RESEARCH PAPER

Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines

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Abstract Reproductive tactics and migratory strategies in Pacific and Atlantic salmonines are inextricably linked through the effects of migration (or lack thereof) on age and size at maturity. In this review, we focus on the ecological and evolutionary patterns of freshwater maturation in salmonines, a key process resulting in the diversification of their life histories. We demonstrate that the energetics of maturation and reproduction provides a unifying theme for understanding both the proximate and ultimate causes of variation in reproductive schedules among species, populations, and the sexes. We use probabilistic maturation reaction norms to illustrate how variation in individual condition, in terms of body size, growth rate, and lipid storage, influences the timing of maturation. This useful framework integrates both genetic and environmental contributions to conditional strategies for maturation and, in doing so, demonstrates how flexible life histories can be both heritable and subject to strong environmental influences. We review evidence that the propensity for freshwater maturation in partially anadromous species is predictable across environmental gradients at geographic and local spatial scales. We note that growth is commonly associated with the propensity for freshwater maturation, but that life-history responses to changes in growth caused by temperature may be strikingly different than changes caused by differences in food availability. We conclude by exploring how contemporary management actions can constrain or

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promote the diversity of maturation phenotypes in Pacific and Atlantic salmonines and caution against underestimating the role of freshwater maturing forms in maintaining the resiliency of these iconic species.

Keywords Salmon · *Oncorhynchus* · *Salmo* · Conservation · Maturation · Life history · Diversity · *Oncorhynchus* Resilience

Introduction

Reproductive tactics and migratory strategies in Pacific and Atlantic salmonines are inextricably linked through the effects of migration on age and size at maturity. Salmonines exhibit a broad array of migratory behavior, from obligate anadromy in pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), for which no individuals in their natural range are known to mature in freshwater, to species in which some populations persist entirely in freshwater environments (e.g., stream resident forms of *O. mykiss*). In between these extremes lies a diverse suite of life histories exhibited by species that display varying "degrees of anadromy" (sensu Rounsefell 1958; Quinn and Myers 2004). Because of large differences in growth opportunities provided by temperate oceans and freshwater ecosystems, these degrees of anadromy contribute to an incredible range in the age and size at maturity in exhibited by salmonines, and provide an opportunity for the evolution of diverse reproductive tactics (Fleming and Reynolds 2004). The diversification of migratory strategies and reproductive tactics has important implications for the effective management of freshwater and marine ecosystems, for it potentially affects salmonine population dynamics, population productivity, ecosystem functioning, and adaptability to changing climatic conditions (e.g., Thériault et al. 2008; Schindler et al. 2010; Bottom et al. 2011).

In this review, we focus specifically on the ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines, a key process resulting in the diversification of their life histories (Docker and Heath 2003). We interpret patterns of freshwater maturation in the context of ultimate considerations (i.e., as a function of relative costs and benefits) as well as proximate considerations (i.e., individual responses to internal and external stimuli).

First, we briefly review the proximate mechanisms underlying the process of maturation in salmonines, as well as ultimate factors influencing maturation schedules. In this context, we describe a conceptual framework for understanding ecological and evolutionary patterns in freshwater maturation based on probabilistic maturation reaction norms. We then use this framework to explore phylogenetic and ecological patterns of freshwater maturation in Pacific and Atlantic salmonines. We conclude by discussing how this view of freshwater maturation can be applied in efforts to protect and restore diversity within these iconic species.

Maturation processes in Pacific and Atlantic salmonines

Sexual maturation is a process that leads to a fundamental change in individual state, marking the transition of juveniles into adulthood (Dieckman and Heino 2007). During maturation, energy is allocated to the development of germinal tissue and the production of gametes so that, ultimately, the individual is capable of sexual reproduction (Thorpe 2007). In salmonines, differentiation of germinal tissues begins early in development (Devlin and Nagahama 2002), with maturation proceeding intermittently over a period of months to years until an individual reaches maturity and is capable of sexual reproduction (Thorpe 2007). The onset and completion of reproductive development is regulated by the endocrine system, and maturation is initiated with hormonal signaling from the brain to the gametocytes, which in turn produce hormones stimulating gametic growth and transformation (Okuzawa 2002; Taranger et al. 2010). The final stages of maturation occur once individuals have achieved sufficient body size and energy reserves to meet the energetic requirements for sexual reproduction (Taranger et al. 2010). Although the stages of reproductive development and the general linkages between hormones and sexual organs are well established, and there are numerous models positing associations between energy storage and maturity (e.g., Thorpe et al. 1998; Rikardsen et al. 2004), the physiological mechanisms linking individual condition (e.g., somatic growth, size, and lipid reserves) and the process of maturation are not fully understood.

Thorpe (2007) hypothesized that the physiological capacity for maturation is continually assessed

internally by the body and the brain until an adequate level of energy reserves is available for development of reproductive organs. Metabolic hormones and growth factors related to individual condition may act in several different ways to promote the onset of puberty. For example, faster growing fish and those with high levels of lipid reserves produce high levels of insulin-like growth factor-I, which may increase the ability of the pituitary to respond to seasonal cues with sufficient releases of hormones permitting initiation or continuation of puberty (Luckenbach et al. 2010). Additionally, some pituitary hormones are actively regulated during maturation and may signal the status of visceral fat reserves during periods when fish are sensitive to reproductive development (Taranger et al. 2010). These findings support expectations that changes in blood chemistry (a reflection of nutrition, growth, and lipid reserves) provide cues that promote the onset and completion of sexual development in salmonines. It is not surprising then, that a large body of research has found that the final stages of maturation are strongly linked with traits reflecting individual condition, such as body size, growth rate, and whole body lipid content (e.g., Saunders et al. 1982; Shearer and Swanson 2000; McMillan et al. 2012). These measures of condition are direct or correlated indicators of an individual's recent energy acquisition, and therefore provide important cues for determining the optimal time for allocating energy towards reproduction (Thorpe 2007).

When should individuals mature? Salmonine energy allocation and maturation schedules

The timing of reproduction represents a classic life history tradeoff (Schluter et al. 1991; Stearns 1992). Because the energy required for sexual maturation comes at a cost to other functions that influence fitness, the benefits of allocating energy to current reproduction are balanced against the fitness benefits of otherwise investing energy in improvements to growth, condition, and the chance of surviving to reproduce at a later point in time (Dieckman and Heino 2007). Consequently, energy allocation schedules underlie variation in the timing of maturation and reflect an evolutionary response to age- and size-mediated components of fitness such as survival, fecundity, and access to mates (Bernardo 1993; Bernardo and Reagan-Wallin 2002). Energy allocation

schedules may also evolve in response to potential ecological opportunities for energy acquisition afforded by complementary habitats. This last point is particularly relevant to the discussion of salmonine life histories because maturation schedules are shaped within the context of the potential costs and benefits of migrating between freshwater and marine environments and the differences in growth and developmental opportunities that these habitats provide. For example, migration to the food-rich marine environment delays maturation, lowers the probability of surviving to reproduce, but typically results in a much larger size and greater energy stores at reproduction (Fleming and Reynolds 2004). Importantly, in some salmonine species some individuals forego marine migrations and mature under the energetic constraints of relatively low-productivity freshwater environments, while other
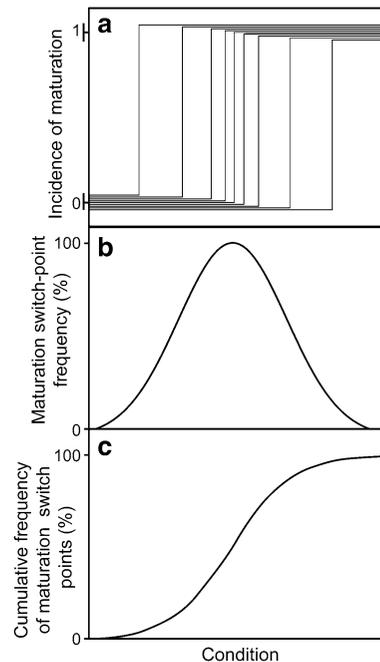

Fig. 1 Individual threshold reaction norms and the frequency distributions of conditional switch points for maturation redrawn from Hazel et al. (1990). **a** An example of a family of discrete threshold (step function) reaction norms for maturation of individuals. *Each vertical line* is a reaction norm switch point representing the condition that triggers maturation for an individual within a population. **b** A case in which switch points are assumed to vary continuously and approximate a normal distribution. **c** Cumulative frequency distribution representing the increase in the proportion of maturing phenotypes with increasing environmental opportunity for growth and development

species lack freshwater maturing forms entirely (Groot and Margolis 1991; Jonsson and Jonsson 1993; Behnke 2002). In the following sections, we describe a framework for understanding potential genetic and ecological factors underlying these differences in life history expression among species and populations.

Conceptual framework for understanding patterns of salmonine maturation

Any framework which seeks to understand patterns of salmonine maturation must consider its genetic basis and how this is affected by the environment. There is clearly an important genetic influence on the age and size at reproduction, with evidence accumulating that the underlying expression of alternative maturation phenotypes in salmonines has a fairly high heritable component (h^2 is typically 0.3–0.6; reviewed in Dodson et al. 2013). Furthermore, evidence is mounting that freshwater maturation is under complex polygenic control, with the number of genes, their specific effects on maturation expression, and the magnitude of their individual effects, being dependent on the salmonine species (Reid et al. 2005; Nichols et al. 2008) and the population (Hecht et al. 2013; Perrier et al. 2013). Despite the strong genetic contribution to maturation, however, most salmonine populations exhibit considerable plasticity in maturation phenotypes, reflecting an important role for genotype-by-environment interactions operating through effects on individual growth and energy storage (Taranger et al. 2010). The capacity for such interactions between genotype and environment allows the timing of maturation to vary in response to an individual's condition, a process that can be illustrated using the reaction norm framework (Hazel et al. 1990; Roff 1996; Hutchings 2011; Fig. 1a).

Genetically-determined maturation reaction norms describe how the timing of maturation responds to environmental influences on fish growth and energy storage (Taranger et al. 2010). Individuals initiate maturation once they exceed a threshold value for traits that are associated with an individual's body size and energy reserves (e.g., McMillan et al. 2012). Individuals that do not exceed the threshold delay maturation until such time as their condition warrants maturation. Traits associated with an individual's condition, such as size, instantaneous growth rate, and

lipid content, are strongly influenced by the environment, and are considered suitable proxies for the actual liability traits controlling maturation (Roff 1996), though they may or may not directly influence the maturation process. Individuals may differ in the condition (e.g., body size, lipid reserves) triggering maturation, reflecting genetic variation in reaction norm thresholds (Hazel et al. 1990; Hutchings and Myers 1994; Piché et al. 2008; Fig. 1a). These thresholds are inherited as typical polygenic traits, generating within a population a normal distribution of individual maturation switch points illustrated in Fig. 1b (Hazel et al. 1990; Roff 1996). The cumulative frequency distribution for such a normal distribution is a sigmoidal curve (Fig. 1c) that can be described as:

$$\Phi(z) = \frac{1}{2}\left(1 + \mathrm{erf}\left[\frac{1}{\sqrt{2}}\left(\frac{z - \bar{z}}{\sigma}\right)\right]\right), \tag{1}$$

where $\Phi(z)$ is the cumulative frequency of individual maturation switch points equal to or less than a value of fish condition z, erf is the normal distribution error function (Shynk 2012), $\bar{z}$ is the mean of the distribution of individual maturation switch points within the population, and σ is the standard deviation of the distribution. We define functional bounds to the
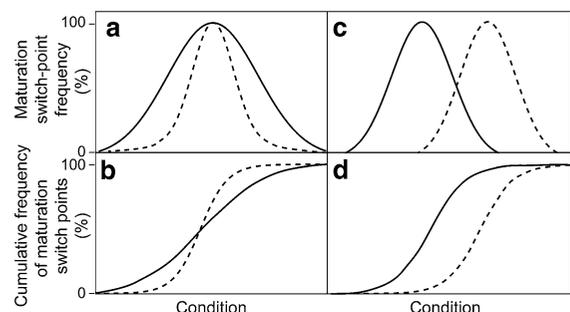

Fig. 2 Differences in the distributions of maturation switch points among populations. **a**, **b** Populations share mean values but differ in the variance of the underlying distribution of maturation switch points. A reduction in the variance of switch points may accompany stabilizing selection on thresholds for maturation. **b** Effects of reduced variance in switch points for populations illustrated in **a** include an increase in the slope of the cumulative frequency distribution of maturation switch points. **c**, **d** Populations differ in mean values but have equal variance in the underlying distribution of maturation switch points. An increase in mean values for maturation switch points may accompany directional selection on thresholds for maturation. **d** Effects of an increase in the mean maturation switch point for populations illustrated in **c** include an increase in the minimum individual condition triggering maturation (z_0 in Eq. 1)

distribution of maturation switch points as $z_0 = \bar{z} - 3\sigma$ and $z_1 = \bar{z} + 3\sigma$, or approximately 99 % confidence intervals around the mean ($\bar{z}$). These bounds represent the minimum conditional threshold for maturation within a population (z_0), and the level of condition that would be expected to trigger maturation in all individuals within a population (z_1).

The effects of variation in the minimum conditional thresholds for maturation (z_0) and standard deviation of the distribution of maturation switch points (σ) are illustrated in Fig. 2. High values of σ indicate greater variation among individuals in thresholds for maturation, which will result in greater variation in individual condition (e.g., size, growth rate, lipid content) at maturity (Fig. 2a, b). Lower values of σ indicate reduced variation in the distribution of maturation switch points within a population (Fig. 2a, b), an expected response to stabilizing selection on conditional thresholds for maturation. Higher values of z_0 reflect a higher minimum conditional threshold for the initiation of maturation within a population (Fig. 2c, d), an expected response to positive directional selection on maturation switch points. Together, these parameters provide useful benchmarks for comparing the distribution of maturation thresholds among species and populations.

To understand how interactions between environmental influences and genetically-determined maturation thresholds determine the incidence of freshwater maturation within populations, an additional component representing the freshwater environmental potential for growth and development must be introduced to the maturation reaction norm framework (Fig. 3). Factors such as temperature, prey abundance, and intra- or interspecific competition inevitably limit the maximum potential condition realized by individuals in freshwater. If individuals experience a freshwater environment conferring a maximum condition "E_{max}", then the propensity for freshwater maturation within the population is determined by the distribution of maturation switch points relative to E_{max} (Fig. 3). Individuals whose switch points fall below E_{max} may potentially mature in freshwater, whereas those whose switch points exceed E_{max} must migrate to better growth (e.g., marine) environments prior to maturation (Fig. 3). Thus, when $z_0 < E_{max}$, the occurrence of freshwater maturation is >0, and the frequency of resident life histories is determined by the cumulative frequency distribution
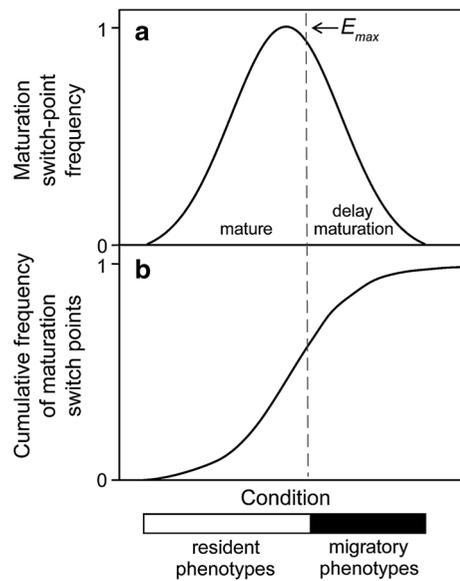

Fig. 3 A conditional strategy for freshwater maturing and anadromous phenotypes. **a** In a freshwater habitat where environmental constraints set an upper limit to the conditional state individuals may achieve (E_{max}), individuals whose developmental switch points lie to the left of E_{max} express freshwater maturing phenotypes, whereas those whose switch points exceed E_{max} must migrate to better growth environments prior to maturation. **b** The relative proportion of resident and anadromous phenotypes in a population experiencing an environment having the constraint E_{max} can be determined by the intersection of E_{max} and the cumulative frequency distribution of developmental switch points. Relative proportions of freshwater maturing and migratory phenotypes are illustrated in the *bar* below (**b**)

of maturation switch points in the interval between z_0 and E_{max}. In populations where $z_0 > E_{max}$, the incidence of freshwater maturation is functionally zero.

The intersection of these functions (E_{max} and the distribution of maturation switch points) provides a conceptual framework for understanding broad patterns in Pacific and Atlantic salmonine life histories. Because maturation switch points reflect underlying genetic variation within a population, they are heritable and therefore can respond to selection (Hazel et al. 1990). Hazel et al. (1990) describe the theory for the evolution of the distribution of switch points to new optima under changing environmental conditions. Hutchings and Myers (1994) and Piché et al. (2008) provide empirical evidence that such a model for conditional strategies is an appropriate framework for analyzing salmonine maturation patterns. In the following sections, we use this conceptual framework to

explore phylogenetic and ecological patterns of freshwater maturation in Pacific and Atlantic salmonines.

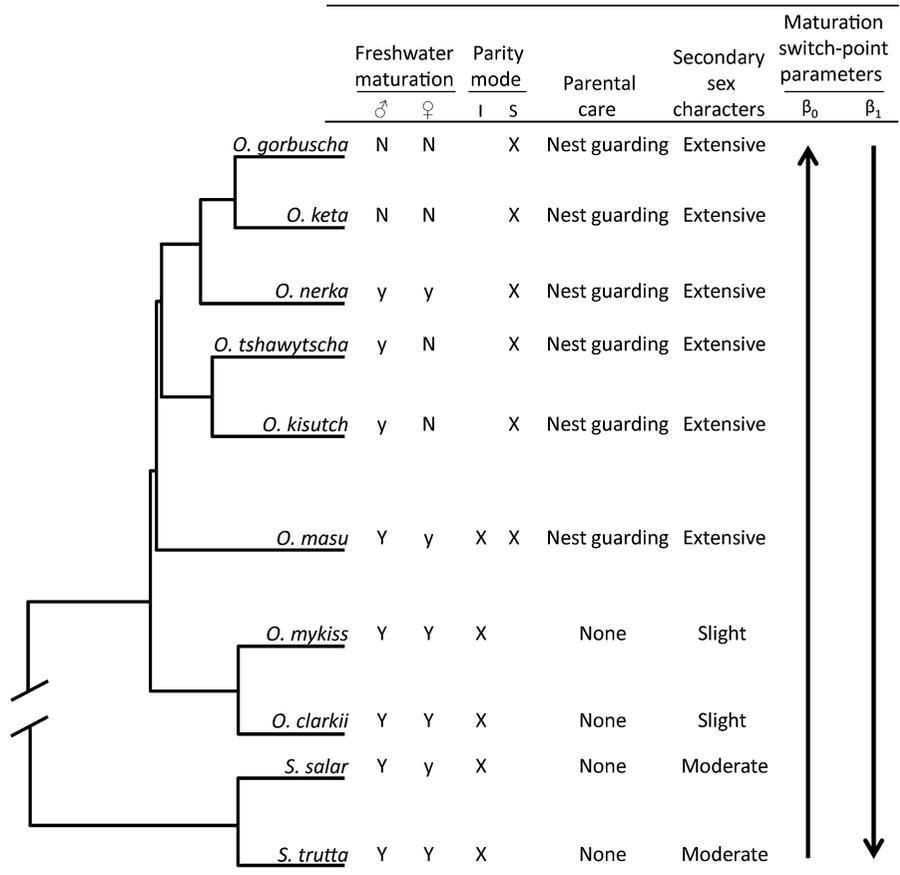## Macro-evolutionary patterns of salmonine life histories

Variation in the age and size at maturity is ubiquitous in salmonines, even within species such as pink salmon that display among the most rigid life histories of any salmonine (Heard 1991). For some species, this variation is dramatic, as in alternative male reproductive phenotypes of Atlantic salmon (*Salmo salar*) in which the mass of mature parr and anadromous adults can differ by more than two orders of magnitude (Fleming 1996). Rounsefell (1958) categorized variation in Pacific and Atlantic salmonine life histories according to their "degree of anadromy" based on six criteria: (1) extent of migrations at sea, (2) duration of stay at sea, (3) state of maturity attained at sea, (4) spawning habits and habitats, (5) post-spawning mortality, and (6) occurrence of freshwater forms of the species. At one extreme are pink and chum salmon. These species may spawn in the intertidal reaches of coastal streams and juveniles emigrate to the marine environment immediately following emergence, so that some individuals may never inhabit strictly fresh water during their life span (Rounsefell 1958). Pink and chum salmon undergo extensive marine migrations, complete most stages of maturation within saltwater, invariably die after spawning (semelparity), and have no known freshwater maturing forms within their natural range, all of which led Rounsefell to consider these species as obligatorily anadromous. At the other extreme, coastal cutthroat trout (*O. clarkii*) may be anadromous, but remain near shore, return to freshwater well in advance of reproduction, can spawn repeatedly (iteroparity), and commonly persist as wholly freshwater resident populations (Hall et al. 1997).

In between these extremes, the salmonines exhibit a continuum of mating systems and migratory strategies. Phylogenetic trends illustrate an increased expression of anadromy and a shift from iteroparous to semelparous reproduction among more derived salmonines, with these transitions occurring within the *Oncorhynchus* clade (Fig. 4). Accompanying these transitions is a loss of resident life histories

within the Pacific salmon, particularly in females. The transition from iteroparity to semelparity is also correlated with an increase in the energetic investment in reproduction per breeding episode, consistent with life history theory (Roff 2002). For example, some semelparous Pacific salmon expend nearly 80 % of their total body energy on reproduction (Hendry and Berg 1999; Fleming and Reynolds 2004). By comparison, resident forms of partially anadromous species expend as little as 13 % of their total energy on reproduction (Hendry and Berg 1999). Although the available literature does not represent a random sample from among the salmonines, reviews by Hendry and Berg (1999) and Fleming and Reynolds (2004) suggest that semelparous salmonines may expend, on average, approximately 20 % more of their total body energy on reproduction than iteroparous salmonines.

The increased energetic investment in reproduction in semelparous salmonines has not been accompanied by an increase in fecundity (Crespi and Teo 2002), as might be expected with "big-bang" reproduction (Roff 2002). Rather, semelparous species appear to invest considerable energy into competition for nest sites and mates, which can be intense under the high local breeding densities in many populations (Fleming 1998). Males often develop exaggerated secondary sexual characters as status symbols and for use as specialized weapons and armor for fighting (Johnson et al. 2006). These traits include enlarged, canine-like "breeding teeth", elongated, hooked jaws, or "kypes", cartilaginous dorsal humps, embedded scales, thickened skin, and changes in skin coloration (Fleming and Reynolds 2004). Semelparous females compete for nest sites that they aggressively defend until death (Fleming and Reynolds 2004). This energetic investment in parental care is undoubtedly costly given the typically high breeding densities (and high risk of nest superimposition) in populations of semelparous species (e.g., McNeil 1964; Fukushima et al. 1998). In addition to nest defense, semelparous females increase energy allocation to gametes on a per-offspring basis, by developing larger eggs (Crespi and Teo 2002; Quinn 2005). Increased per-offspring energy allocation may improve offspring fitness, as larger eggs may result in greater juvenile growth and survivorship (Crespi and Teo 2002; Einum et al. 2004). Conspecific density may be responsible for driving salmonines towards higher levels of energetic

Fig. 4 Partial phylogeny of Pacific and Atlantic salmonines and corresponding reproductive traits. The *Salvelinus* clade is omitted to emphasize trends in reproductive traits within the genus *Oncorhynchus*. Reproductive traits include the presence of freshwater maturing forms (Y = yes, N = no; *lower case letters* indicate that the occurrence of freshwater maturing forms is uncommon); parity mode (i = iteroparous, s = semelparous), form of parental care, development of secondary sexual characteristics, and trends in the parameters defining the distribution of maturation switch points (z_0 = minimum conditional threshold for maturation; σ = standard deviation of the distribution of maturation switch points). *Arrows* indicate the direction that parameter values are hypothesized to increase

	Freshwater maturation		Parity mode		Parental care	Secondary sex characters	Maturation switch-point parameters	
	♂	♀	i	s			β_0	β_1
O. gorbuscha	N	N		X	Nest guarding	Extensive		
O. keta	N	N		X	Nest guarding	Extensive		
O. nerka	y	y		X	Nest guarding	Extensive		
O. tshawytscha	y	N		X	Nest guarding	Extensive		
O. kisutch	y	N		X	Nest guarding	Extensive		
O. masu	Y	y	X	X	Nest guarding	Extensive		
O. mykiss	Y	Y	X		None	Slight		
O. clarkii	Y	Y	X		None	Slight		
S. salar	Y	y	X		None	Moderate		
S. trutta	Y	Y	X		None	Moderate		

investment in reproduction, as reproductive success under intense intraspecific competition depends on an individual's relative (rather than absolute) energy expenditure (Schaffer 2004). This remains a compelling hypothesis for the origins of semelparity in salmonines, despite substantial uncertainties concerning cause and effect (Crespi and Teo 2002; Schaffer 2004).

In terms of our conceptual framework, phylogenetic trends suggest two hypotheses related to the expression of resident and anadromous life histories in salmonines. First, the increased energetic capital necessary for successful reproduction in semelparous populations likely far exceeds that which can be acquired within most lotic ecosystems, especially after accounting for density-dependent effects on growth and survival (Hendry et al. 2004). That is, semelparous salmonines have evolved high minimal thresholds for maturation that require a substantially greater level of energy investment, so that $z_0 > E_{max}$ (Fig. 4). Second, a decrease in plasticity for age and size at maturation

may accompany an increase in the degree of anadromy (Rounsefell 1958; Quinn and Myers 2004), so that the variation in thresholds for maturation (Fig. 4) decreases in more derived species. In other words, semelparous species may be characterized by a narrower distribution of conditional switch points for maturation (e.g., Fig. 2 a, b) in addition to possessing elevated minimum thresholds (z_0).

Sex-specific constraints to freshwater maturation

Energetic investment in reproduction also helps to explain differences in the propensity for males and females to express resident life histories. Females are more likely than males to adopt anadromy and less likely to mature in freshwater (Hendry et al. 2004). Between the sexes, females characteristically invest more in offspring production (e.g., Hayward and Gilloly 2011). Females invest up to 25 % of their body weight into gonads, whereas male investment is

typically closer to 5 % (Fleming 1996; Fleming and Reynolds 2004). Females also devote considerably more energy to the production of gametes on a per-unit-weight basis, as ovaries have about 1.5 times the energy density of testes (Jonsson et al. 1991; Fleming 1996). In terms of overall investment in offspring production, females expend approximately 10 % more total energy than males after accounting for the cost of reproductive behaviors such as nest building and defense (Hendry and Berg 1999).

This greater energetic investment in reproduction by females is an evolutionary response to female reproductive success typically being more limited by gamete production and offspring quality than by access to mates. Because both fecundity and the total energy available for reproduction increase with body size, attaining a large size at maturity is critical to maximizing reproductive success in females. Accordingly, the greater prevalence of anadromy in females is likely a consequence of the fitness benefits of attaining a larger body size (Jonsson and Jonsson 1993). Females that remain in freshwater may enjoy a higher probability of survival to reproduction, as well as a higher probability of repeated reproduction (iteroparity), but they typically mature at a much smaller body size, with exponentially reduced fecundity (Fleming and Reynolds 2004).

In contrast to females, reproductive success in males is typically limited by access to mates rather than gamete production (Gross 1985; Quinn 2005). Consequently, in most salmonines, males employ multiple behavioral tactics to gain access to females, which are in part linked to body size. Larger individuals attempt to dominate access to females through aggressive competition, whereas smaller freshwater maturing parr rely more on sneaking tactics to surreptitiously fertilize eggs during spawning (Esteve 2005). The size difference between males adopting these alternative behaviors can be considerable, as the body mass of sneaking mature male parr is often two orders of magnitude lower than anadromous "fighter" males (Fleming and Reynolds 2004). Despite the discrepancy in size, mature male parr can have significant reproductive success, and may fertilize over 50 % of the eggs in some salmon populations (Morán et al. 1996; Martinez et al. 2000; Garcia–Vazquez et al. 2001). Thus, the relatively low energetic cost of sperm production provides a proximate mechanism facilitating the development of

lower conditional thresholds for male maturation and the reproductive success of the sneaker tactic provides an ultimate mechanism that drives its evolution. Consequently, for the majority of salmonines, lower costs of gamete production for males, combined with lower selective pressures for large body size, have resulted in a greater propensity for males to mature within the environmental constraints of freshwater habitats relative to females. Furthermore, in at least some iteroparous salmonines, males can apparently experience both freshwater maturation and subsequent anadromy. Although freshwater maturation typically precludes subsequent smolting in most salmonines, a high percentage of male Atlantic salmon smolts from some Norwegian populations have previously matured in freshwater as parr (Bohlin et al. 1986; Jonsson and Jonsson 2011). Thus, freshwater maturation may allow male Atlantic salmon only the first of multiple tactics for reproductive success.

These sex-specific selective pressures help explain why freshwater maturing males have been documented in nearly every salmonine species (Fig. 4). Even among semelparous salmonines, for which, with the exception of sockeye salmon (O. nerka; "kokanee"; Wood et al. 2008) and some populations of masue salmon (O. masou; Morita and Nagasawa 2010), freshwater maturation of females is extremely rare within their natural range, males may mature in freshwater, albeit with less frequency than in iteroparous salmonines. In fact, given several advantages of early maturation (e.g., improved survival to reproduction, reduced generation time, higher incidence of repeat spawning in iteroparous species), it is perhaps surprising that any salmonine species lacks resident male life histories. Although causes for the loss of freshwater maturing males are speculative, it is noteworthy that species lacking freshwater maturing males (i.e., pink and chum salmon) migrate to the ocean as fry (Groot and Margolis 1991). Perhaps this behavior simply pre-empts potential environmental opportunities for freshwater maturation. This may also explain why freshwater maturing parr are more common in stream-type Chinook salmon (O. tshawytscha), which rear for over one year in freshwater before smolting, than in ocean-type Chinook salmon, which predominately migrate within a few months of emergence (Healey 1991). Nevertheless, differences between the propensity for males and females to mature in freshwater represent sex-specific constraints
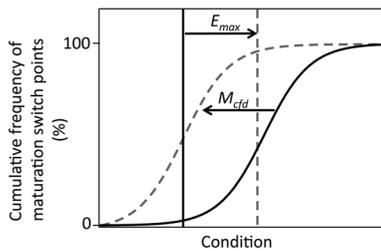
Fig. 5 A conceptual model for habitat and genotype management of Pacific and Atlantic salmonine maturation phenotypes. *Vertical lines* represent freshwater environmental constraints to individual condition (E_{max}). Sigmoidal curves represent cumulative frequency distributions of conditional maturation switch points (M_{cfd}) for individuals within hypothetical populations. Under some conditions (*solid black lines*), freshwater maturing phenotypes may be rare because most individuals have conditional maturation switch points that exceed the level of individual condition that can be achieved in freshwater. Habitat management may relax freshwater constraints on individual condition (e.g., *dashed gray vertical line*), which can increase the proportion of freshwater maturing phenotypes. Genotype management may shift the cumulative frequency distribution of maturation switch points. A shift in the distribution of switch points towards lower conditional maturation thresholds (*dashed gray curve*) will increase the proportion of freshwater maturing phenotypes

to life history plasticity that have important repercussions for the conservation and management of salmonines (Fraser in press).

Patterns in partial anadromy across environmental gradients

As described above, environmental variation can exert a strong influence on salmonine life histories. Factors such as temperature, photoperiod, food availability, and fish density dictate the opportunity for juvenile growth and development, thereby defining the position of E_{max} (Fig. 3). For a given distribution of conditional maturation switch points, shifts in E_{max} along environmental gradients result in environmentally-induced changes in the prevalence of freshwater maturing phenotypes among and within populations (Fig. 5). The incidence of freshwater maturation reflects the influence of environmental variation at multiple spatial scales, from individual watersheds to broad geographic scales encompassing species' ranges. In this section, we explore how shifts in E_{max} along environmental gradients at geographic and watershed

scales influence patterns of freshwater maturation in salmonines.

Geographical variation in freshwater maturation

Research at geographic scales has often focused on latitudinal clines in salmonine life history traits (e.g., Metcalfe and Thorpe 1990; Fleming and Gross 1990), including variation in the rate of freshwater maturation among partially anadromous populations (Valiente et al. 2005; Morita and Nagasawa 2010). Latitudinal clines in salmonine life history traits can reflect a decrease in freshwater growth opportunities at higher latitudes due to colder temperatures and a shorter growing season (Metcalfe and Thorpe 1990). Morita and Nagasawa (2010), for example, found that colder stream temperatures were associated with decreased fish growth and lower rates of freshwater maturation of both males and females in more northerly populations of masu salmon in Japan. Similarly, in a review of Atlantic salmon populations spanning a range of 23° latitude, Valiente et al. (2005) found significantly lower rates of freshwater maturation in males in more northerly rivers. Decreases in freshwater growth opportunities at higher latitudes are also paralleled by increases in ocean productivity, and this combination has been hypothesized to favor the expression of anadromy (i.e., the "food availability hypothesis"; Gross et al. 1988). Consistent with this hypothesis are previous observations of an increase in the degree of anadromy at higher latitudes first suggested by Rounsefell (1958) for North American salmonines, and subsequently described for brown trout (*Salmo trutta*) in Europe (Elliott 1994), and masu salmon in Asia (Malyutina et al. 2009; Morita and Nagasawa 2010).

Some salmonines exhibit exceptions to the general pattern of increased anadromy with latitude. In western Alaska, many *O. mykiss* populations near the species' northern distributional boundary are dominated by freshwater resident life histories (e.g., Meka et al. 2003; Schwanke and Hubert 2003). These populations tend to inhabit watersheds that support extremely productive populations of sockeye salmon. Consequently, they experience uncharacteristically high freshwater growth opportunities provided by marine-derived resources such as salmon eggs and flesh from the carcasses of post-spawning adults. Similarly, in Kamchatka, Russia, patterns of freshwater productivity do not follow general latitudinal trends. Freshwater

maturing life histories dominate in some of the most northerly Kamchatkan *O. mykiss* populations, where stable hydrogeomorphic conditions combine with abundant salmon returns to provide excellent freshwater growth opportunities (Pavlov and Savvaitova 2008). These examples underscore the importance of local processes that may override the effect of latitude on environmental gradients influencing growth. However, these apparent exceptions also help support a general rule for salmonine life histories: spatial patterns in life history expression are strongly influenced by opportunities for freshwater growth, whether these opportunities conform to broad-scale environmental gradients (e.g., latitudinal variation in climate) or local biophysical controls.

In addition to freshwater growth opportunities, latitudinal gradients in freshwater-marine connectivity can influence the prevalence of freshwater maturation. In the Mediterranean and semi-arid climates that characterize the southern distributions of some salmonines, low stream flows and warm temperatures limit seasonal migration opportunities. Coastal lagoon sandbar formation and seasonally dry stream reaches may constrain both the immigration of anadromous adults and emigration of smolts to very short windows when stream flows and temperatures are suitable (Boughton et al. 2005). For example, in Topanga Creek, CA, USA, near the southern distribution limit for *O. mykiss*, there are commonly <20 days of potential fish migration opportunity annually (Bell et al. 2011). In some systems, periods of drought may result in several consecutive years when migration is impossible (Titus et al. 2000). The reduction in migration opportunity should strongly favor freshwater maturing life histories. Under such conditions, selection for freshwater residents may act to shift the distribution of maturation switch points so that a higher proportion of individuals have switch points below E_{max} (Fig. 5).

Finally, it is important to consider the increase in human population density towards the southern extent of salmonine distributions and the resulting influence on salmonine life histories. Land conversion, water extraction, and barriers to migration (from large dams to poorly designed road crossings), reduce freshwater-marine connectivity, and are likely to disproportionately impact anadromous phenotypes in the southern portion of species' ranges and favor freshwater maturation. Many watersheds that now produce almost entirely (or

exclusively) freshwater maturing phenotypes historically supported abundant anadromous runs (e.g., Titus et al. 2000; Alagona et al. 2012). So, while there is strong evidence that climatic gradients influence salmonine life histories at geographic spatial scales, we recognize that anthropogenic stressors covary with climate, and caution against underestimating the environmental potential for anadromy at more southerly latitudes in the absence of human influences.

Environmental gradients within watersheds

Watershed-scale variation in life history expression is also observed within salmonine populations (Baum et al. 2005; Aubin-Horth et al. 2006). Considering the positive influence of growth opportunity on rates of freshwater maturation observed among populations, watershed-scale variation in factors that affect individual fish growth, such as food availability, fish density, and temperature, should also influence spatial variability in rates of freshwater maturation within populations. Increased food availability favors freshwater maturation through its positive influence on the potential energy for growth and development (Jonsson and Jonsson 1993; Hendry et al. 2004). Experimentally reducing food rations can decrease the proportion of freshwater maturing males in hatchery Atlantic salmon (Rowe and Thorpe 1990; Thorpe et al. 1990), Chinook salmon (Hopkins and Unwin 1997; Larsen et al. 2006; Larsen et al. 2013), steelhead trout (Tipping and Byrne 1996), and brown trout (Pirhonen and Forsman 1999). Laboratory experiments with Arctic charr (*Salvelinus alpinus*) (Nordeng 1983) and brown trout (Jonsson 1989; Olsson et al. 2006) also demonstrate significant effects of food availability on the adoption of migratory or resident phenotypes.

Per-capita reductions in food availability, operating through density-dependent resource competition, may similarly influence salmonine life history expression. Density-dependent growth is well-documented in juvenile salmonids (Keeley 2001; Imre et al. 2005; Einum et al. 2006), and changes in per-capita food availability can also influence developmental rates. For example, Letcher and Terrick (1998) observed an approximately 70 % increase in the rate of freshwater maturation of age-0 Atlantic salmon associated with increased juvenile growth following a catastrophic flood that substantially reduced inter- and intra-specific fish density. Morita et al. (2000) used a

transplant experiment to demonstrate that reduced fish density promoted faster juvenile growth and increased freshwater residency in partially anadromous white spotted charr (*S. leucomaenis*). In an observational study, Olsson and Greenberg (2004) also found that individual brown trout from stream reaches with a low density of conspecifics were more likely to remain as residents than those from reaches with high fish density. These results are consistent with the food availability hypothesis posed to explain patterns of anadromy and residency at geographic spatial scales (Gross et al. 1988). Individuals experiencing good feeding opportunities should forego migration and invest energy in gonadal development, whereas those experiencing poor feeding opportunities should delay maturation and prepare for smolting (Jonsson and Jonsson 1993; Hendry et al. 2004).

Thermal regimes also directly influence fish development and growth and may, therefore, be expected to affect rates of freshwater maturation. Incubation temperature strongly influences rates of embryonic development and emergence timing (Beacham and Murray 1990). The timing of emergence determines both seasonal opportunities for growth, as well as physiological responses to interactions between growth rate, energy storage, and photoperiod that can strongly influence salmonine life-history trajectories, including the potential for early male maturation (Beckman et al. 2007). Temperature also influences salmonine energy allocation strategies. During juvenile rearing, salmonines exposed to lower stream temperatures tend to increase energy allocation towards storage, particularly as mobilizible lipid reserves, at a cost to somatic growth (Tocher 2003). This pattern is observed across latitudinal and altitudinal gradients (Berg et al. 2011), and within watersheds among streams with contrasting thermal regimes (McMillan et al. 2012). The tradeoff between somatic growth and energy storage across different thermal environments is important for understanding watershed-scale patterns of freshwater maturation because it is energy from lipid reserves that is mobilized to fuel the development of gametes. In a field study in the John Day River, OR, USA, McMillan et al. (2012) found that fish exposed to warmer temperature regimes increased somatic growth at the expense of lipid storage, which reduced the probability of freshwater maturation. They further demonstrated that an increase in whole-body lipid levels in fish

inhabiting cold streams decreased the estimated body-length threshold for maturation relative to that in warmer streams. Similarly, male and female *O. mykiss* from the Clackamas River, OR, USA, experimentally reared under cold thermal regimes had significantly higher levels of whole body lipids, lower somatic growth, increased rates of freshwater maturation, and decreased rates of anadromy compared with those reared under warm thermal regimes (Sloat and Reeves 2014). These studies indicate that thermally-induced reductions in somatic growth do not necessarily decrease the incidence of freshwater maturation. In fact, the opposite can be true. Consequently, life history responses to thermally induced changes in growth rates can be strikingly different than the response to changes in growth due to food availability (Berrigan and Charnov 1994).

Given that stream temperatures within watersheds typically decrease with altitude, the effect of temperature on salmonine energy allocation may help explain why researchers often find higher rates of freshwater maturation with increasing altitude (Bohlin et al. 2001; Narum et al. 2008), despite observing lower rates of somatic growth in headwater habitats. For example, Baum et al. (2005) found that male Atlantic salmon at higher altitude sites had lower somatic growth rates but were more likely to mature in freshwater. In a similar study, Aubin-Horth et al. (2006) found a higher incidence of freshwater maturity and a lower body length threshold for freshwater maturation in male Atlantic salmon at higher-altitude sites. These observations seem to contradict the generally positive association between increased somatic growth and rates of freshwater maturation observed at geographic spatial scales. Consequently, the effects of temperature on somatic growth, energy allocation, and salmonine life histories are worthy of further research. First, temperature may be an especially important environmental influence on watershed-scale patterns in salmonine life history expression, especially freshwater maturation. This is particularly relevant to salmonine management, given projected changes in stream temperatures due to climate change. Second, because somatic growth is positively associated with freshwater maturation at geographic spatial scales, but may be negatively associated with somatic growth within watersheds, this suggests a scale-dependent process reversal that warrants further investigation.

The preceding discussion is focused on salmonines in streams, but use of other freshwater habitats can be important, notably lakes and reservoirs. Where these habitats are available, salmonines may use them extensively (Hutchings 1986; Quinn 2005; Jonsson and Jonsson 2011), with development of freshwater residency in lakes following postglacial formation of such habitats (e.g., Berg 1985), as well as rapid development of such life histories in some species following recent impoundment of rivers formerly supporting anadromous life histories (e.g., Clemento et al. 2009; Holecek and Scarnecchia 2013). Although broad-scale analyses indicate rivers can be much more productive than lakes (Randall et al. 1995), comparative studies of the condition of young salmonines in streams and lakes downstream suggest the latter may have greater energy stores (Dempson et al. 2004), which may increase the probability of freshwater maturation (see above). Given the high degree of variability in conditions offered by lakes, as well as interactions between streams and lakes (e.g., Jones 2010), it is difficult to envision a consistent pattern of freshwater maturation in relation to these habitat types. Similar analogies apply to estuaries, temporary lagoons, or other habitats outside of running waters (e.g., Hayes et al. 2008; Jonsson and Jonsson 2011). In some cases, species normally considered to adopt primarily anadromous life histories have successfully colonized very large freshwater systems (e.g., pink salmon, *O. gorbuscha* in the North American Great Lakes; Crawford 2001), which may effectively provide growth and survival opportunities that are analogous to marine environments. In short, patterns of freshwater maturation within watersheds are likely driven by bioenergetic factors (e.g., productivity, temperature, activity costs) that can be consistently linked to environmental gradients that influence them, regardless of habitat type considered.

Finally, spatial habitat structure can influence patterns of salmonine life histories. Migration distance is known to influence patterns of residency and anadromy in partially migratory populations by increasing migration costs for anadromous individuals (Bohlin et al. 2001; Finstad and Hein 2012). Recent evidence also demonstrates that migration distance can influence reaction norms for freshwater maturation in male charr and salmon (Sahashi and Morita 2013). More complex spatial processes, including landscape complementation and neighborhood

effects, are likely to influence basin-scale patterns of life history expression (Falke et al. 2013). Though rarely studied in partially migratory salmonines, these processes may influence, for example, spawning habitat selection by anadromous females (Falke et al. 2013), with potential effects on female intraspecific competition among alternative maturation phenotypes (Dodson et al. 2013).

Partial anadromy and the conservation of Pacific and Atlantic salmonines

Understanding the patterns and processes underlying Pacific and Atlantic salmonine life histories is central to their conservation and management in several contexts. Among populations, for example, diversity in life histories is known to facilitate complementary and/or independent dynamics that help to generate more temporally stable ecosystem services (e.g. fisheries yield; Hilborn et al. 2003). Within populations, life history diversity can facilitate resilience to environmental change (Greene et al. 2010), and the erosion of this diversity may act as a harbinger of population collapse (Moore et al. 2010; Carlson and Satterthwaite 2011; Fraser in press). Partial anadromy, in which some individuals forego marine migrations and mature within freshwater, can be a particularly effective form of bet hedging, minimizing the risk of localized population extinction by spreading populations across spatially heterogeneous habitats and varying the age at reproduction among individuals. Freshwater maturing forms within otherwise anadromous populations provide a demographic and genetic buffer during periods of poor ocean productivity (Christie et al. 2011). For example, populations of partially anadromous species may persist as freshwater residents for decades or centuries following isolation from the ocean (e.g., Thrower et al. 2004). Likewise, anadromous forms can be effective at recolonizing freshwater systems subject to stochastic and catastrophic disturbances (Reeves et al. 1995).

In the most basic sense, plasticity in freshwater maturation depends on complementary interactions between environmental opportunities for growth and development in freshwater (E_{max}) and macro- and microevolutionary influences on the distribution of genetically-determined maturation switch points characteristic of populations (Fig. 5). Humans influence both the freshwater environment that salmonines

experience (McClure et al. 2008), as well as contemporary selective pressures on life history traits (Thériault et al. 2008), and therefore may exert strong influences on the incidence of freshwater maturation within partially anadromous salmonines. We argue that a better understanding of factors that constrain or promote plasticity in maturation switch points may be crucial for assessing the potential for salmonines to persist or recover following environmental change. Further, we suggest that the persistence of partially anadromous populations may depend on proactive management actions that maintain a mix of freshwater maturing and anadromous phenotypes given that: (1) rates of anthropogenic influences on marine and freshwater environments are increasing (McClure et al. 2008); (2) contemporary fisheries management exerts strong influences on salmonine life histories, often with unintended consequences; and (3) reaction norms for certain salmonine life history traits can become invariant over short timescales (Haugen & Vollestad 2000).

Maintenance of freshwater maturing and anadromous phenotypes may be achieved through two potentially complementary approaches (Fig. 4). The first approach focuses on the role of environmental heterogeneity in the maintenance of phenotypic diversity in wild populations (Watters et al. 2003). Due to individual differences in behavior, physiology, and morphology, different phenotypes may be favored across different types of habitats (McClure et al. 2008). Habitat homogenization can diminish phenotypic diversity by either constraining phenotypic expression, limiting survival to a narrow range of phenotypes, or both. Human-induced habitat loss has not been equal across all habitat types and therefore has disproportionally affected individuals with different phenotypic attributes (McClure et al. 2008). At regional scales, habitats currently available to partially anadromous salmonids tend to be lower in elevation, wetter, and have less intra-annual climate variability compared to inaccessible historical habitats (e.g., due to dams; McClure et al. 2008). At the watershed scale, diking and channelization have reduced the availability of off-channel habitats such as floodplains, sloughs, and backwaters (e.g., Beechie et al. 2001; Pess et al. 2002). Historically, a wider range of growth environments were available within a shifting mosaic of aquatic habitats (Stanford et al. 2005). The loss of such habitat diversity, and

associated growth opportunities, has likely decreased environmental opportunities for the expression of alternative salmonine maturation phenotypes (e.g., decreased E_{max}; Fig. 5). The reduction in North American beaver populations (*Castor canadensis*) is another example of historical change that has altered the biophysical complexity of aquatic ecosystems (Naiman et al. 1988) with consequences for phenotypic expression in salmonines. For example, beaver ponds can facilitate faster fish growth and approximately double the rate of male parr maturity in Atlantic salmon (Sigourney et al. 2006). Consequently, one way to conserve or restore life history diversity in Pacific and Atlantic salmonines is to maintain or restore heterogeneous freshwater habitats that increase opportunities for growth and development (Watters et al. 2003).

A second approach to maintenance of both freshwater maturing and anadromous phenotypes focuses on the maintenance of genetic variation underlying maturation switch points (Fig. 5). The importance of freshwater maturing forms may be critical in several regions where changes to the marine environment are substantially reducing marine survival of salmonines (COSEWIC 2006; Welch et al. 2009), in some cases to the point of being negligible (Fraser in press). Because freshwater maturation may be the only means to avoid marine mortality, phylogenetic and/or sex-specific constraints to freshwater maturation will decrease the probability that some salmonines will persist in these regions. If such changes to the marine environment continue or become more widespread, then in certain instances, populations harboring any genetic variation for freshwater maturation might represent important gene pools for species persistence and perhaps recovery. An example of this might be the few fluvial Atlantic salmon populations that contain females maturing as parr. Sutterlin and MacLean (1984) successfully cross-bred adults from a fluvial freshwater resident and an anadromous population of Atlantic salmon to produce male and female offspring with intermediate conditional switch points for maturation, which facilitated freshwater maturation of 53 % of hybrid females. Thus, where it would be beneficial for population resilience or reestablishment, artificial breeding programs could be managed to increase genetic variation underlying the distribution of maturation switch points in order to produce a mix of freshwater maturing and anadromous individuals.

Historically, however, there has been a sustained effort by hatchery production and supplementation programs to reduce the incidence of freshwater maturation in partially anadromous salmonines (e.g., Myers and Hutchings 1985; Sharpe et al. 2007; Bastien et al. 2011). Freshwater maturing individuals, termed "residuals" within the context of hatchery supplementation, are considered a biological nuisance as they represent a direct loss to the production of anadromous adults (Beckman and Larsen 2005). Reducing "residualism" is an understandable goal where hatchery stocks pose significant ecological and genetic risks to sympatric wild populations. However, selection against freshwater maturing phenotypes within domesticated populations may have unintended consequences for the persistence of wild populations, because experience has shown that hatchery fish cannot be fully segregated from wild populations. Thus, if domestication selects for higher conditional maturation switch points through selective breeding of anadromous phenotypes, this genetic effect may enter wild populations through hybridization with hatchery fish spawning in the wild. In other words, domestication selection on traits influencing migratory and maturation phenotypes cannot be contained within hatchery populations. Artificial breeding programs may be affecting reproductive phenotypes in more subtle ways, as well. Semelparity is thought to be an adaptive response to high juvenile survival and low adult post-reproductive survival (Roff 2002). Under current conditions, salmonines may experience decreased post-reproductive adult survival as a result of habitat degradation (e.g., increase migration costs due to dams, increased water temperature) and increased juvenile survival facilitated by hatchery rearing. Consequently, Crespi and Teo (2002) have argued that these compounding human influences may be selecting strongly for semelparity in otherwise iteroparous species such as steelhead trout and Atlantic salmon.

A last example of anthropogenic effects comes from the perspective that human activities often induce rapid evolutionary change in the expression of life history variation. Because the mode of maturation is associated with survival and a threshold body size influenced by both genetic and plastic effects (Thériault et al. 2008), human activities such as fisheries harvest and hydroelectric dam development can result in genetically-based shifts in life history expression. Namely, these activities frequently select against anadromous individuals. Fisheries harvesting in the sea or during spawning migration also increases mortality of anadromous individuals (Thériault et al. 2008). And dam construction, which prevents migration or makes it challenging, might either increase mortality or decrease reproductive success of anadromous fish. These factors, and the previously discussed human impacts to freshwater-marine connectivity, are likely to disproportionately impact anadromous individuals and may place even greater conservation value in the maintenance of freshwater maturing phenotypes.

Conclusions

In the past 25 years ($\sim$6–8 salmon generations) there has been an increasing awareness that human-induced environmental change affects not only the abundance but also the phenotypic and genetic diversity of salmonine populations (Waples 1991; Nielsen 1999). Most contemporary management implicitly or explicitly exerts strong influences on salmonine phenotypes, and these influences affect population resiliency (Bottom et al. 2011). Management actions can change the force of natural selection by changing the relationships between the environment, phenotypes, and components of fitness (Young 2004). This recognition has led to suggestions that conservation of salmonines may depend largely on the management of phenotypic diversity (Watters et al. 2003). In this review, we provide a framework for understanding the proximate and ultimate influences on a major component of salmon life history diversity: the propensity for freshwater maturation. The expression of freshwater maturation in partially anadromous species provides a demographic and genetic buffer during periods of poor ocean conditions, and therefore is a key life history trait influencing the resiliency of some salmonines. Those species without freshwater maturing forms may have compensatory life history traits allowing them to thrive in many ecological settings, but they remain particularly vulnerable to changes in the marine environment. We suggest that managers should not underestimate the importance of freshwater maturing forms for the persistence of partially anadromous species. An improved understanding of the factors underlying freshwater maturation should increase recognition of contemporary management actions that

either constrain or promote the diversity of maturation phenotypes in Pacific and Atlantic salmonines.

References

Alagona PS, Cooper S, Stoecker M, Beedle P, Capelli M (2012) The history of steelhead and rainbow trout in the Santa Ynez River watershed. Bull South Calif Acad Sci 11:163–222

Aubin-Horth N, Bourque J-F, Daigle G, Hedger R, Dodson JJ (2006) Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 63:2067–2075. doi:10.1139/F06-103

Bastien A, Perry GM, Savaria J-Y, Bernatchez L, Audet C (2011) Genetic gain for growth and delayed sexual maturation using a feral strain of anadromous brook trout. N Am J Aquac 73:24–33

Baum D, Laughton R, Armstrong JD, Metcalfe NB (2005) The effect of temperature on growth and early maturation in a wild population of Atlantic salmon parr. J Fish Biol 67:1370–1380. doi:10.1111/j.0022-1112.2005.00832.x

Beacham TD, Murray CB (1990) Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Trans Am Fish Soc 119:927–945

Beckman BR, Larsen DA (2005) Upstream migration of mini-jack (Age-2) Chinook salmon in the Columbia River: behavior, abundance, distribution, and origin. Trans Am Fish Soc 134:1520–1541. doi:10.1577/T05-036.1

Beckman BR, Gadberry B, Parkins P, Cooper KA, Arkush KD (2007) State-dependent life history plasticity in Sacramento River winter-run Chinook Salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation. Can J Fish Aquat Sci 64:256–271

Beechie TJ, Collins BD, Pess GR (2001) Holocene and recent geomorphic processes, land use, and salmonid habitat in two north Puget Sound river basins. In: Dorava JM, Montgomery DR, Palcsak B, Fitzpatrick F (eds) Geomorphic processes and riverine habitat. American Geophysical Union, Washington, pp 37–54

Behnke RJ (2002) Trout and salmon of North America, 1st edn. Free Press, New York

Bell E, Dagit R, Ligon F (2011) Colonization and persistence of a southern California steelhead (*Oncorhynchus mykiss*) population. Bull South Calif Acad Sci 110:1–16

Berg OK (1985) The formation of non-anadromous populations of Atlantic salmon, *Salmo salar* L., in Europe. J Fish Biol 27:805–815

Berg OK, Rød G, Solem Ø, Finstad AG (2011) Pre-winter lipid stores in brown trout *Salmo trutta* along altitudinal and latitudinal gradients. J Fish Biol 79:1156–1166

Bernardo J (1993) Determinants of maturation in animals. Trends Ecol Evol 8:166–173. doi:10.1016/0169-5347(93)90142-C

Bernardo J, Reagan-Wallin NL (2002) Plethodontid salamanders do not conform to "general rules" for ectotherm life histories: insights from allocation models about why simple models do not make accurate predictions. Oikos 97:398–414

Berrigan D, Charnov EL (1994) Reaction norms for age and size at maturity in response to temperature a: puzzle for life historians. Oikos 70:474–478

Bohlin T, Delleforo C, Faremo U (1986) Early sexual maturation of male sea trout and salmon—an evolutionary model and some practical implications. Rep Inst Freshw Res Drottningholm 66:17–25

Bohlin T, Pettersson J, Degerman E (2001) Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. J Anim Ecol 70:112–121. doi:10.1046/j.1365-2656.2001.00466.x

Bottom DL, Jones KK, Simenstad CA, Smith CL, Cooper R (eds) (2011) Pathways to resilience: sustaining salmon ecosystems in a changing world. Oregon Sea Grant, Corvallis

Boughton DA, Fish H, Pipal K, Goin J, Watson F, Casagrande J, Casagrande J, Stoecker M (2005) Contraction of the southern range limit for anadromous *Oncorhynchus mykiss*. NOAA Tech Memo. NMFS-SWFSC-380

Carlson SM, Satterthwaite WH (2011) Weakened portfolio effect in a collapsed salmon population complex. Can J Fish Aquat Sci 68:1579–1589

Christie MR, Marine ML, Blouin MS (2011) Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Mol Ecol 20:1263–1276

Clemento AJ, Anderson EC, Boughton D, Girman D, Garza JC (2009) Population genetic structure and ancestry of *Oncorhynchus mykiss* populations above and below dams in south-central California. Conserv Genet 5:1321–1336

Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2006) Inner Bay of Fundy Atlantic salmon status report. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada

Crawford SS (2001) Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects. Canadian Special Publication of Fisheries and Aquatic Sciences 132. National Research Council Canada Monograph Series, NRC Research Press, Ottawa, Canada

Crespi BJ, Teo R (2002) Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56:1008–1020

Dempson JB, Schwarz CJ, Shears M, Furey G (2004) Comparative proximate body composition of Atlantic salmon with emphasis on parr from fluvial and lacustrine habitats. J Fish Biol 64:1257–1271

Devlin RH, Nagahama Y (2002) Sex determination and sex differentiation in fish: an overview of genetic,

physiological, and environmental influences. Aquaculture 208:191–364

Dieckman U, Heino M (2007) Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar Ecol-Prog Ser 335:253–269

Docker MF, Heath DD (2003) Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia. Conserv Genet 4:227–231

Dodson JJ, Aubin-Horth N, Thériault V, Paez D (2013) The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biol Rev. doi:10.111/brv.12019

Einum S, Kinnison MT, Hendry AP (2004) Evolution of egg size and number. In: Hendry AP, Stearns SC (eds) Evolution illuminated: salmon and their relatives. Oxford University Press, USA, pp 126–153

Einum S, Sundt-Hansen L, Nislow KH (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113:489–496. doi:10.1111/j.2006.0030-1299.14806.x

Elliott JM (1994) Quantitative ecology and the brown trout. Oxford University Press, USA

Esteve M (2005) Observations of spawning behaviour in salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. Rev Fish Biol Fisher 15:1–21. doi:10.1007/s11160-005-7434-7

Falke JA, Dunham JB, Jordan CE, McNyset KM, Reeves GH (2013) Spatial ecological processes and local factors predict the distribution and abundance of spawning by steelhead (*Oncorhynchus mykiss*) across a complex riverscape. PLoS One 8(11):e79232. doi:10.1371/journal.pone.0079232

Finstad AG, Hein CL (2012) Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char. Glob Chang Biol 18:2487–2497. doi:10.1111/j.1365-2486.2012.02717.x

Fleming IA (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. Rev Fish Biol Fisher 6:379–416

Fleming IA (1998) Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Can J Fish Aquat Sci 55:59–76. doi:10.1139/cjfas-55-S1-59

Fleming IA, Gross MR (1990) Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology 71:1–11

Fleming IA, Reynolds JD (2004) Salmonid breeding systems. In: Hendry AP, Stearns SC (eds) Evolution illuminated: salmon and their relatives. Oxford University Press, USA, pp 264–294

Fraser DJ (in press) Evolutionary hypotheses for a constraint to life history resilience in depleted Atlantic salmon (*Salmo salar*) populations. J Fish Biol

Fukushima M, Quinn TJ, Smoker WW (1998) Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. Can J Fish Aquat Sci 55:618–625. doi:10.1139/cjfas-55-3-618

Garcia-Vazquez E, Moran P, Martinez JL, Perez J, de Gaudemar B, Beall E (2001) Alternative mating strategies in Atlantic salmon and brown trout. J Hered 92:146–149. doi:10.1093/jhered/92.2.146

Greene CM, Hall JE, Guilbault KR, Quinn TP (2010) Improved viability of populations with diverse life-history portfolios. Biol Lett 6:382–386. doi:10.1098/rsbl.2009.0780

Groot C, Margolis L (1991) Pacific salmon life histories, 1st edn. UBC Press, Vancouver

Gross, MR (1985) Disruptive selection for alternative life histories in salmon. Nature 313:47–48

Gross MR, Coleman RM, McDowall RM (1988) Aquatic productivity and the evolution of diadromous fish migration. Science 239:1291–1293

Hall JD, Bisson PA, Gresswell RE (1997) Sea-run cutthroat trout: biology, management, and future conservation: proceedings of a symposium, Reedsport, Oregon, October 12–14, 1995. Oregon Chapter of the American Fisheries Society

Haugen TO, Vollestad LA (2000) Population differences in early-life history traits in grayling. J Evol Biol 13:897–905

Hayes SA, Bond MH, Hanson CV, Freund EV, Smith JJ, Anderson EC, Ammann AJ, MacFarlane RB (2008) Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. Trans Am Fish Soc 137:114–128

Hayward A, Gillooly JF (2011) The cost of sex: quantifying energetic investment in gamete production by males and females. PLoS One 6:e16557. doi:10.1371/journal.pone.0016557

Hazel WN, Smock R, Johnson MD (1990) A polygenic model for the evolution and maintenance of conditional strategies. Proc R Soc Lond B Biol 242:181–187

Healey MC (1991) Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In: Groot C, Margolis L (eds) Pacific salmon life histories, 1st edn. UBC Press, Vancouver, pp 311–394

Heard WR (1991) Life history of pink salmon (*Oncorhynchus gorbuscha*). In: Groot C, Margolis L (eds) Pacific salmon life histories, 1st edn. UBC Press, Vancouver, pp 119–230

Hecht BC, Campbell NR, Holecek DC, Narum SR (2013) Genome-wide association reveals genetic basis for the propensity to migrate in wild populations of rainbow trout and steelhead. Mol Ecol 22:3061–3076

Hendry AP, Berg OK (1999) Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Can J Zool 77:1663–1675

Hendry AP, Bohlin T, Jonsson B, Berg OK (2004) To sea or not to sea? Anadromy versus non-anadromy in salmonids. In: Hendry AP, Stearns S (eds) Evolution illuminated: salmon and their relatives. Oxford University Press, USA, pp 92–125

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad Sci USA 100:6564–6568. doi:10.1073/pnas.1037274100

Holecek DE, Scarnecchia DL (2013) Comparison of two life history strategies after impoundment of a historically anadromous stock of Columbia river redband trout. Trans Am Fish Soc 142:1157–1166

Hopkins CL, Unwin MJ (1997) The effect of restricted spring-time feeding on growth and maturation of freshwater-reared chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Aquac Res 28:545–549. doi:10.1111/j.1365-2109.1997.tb01072.x

Hutchings JA (1986) Lakeward migrations by juvenile Atlantic salmon, *Salmo salar*. Can J Fish Aquat Sci 43:732–741

Hutchings JA (2011) Old wine in new bottles: reaction norms in salmonid fishes. Heredity 106:421–437

Hutchings JA, Myers RA (1994) The evolution of alternative mating strategies in variable environments. Evol Ecol 8:256–268

Imre I, Grant JWA, Cunjak RA (2005) Density dependent growth of young-of-the-year Atlantic salmon (Salmo salar) in Catamaran Brook, New Brunswick. J Anim Ecol 74:508–516

Johnson SP, Carlson SM, Quinn TP (2006) Tooth size and skin thickness in mature sockeye salmon: evidence for habitat constraints and variable investment between the sexes. Ecol Freshw Fish 15:331–338

Jones NE (2010) Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream-lake networks. Can J Fish Aquat Sci 67:1350–1362

Jonsson B (1989) Life history and habitat use of Norwegian brown trout (Salmo trutta). Freshw Biol 21:71–86

Jonsson B, Jonsson N (1993) Partial migration—niche shift versus sexual-maturation in fishes. Rev Fish Biol Fisher 3:348–365. doi:10.1007/BF00043384

Jonsson B, Jonsson N (2011) Ecology of Atlantic salmon and brown trout. Springer, New York

Jonsson N, Jonsson B, Hansen L (1991) Energetic cost of spawning in male and female Atlantic salmon (Salmo salar L.). J Fish Biol 39:739–744. doi:10.1111/j.1095-8649.1991.tb04403.x

Keeley ER (2001) Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82:1247–1259

Larsen DA, Beckman BR, Strom CR, Parkins PJ, Cooper KA, Fast DE, Dickhoff WW (2006) Growth modulation alters the incidence of precocious male maturation and physiological development of hatchery reared spring Chinook salmon: a comparison with natural origin fish. Trans Am Fish Soc 135:1017–1032

Larsen DA, Harstad DL, Strom CR, Johnston MV, Knudsen CM, Fast DE, Pearson TN, Beckman BR (2013) Early life history variation in hatchery—and natural-origin spring chinook salmon in the Yakima River, Washington. Trans Am Fish Soc 142:540–555

Letcher BH, Terrick TD (1998) Maturation of male age-0 Atlantic salmon following a massive, localized flood. J Fish Biol 53:1243–1252

Luckenbach JA, Dickey JT, Swanson P (2010) Regulation of pituitary GnRH receptor and gonadotropin subunits by IGF1 and GnRH in prepubertal male coho salmon. Gen Comp Endocr 167:387–396

Malyutina AM, Savvaitova KA, Kuzishchin KV, Gruzdeva MA, Pavlov DS (2009) Population structure of the masu salmon Oncorhynchus masou from the Kol River (Western Kamchatka) and geographic variation in the species area. J Ichthyol 49:390–402. doi:10.1134/S0032945209050051

Martinez JL, Moran P, Perez J, de Gaudemar B, Beall E, Garcia-Vazquez E (2000) Multiple paternity increases effective size of southern Atlantic salmon populations. Mol Ecol 9:293–298. doi:10.1046/j.1365-294x.2000.00857.x

McClure MM, Carlson SM, Beechie TJ, Pess GR, Jorgensen JC, Sogard SM, Sultan SE, Holzer DM, Travis J, Sanderson BL, Power ME, Carmichael RW (2008) Evolutionary consequences of habitat loss for Pacific anadromous salmonids. Evol Appl 1:300–318. doi:10.1111/j.1752-4571.2008.00030.x

McMillan JR, Dunham JB, Reeves GH, Mill JS, Jordan CE (2012) Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, Oncorhynchus mykiss. Environ Biol Fishes 93:343–355. doi:10.1007/s10641-011-9921-0

McNeil WJ (1964) Redd superimposition and egg capacity of pink salmon spawning beds. J Fish Res Board Can 21:1385–1396. doi:10.1139/f64-119

Meka JM, Knudsen EE, Douglas DC, Benter RB (2003) Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Trans Am Fish Soc 132:717–732. doi:10.1577/T01-166

Metcalfe NB, Thorpe JE (1990) Determinants of geographical variation in the age of seaward-migrating salmon, Salmo salar. J Anim Ecol 59:135–145

Moore JW, McClure M, Rogers LA, Schindler DE (2010) Synchronization and portfolio performance of threatened salmon. Conserv Lett 3:340–348

Morán P, Pendas A, Beall E, García-Vazquez E (1996) Genetic assessment of the reproductive success of Atlantic salmon precocious parr by means of VNTR loci. Heredity 77:655–660

Morita KMK, Nagasawa TNT (2010) Latitudinal variation in the growth and maturation of masu salmon (Oncorhynchus masou) parr. Can J Fish Aquat Sci 67:955–965

Morita K, Yamamoto S, Hoshino N (2000) Extreme life history change of white-spotted char (Salvelinus leucomaenis) after damming. Can J Fish Aquat Sci 57:1300–1306. doi:10.1139/cjfas-57-6-1300

Myers RA, Hutchings JA (1985) Selection against parr maturation in Atlantic salmon. Aquaculture 53:313–320

Naiman RJ, Johnston CA, Kelley JC (1988) Alteration of North American streams by beaver. Bioscience 38:753–762

Narum SR, Zendt JS, Graves D, Sharp WR (2008) Influence of landscape on resident and anadromous life history types of Oncorhynchus mykiss. Can J Fish Aquat Sci 65:1013–1023

Nichols KM, Edo AF, Wheeler PA, Thorgaard GH (2008) The genetic basis of smoltification-related traits in Oncorhynchus mykiss. Genetics 179:1559–1575

Nielsen JL (1999) The evolutionary history of steelhead (Oncorhynchus mykiss) along the US Pacific Coast: developing a conservation strategy using genetic diversity. ICES J Mar Sci 56:449–458

Nordeng H (1983) Solution to the char problem based on Arctic char (Salvelinus alpinus). Can J Fish Aquat Sci 40:1372–1387. doi:10.1139/f83-159

Okuzawa K (2002) Puberty in teleosts. Fish Physiol Biochem 26:31–41

Olsson IC, Greenberg LA (2004) Partial migration in a landlocked brown trout population. J Fish Biol 65:106–121. doi:10.1111/j.1095-8649.2004.00430.x

Olsson IC, Greenberg LA, Bergman E, Wysujack K (2006) Environmentally induced migration: the importance of food. Ecol Lett 9:645–651. doi:10.1111/j.1461-0248.2006.00909.x

Pavlov DS, Savvaitova KA (2008) On the problem of ratio of anadromy and residence in salmonids (Salmonidae). J Ichthyol 48:778–791

Perrier C, Bourret V, Kent M, Bernatchez L (2013) Parallel and nonparallel genome-wide divergence among replicate population pairs of freshwater and anadromous Atlantic salmon. Mol Ecol. doi:10.1111/mec.12500

Pess GR, Montgomery DR, Steel EA, Bilby RE, Feist BE, Greenberg HM (2002) Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., USA. Can J Fish Aquat Sci 59:613–623

Piché J, Hutchings JA, Blanchard W (2008) Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proc R Soc Lond B Biol 275:1571–1575

Pirhonen J, Forsman L (1999) Can smolting and maturation of hatchery-reared brown trout *Salmo trutta* L. be affected by food deprivation during the first and second years of rearing? Aquac Res 30:611–620. doi:10.1046/j.1365-2109.1999.00380.x

Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. Univ. Press, Seattle, p 320

Quinn TP, Myers KW (2004) Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Rev Fish Biol Fisher 14:421–442. doi:10.1007/s11160-005-0802-5

Randall RG, Kelso JRM, Minns CK (1995) Fish production in freshwaters: are rivers more productive than lakes? Can J Fish Aquat Sci 52:631–643

Reeves GH, Benda LE, Burnett KM, Bisson PA, Sedell JR (1995) A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Am Fish Soc Symp 17:334–349

Reid DP, Szanto A, Glebe BD, Danzmann RG, Ferguson MM (2005) QTL for body weight and condition factor in Atlantic salmon (*Salmo salar*): comparative analysis with rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*). Heredity 94:166–172

Rikardsen AH, Thorpe JE, Dempson JB (2004) Modelling the life-history variation of Arctic charr. Ecol Freshw Fish 13:305–311

Roff DA (1996) The evolution of threshold traits in animals. Q Rev Biol 71:3–35. doi:10.2307/3037828

Roff DA (2002) Life history evolution, 1st edn. Sinauer Associates, Sunderland

Rounsefell GA (1958) Anadromy in North American salmonidae. U.S. G.P.O, Washington

Rowe D, Thorpe J (1990) Differences in growth between maturing and nonmaturing male Atlantic Salmon, *Salmo salar* L., parr. J Fish Biol 36:643–658. doi:10.1111/j.1095-8649.1990.tb04319.x

Sahashi G, Morita K (2013) Migration costs drive convergence of threshold traits for migratory tactics. Proc R Soc B 280:20132539. doi:10.1098/rspb.2013.2539

Saunders RL, Henderson EB, Glebe BD (1982) Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). Aquaculture 28:211–229. doi:10.1016/0044-8486(82)90024-2

Schaffer WM (2004) Life histories, evolution, and salmonids. In: Hendry AP, Stearns SC (eds) Evolution illuminated: salmon and their relatives. Oxford University Press, USA, pp 20–51

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465:609–613

Schluter D, Price TD, Rowe L (1991) Conflicting selection pressures and life history trade-offs. Proc R Soc Lond B Biol 246:11–17

Schwanke CJ, Hubert WA (2003) Structure, abundance, and movements of an allacustrine population of rainbow trout in the Naknek River, Southwest Alaska. Northwest Sci 77:340–348

Sharpe CS, Beckman BR, Cooper KA, Hulett PL (2007) Growth modulation during juvenile rearing can reduce rates of residualism in the progeny of wild steelhead broodstock. N Am J Fish Manag 27:1355–1368

Shearer KD, Swanson P (2000) The effect of whole body lipid on early sexual maturation of 1+ age male chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture 190:343–367

Shynk JJ (2012) Probability, random variables, and random processes: theory and signal processing applications. Wiley, New York

Sigourney DB, Letcher BH, Cunjak RA (2006) Influence of beaver activity on summer growth and condition of age-2 Atlantic salmon parr. Trans Am Fish Soc 135:1068–1075

Sloat MR, Reeves GH (2014) Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (Oncorhynchus mykiss) life histories. Can J Fish Aquat Sci. doi:10.1139/cjfas-2013-0366

Stanford JA, Lorang MS, Hauer FR (2005) The shifting habitat mosaic of river ecosystems. Verh Int Verein Limnol 29:123–136

Stearns SC (1992) The evolution of life histories. OUP, Oxford

Sutterlin AM, MacLean D (1984) Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Can J Fish Aquat Sci 41:1139–1149

Taranger GL, Carrillo M, Schulz RW, Fontaine P, Zanuy S, Felip A, Weltzien F-A, Dufour S, Karlsen O, Norberg B, Andersson E, Hansen T (2010) Control of puberty in farmed fish. Gen Comp Endocr 165:483–515

Thériault V, Dunlop E, Dieckmann U, Bernatchez L, Dodson JJ (2008) The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evol Appl 1:409–423

Thorpe JE (2007) Maturation responses of salmonids to changing developmental opportunities. Mar Ecol Prog Ser 335:285–288

Thorpe JE, Talbot C, Miles MS, Keay DS (1990) Control of maturation in cultured Atlantic salmon in pumped seawater tanks, by restricting food intake. Aquaculture 86:315–326

Thorpe JE, Mangel M, Metcalfe NB, Huntingford FA (1998) Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evol Ecol 12:581–599

Thrower FP, Hard JJ, Joyce JE (2004) Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead. J Fish Biol 65:286–307

Tipping JM, Byrne JB (1996) Reducing feed levels during the last month of rearing enhances emigration rates of hatchery-reared steelhead smolts. Prog Fish-Cult 58:128–130

Titus RG, Erman DC, Snider WM (2000) History and status of steelhead in California coastal drainages south of San Francisco Bay. California Department of Fish and Game Fish Bulletin

Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fish. Rev Fish Sci 11:107–184

Valiente AG, Juanes F, Garcia-Vazquez E (2005) Reproductive strategies explain genetic diversity in Atlantic Salmon, *Salmo salar*. Environ Biol Fish 74:323–334. doi:10.1007/s10641-005-1331-8

Waples RS (1991) Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Mar Fish Rev 53:11–22

Watters JV, Lema SC, Nevitt GA (2003) Phenotype management: a new approach to habitat restoration. Biol Conserv 112:435–445

Welch DW, Melnychuk MC, Rechisky RW, Jacobs MC, Ladouceur M (2009) Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Can J Fish Aquat Sci 66:736–750

Wood CC, Bickham JW, Nelson J, Foote CJ, Patton JC (2008) Recurrent evolution of life history ecotypes in sockeye salmon: implications for conservation and future evolution. Evol Appl 1:207–221. doi:10.1111/j.1752-4571.2008.00028.x

Young KA (2004) Towards evolutionary management: lessons from salmonids. In: Hendry AP, Stearns SC (eds) Evolution illuminated: salmon and their relatives. Oxford University Press, New York, pp 358–376