriate data into models, and thus research on wild animals is necessary (Lindsjö, Fahlman & Törnqvist, 2016). Animal care protocols should ensure that the number of fish included in studies is appropriate and necessary, and techniques should be refined, particularly as they are changing and being optimized. There have been great advances recently in

Table 1. Species for which studies have investigated the role of physiology in life-history strategies, and species for which more studies are needed. NA represents cases where the particular life-history choice is not present for a given species. Note that this table summarizes where the majority of studies have focused, and does *not* suggest that more studies should not be undertaken for species that have been investigated. Rather, this table summarizes species for which studies on each topic are rare or non-existent

	Anadromy *versus* residency	Juvenile outmigration	Sexual maturation	Return migration	Reproductive investment	Repeat spawners
Brown/sea trout *Salmo trutta*	Investigated	Investigated	Investigated	Needs further investigation	Investigated	Investigated
Atlantic/Oananiche salmon *Salmo salar*	Investigated	Investigated	Investigated	Needs further investigation	Needs further investigation	Investigated
Arctic charr *Salvelinus alpinus*	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation
Brook trout *Salvelinus fontinalis*	Investigated	NA	Needs further investigation	NA	Needs further investigation	Needs further investigation
Lake trout *Salvelinus namaycush*	NA	NA	Needs further investigation	NA	Needs further investigation	Needs further investigation
Dolly Varden *Salvelinus malma*	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation
Bull trout *Salvelinus confluentus*	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation
Rainbow/steelhead trout *Oncorhynchus mykiss*	Investigated	Investigated	Investigated	Needs further investigation	Needs further investigation	Needs further investigation
Cutthroat trout *Oncochyrnchus clarkii*	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation
Sockeye/Kokanee salmon *Oncorhynchus nerka*	Needs further investigation	Investigated	Needs further investigation	Investigated	Investigated	Needs further investigation
Chinook salmon *Oncorhynchus tshawytscha*	NA	Needs further investigation	Needs further investigation	Investigated	Needs further investigation	NA
Pink salmon *Oncorhynchus gorbuscha*	NA	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	NA
Coho salmon *Oncorhynchus kisutch*	NA	Needs further investigation	Needs further investigation	Investigated	Needs further investigation	NA
Chum salmon *Oncorhynchus keta*	NA	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	NA
Masu salmon *Oncorhynchus masou*	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation	Needs further investigation

The colour shading was indicates simply to demonstrate how widely some species have been investigated.

Table 2. Proposed research questions to guide future research on the physiological basis of life-history strategies in salmonids

Life-history decision	Research questions
Anadromy *versus* residency	• What is the role of the stress axis in determining who migrates and who resides? • What are the relative roles and timing of different physiological systems and processes, and their interactions on the decision to migrate or reside? • How will changing environmental conditions (i.e. climate change) influence decisions to migrate or reside, and will that differ over a species' range? • Do physiological challenges experienced early in life affect the decision to migrate or reside?
Timing of juvenile outmigration	• Does disease resistance or pathogen load affect the timing of migration in juveniles? • Can we predict the physiological impact of climate change on smolt quality and survival in the sea? • Are autumn migrants physiologically different from spring migrants, and how? • What are the physiological drivers and processes associated with autumn migration? • What are the physiological consequences of anthropogenic disturbances (delay at barriers, light pollution, etc.) on the timing of outmigration?
Sexual maturation	• How do environmental conditions affect the growth and timing of sexual maturation, and what is the underlying physiological mechanism? • Do the physiological processes underlying sexual maturity differ between iteroparous and semelparous salmonids? • How does metabolic phenotype influence the timing of sexual maturation? • How are the physiological processes involved with sexual maturation influenced by temperature, and what are the broader population consequences of this?
Return migration	• Are individuals with higher parasitic/viral load more likely to stray, or more likely to return earlier to fresh water if infections were incurred at sea? • Does thermal tolerance affect migration timing and distance? • Are fish more likely to stray when river temperatures exceed thermal tolerance? • Does diffuse pollution in fresh water affect the physiological basis of imprinting and straying in adults? • What is the role of nutrition at sea on timing of spawning migrations? • What physiological parameters are involved in determining when to begin the return migration? • How do interacting stressors and physiological systems interact to influence return migration behaviour? • Is return migration behaviour and its physiological underpinnings sufficiently plastic to adjust to environmental change?
Reproductive investment	• Beyond size, what are the physiological mechanisms underlying inter-individual differences in spawning investment? • Does thermal tolerance affect reproductive investment? • Does cardiorespiratory performance determine reproductive investment? • What is the role of nutrition at sea on determining pre-spawning physiological state and does that relate to the level of spawning investment? • How do additional anthropogenic and environmental stressors affect reproductive investment?
Repeat spawning	• How variable is individual post-spawning nutritional state among spawning seasons, and does that relate to prior feeding success and spawning investment decision? • How does the level of previous spawning investment affect post-spawning nutritional state? • Does the initial decision of how much to invest in spawning then dictate post-spawning survival probability at the individual level? • What level of behavioural repeatability/flexibility exist in species that undertake multiple feeding migrations in their lifespan, and what physiological drivers might be involved? • What are the physiological drivers (e.g. nutritional threshold) of consecutive *versus* alternate repeat spawning strategies determining spawning interval? • How do abiotic factors during the spawning migration affect the post-spawning physiological state of individuals, and their chance of repeated spawning? • How do intraspecific factors (e.g. metabolic rate, body size, sex) interact with environmental factors (e.g. temperature, distance) to influence repeat spawning and reproductive success?

approaches for taking non-lethal physiological samples including best practice guides (e.g. blood samples *via* the caudal vasculature; Lawrence *et al*., 2020) with evidence suggesting few to no lasting effects of non-lethal samples (e.g. muscle biopsy in Atlantic salmon; Bøe *et al*., 2020*a*). This mounting evidence, as well as appropriate training of new members by experienced personnel should provide a basis for physiological studies.

In this review, we have explored how physiology influences life-history decisions, but there remains a great deal to be explored – much of which would benefit from an experimental approach (Birnie-Gauvin *et al.*, 2020). Table 2 lists some of the outstanding research questions. Combining an array of tracking technologies with non-lethal samples (e.g. blood samples, gill biopsies, or muscle biopsies) to enable genomic or other mechanistic analysis would allow many of these questions to be explored. We find that few studies on salmonids have used muscle biopsies (though see Bøe *et al.*, 2020*b*), and this method could help answer questions related to chronic stress, trophic ecology and diet.

IV. CONCLUSIONS

(1) Salmonids, being migratory species (at least to some extent), rely on multiple habitat types throughout their life cycle (rivers, lakes, coasts, open ocean), and are thus particularly susceptible to human disturbances such as habitat degradation and fragmentation, as well as climate change (Wilcove & Wikelski, 2008).

(2) However, due to their ability to move and their variable life-history strategies, salmonids can also be viewed as highly adaptable in the face of change.

(3) Migratory animals play important roles in ecosystem processes including the transport of nutrients, energy and pathogens between habitats that would otherwise not be connected (Bauer & Hoye, 2014). In this context, the loss of migrants or migratory behaviour is likely to cause important ramifications for ecological communities (Shaw, 2016).

(4) Our ability to predict species responses to environmental change is linked to our ability to identify species and population environmental tolerances; and these tolerances are a direct consequence of physiological processes. A greater understanding of these processes will support the management and conservation of these species.

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