NRC Research Press

REVIEW

Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns

Neala W. Kendall, John R. McMillan, Matthew R. Sloat, Thomas W. Buehrens, Thomas P. Quinn, George R. Pess, Kirill V. Kuzishchin, Michelle M. McClure, and Richard W. Zabel

Abstract: *Oncorhynchus mykiss* form partially migratory populations with anadromous fish that undergo marine migrations and residents that complete their life cycle in fresh water. Many populations' anadromous components are threatened or endangered, prompting interest in understanding ecological and evolutionary processes underlying anadromy and residency. In this paper, we synthesize information to better understand genetic and environmental influences on *O. mykiss* life histories, identify critical knowledge gaps, and suggest next steps. Anadromy and residency appear to reflect interactions among genetics, individual condition, and environmental influences. First, an increasing body of literature suggests that anadromous and resident individuals differ in the expression of genes related to growth, smoltification, and metabolism. Second, the literature supports the conditional strategy theory, where individuals adopt a life history pattern based on their conditional status relative to genetic thresholds along with ultimate effects of size and age at maturation and iteroparity. However, except for a generally positive association between residency and high lipid content plus a large attainable size in fresh water, the effects of body size and growth are inconsistent. Thus, individuals can exhibit plasticity in variable environments. Finally, patterns in anadromy and residency among and within populations suggested a wide range of possible environmental influences at different life stages, from freshwater temperature to marine survival. Although we document a number of interesting correlations, direct tests of mechanisms are scarce and little data exist on the extent of residency and anadromy. Consequently, we identified as many data gaps as conclusions, leaving ample room for future research.

Résumé : Les truites arc-en-ciel (*Oncorhynchus mykiss*) forment des populations partiellement migratrices incluant des individus anadromes qui effectuent des migrations marines et des individus résidents dont le cycle biologique se déroule entièrement en eau douce. Les éléments anadromes de nombreuses populations sont menacés ou en voie de disparition, ce qui suscite un intérêt envers la compréhension des processus écologiques et évolutionnaires qui sous-tendent l'anadromie et la résidence. Nous présentons une synthèse de l'information disponible dans le but de mieux comprendre les influences génétiques et environnementales sur les cycles biologiques d'*O. mykiss*, de cerner les lacunes critiques en matière de connaissances et de proposer des avenues de recherche future. L'anadromie et la résidence semblent témoigner d'interactions entre la génétique, l'état des individus et des influences environnementales. D'abord, de plus en plus d'études donnent à penser que les individus anadromes et résidents diffèrent sur le plan de l'expression des gènes associés à la croissance, à la smoltification et au métabolisme. Deuxièmement, la documentation appuie la théorie de la stratégie conditionnelle selon laquelle les individus adoptent un motif de cycle biologique basé sur leur état conditionnel par rapport à des seuils génétiques, ainsi que sur les effets finaux de la taille et de l'âge à la maturité et de l'itéroparité. Cependant, à l'exception d'une association généralement positive entre la résidence et un contenu lipidique élevé en plus d'une grande taille pouvant être atteinte en eau douce, les effets de la taille du corps et de la croissance ne sont pas uniformes. Ainsi, des individus peuvent présenter une plasticité dans des milieux variables. Enfin, des motifs d'anadromie et de résidence entre les populations et au sein de ces dernières indiqueraient un grand éventail d'influences environnementales possibles à différentes étapes du cycle de vie, allant de la température de l'eau douce à la survie en mer. Bien que nous documentions un certain nombre de corrélations intéressantes, les tests directs des mécanismes sont rares et peu de données existent sur l'ampleur de la résidence et de l'anadromie. Par conséquent, nous cernons autant de lacunes sur le plan des données que de conclusions, ce qui laisse amplement de place pour des travaux futurs. [Traduit par la Rédaction]

Received 16 April 2014. Accepted 5 October 2014.

Paper handled by Associate Editor Michael Bradford.

N.W. Kendall,[*,†] J.R. McMillan,[*,‡] G.R. Pess, M.M. McClure, and R.W. Zabel. National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112, USA.
M.R. Sloat. Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331-3803, USA.
T.W. Buehrens. Washington Department of Fish and Wildlife, Fish Program, Science Division, 2108 Grand Blvd., Vancouver, WA 98661, USA.
T.P. Quinn. School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA.
K.V. Kuzishchin. Moscow State University, Vorob'evy Gory, Moscow, 119899, Russian Federation.

Corresponding author: Neala W. Kendall (e-mail: neala.kendall@dfw.wa.gov).
[*]Equal authorship.
[†]Present address: Washington Department of Fish and Wildlife, Fish Program, Science Division, 1111 Washington St. SE, Olympia, WA 98501, USA.
[‡]Present address: Trout Unlimited, 1326 5th Avenue, Suite 450, Seattle WA 98101, USA.

Can. J. Fish. Aquat. Sci. **72**: 319–342 (2015) dx.doi.org/10.1139/cjfas-2014-0192

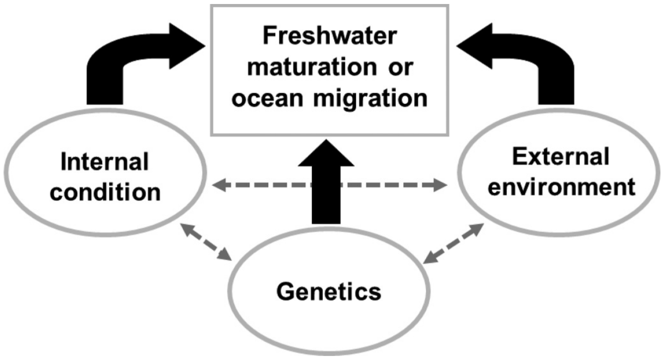
Introduction

Oncorhynchus mykiss is one of several salmonine fishes (*Oncorhynchus*, *Salmo*, *Salvelinus* spp.) that display a form of partial migration; some individuals in a population undergo marine migrations (i.e., anadromy) before returning to fresh water to breed, whereas others complete their entire life cycle within fresh water (i.e., residency; Jonsson and Jonsson 1993; Pavlov and Savvaitova 2008; Quinn and Myers 2004). "Steelhead" and "rainbow trout" are the common North American names for anadromous and freshwater resident life history forms of *O. mykiss*, respectively, whereas both forms are known as "mykizha" in Russia. Anadromous and resident forms are often sympatric, commonly interbreed, and their offspring may adopt either form (Christie et al. 2011; Courter et al. 2013; Sloat and Reeves 2014). The balance of life histories can vary, with some populations supporting more residents and others more anadromous individuals (e.g., Pavlov et al. 2008). Even for populations in close proximity, the proportion of individuals displaying different life histories can vary dramatically, suggesting that complex evolutionary and ecological processes influence the balance between anadromy and residency. Although partial migration is common among salmonines, with a long record of research in some species such as Atlantic salmon (*Salmo salar*; Aubin-Horth et al. 2006; Rowe and Thorpe 1990; Simpson 1992), the processes shaping *O. mykiss* behavior are not completely understood.

Oncorhynchus mykiss display diverse life histories (Behnke 2002), and the extent of anadromy and residency is shaped by interactions among a fish's genotype, individual condition (e.g., size, recent growth rate, and energy stores), and environment (Fig. 1; Sloat et al. 2014). The extent of anadromy and residency has implications for population viability through influences on abundance, intra- and interpopulation diversity, resilience, structure, and productivity (Waples et al. 2008). Understanding partial migration is important from a conservation and management perspective in the same way that understanding the portfolio effect is helpful in financial realms (Koellner and Schmitz 2006; Lehman and Tilman 2000; Schindler et al. 2010). For example, greater life history diversity in *O. mykiss* spreads mortality risk over space and time, thereby dampening population fluctuations and increasing resiliency to environmental variability (Moore et al. 2014). Further, resident males mating with anadromous females (McMillan et al. 2007) and the contribution of anadromous offspring from residents and vice-versa (Christie et al. 2011; Courter et al. 2013; Sloat and Reeves 2014) offer important avenues for buffering genetic and demographic stochasticity that are much less available to other Pacific salmonines (Sloat et al. 2014). Declines in the anadromous component of *O. mykiss* populations in the United States, Canada, and Russia have motivated an increased interest in exploring the factors shaping anadromy and residency, especially as changing climate conditions and anthropogenic activities alter the fitness of these different forms (Benjamin et al. 2013; Satterthwaite et al. 2010).

The purpose of this paper is to review the patterns and processes underlying the expression of anadromy and residency in *O. mykiss* (Fig. 1). A review is important and timely for several reasons. First, because most studies on anadromy and residency in *O. mykiss* are recent, there is an opportunity to summarize the most influential processes and identify knowledge gaps to help guide future research and monitoring. Second, *O. mykiss* inhabit the broadest latitudinal range of environments of any salmonine (Behnke 2002), and the environmental variation may provide clues about which habitat factors affect anadromy and residency (Benjamin et al. 2013; McMillan et al. 2012; Sloat and Reeves 2014), which is especially relevant given the need for understanding the implications of climate change. Third, though genetics (e.g., Nichols et al. 2008) and individual condition early in life (e.g., McMillan et al. 2012) influence anadromy and residency in *O. mykiss* as they do with other salmonines (e.g., Simpson 1992), *O. mykiss* are arguably the most complex of the partially anadromous salmonines. Thus, they may provide additional insights into life history expression that are observed rarely in Atlantic salmon, such as resident maturation by relatively small, young females (Sloat 2013; Sloat and Reeves 2014). Fourth, correlations between individual condition and life history patterns are not always consistent, and the reasons for such differences have not been fully explored. Lastly, research from Russia is not as well disseminated in North America, but it provides valuable information on linkages between the environment and partial migration in relatively healthy populations (McPhee et al. 2014; Pavlov et al. 2001*a*, 2001*b*). This review brings together existing information from both western and eastern Pacific populations and provides a foundation for understanding how future anthropogenic impacts and climate change could influence *O. mykiss* life histories.

Fig. 1. Schematic diagram illustrating how an individual's internal condition, genetic background, and environmental conditions influence whether or not a salmonine matures in fresh water as a resident or becomes anadromous and migrates to the ocean. Black arrows indicate one-way effects, and grey dashed arrows indicate two-way or interactive effects.



Fitness trade-offs in partially migratory salmonines

Although a simple dichotomy between "anadromy" and "freshwater residency" belies the diverse array of developmental pathways exhibited by *O. mykiss* (Shapovalov and Taft 1954), the division does correspond with major differences in selective pressures experienced by these phenotypes (Table 1; Jonsson and Jonsson 1993). Anadromous fish undergo smolt transformation in preparation for the marine environment and typically must delay reproduction to migrate to the rich feeding grounds of the temperate seas, but they benefit from a larger size at maturation. Mortality during the smolt migration and early ocean occupancy may exceed 95%, decreasing mean survival to reproduction for anadromous individuals (Hendry et al. 2004). Resident fish typically have a higher probability of surviving to reproduce multiple times (i.e., iteroparity), but reproduce at smaller sizes (and thus with lower fecundity) than their anadromous counterparts (Fleming and Reynolds 2004). Thus, anadromy and residency are characterized by trade-offs in survival to and size and age at first reproduction along with the probability of iteroparity.

Many factors can modify the strength of these trade-offs, including environmental conditions. For example, increased migration difficulty or poor ocean conditions should decrease benefits of anadromy (Hendry et al. 2004), whereas improved freshwater productivity should increase the benefits of residency (Finstad and Hein 2012). The fitness trade-offs between life histories could therefore be expected to vary spatially and temporally with changes in environmental conditions, including those imposed by anthropogenic actions and climate change.

Table 1. Potential costs and benefits associated with residency and anadromy in partially migratory salmonines.

Life history	Costs	Benefits
Residency	Typically smaller size at maturation: For females, lower fecundity, smaller eggs, producing smaller fry, smaller range of gravel for redds, and shallower redds. For males, decreased chance of competitive dominance and female choice for reproduction.	Reduced mortality with younger age at maturation, avoidance of large marine predators. Reduced cost and length of marine migration. Increased chance of iteroparity.
Anadromy	Increased mortality risk during marine migration. Higher mortality with older age at maturation. Decreased chance of iteroparity.	Reproduction typically at larger size: For females, higher fecundity and access to a larger range of gravel for redds and larger eggs, producing larger fry. For males, increased chance behavioral dominance during mating and female choice.

The balance of fitness trade-offs also differs between males and females because of varying strengths of size-mediated fitness components (Table 1; Hendry et al. 2004). For example, female reproductive success is typically limited by the production of gametes rather than access to mates, as is the case for males, and a larger body size typically equates to greater fecundity (Quinn et al. 2011; Schill et al. 2010). Larger females also attract more potential mates, acquire high-quality spawning sites, mobilize larger substrate, and dig deeper nests (Fleming and Reynolds 2004; Steen and Quinn 1999). Consequently, female salmonines are more frequently anadromous (Morita and Nagasawa 2010; Ohms et al. 2014) and on average mature at larger sizes and older ages than males (Hendry et al. 2004; Jonsson and Jonsson 1993).

Although body size is also important to males, they have evolved tactics that allow different-sized individuals to gain access to females (Table 1; Fleming and Reynolds 2004; Gross 1991). Larger individuals attempt to dominate access to females through aggressive competition, whereas smaller individuals rely more on sneaking tactics to surreptitiously fertilize eggs during spawning (Fleming 1996). The size differences of males using alternative mating tactics can be great (Fleming and Reynolds 2004), though small sneaking males can still have significant reproductive success (Christie et al. 2011; Martinez et al. 2000; Morán et al. 1996; Seamons et al. 2004). Males therefore more frequently become residents because they are less dependent on large body size for reproductive success than females, and as a result, they mature across a much greater range of ages and sizes (Jonsson and Jonsson 1993; Roni and Quinn 1995).

Partial migration in *O. mykiss*

Anadromous and resident life histories

All *O. mykiss* spawn and rear in fresh water, but in the time between emergence and spawning there is tremendous variation in their migration patterns, age at smolt transformation, and age and size at maturation (Behnke 2002; Kuzishchin et al. 2007; Savvaitova et al. 2002; Shapovalov and Taft 1954). For example, on the Kamchatka Peninsula, Russia, populations may consist of individuals that spend several years in the open ocean before returning to fresh water for spawning (typical anadromous); others that make nonreproductive migrations to fresh water several months after their initial ocean entry, overwinter there, and then return to the ocean the following spring (half-pounder); others that seasonally enter estuaries repeatedly over successive years before maturing (estuarine) or alternate years between estuaries and rivers throughout their life (river–estuarine); and residents that spend their entire lives in fresh water (Kuzishchin et al. 2007; Pavlov et al. 2008; Savvaitova et al. 2003). Analogous life histories have been documented to varying degrees in North American populations (e.g., Hodge 2010) and may be more common than is currently recognized because such aspects of *O. mykiss* life histories are less studied than in Russia (e.g., Behnke 2002; Busby et al. 1996; Hard et al. 2007; Quinn and Myers 2004).

The various life histories are typically characterized by differences in sizes and ages at maturation. Fully anadromous individuals spend 1–4 years in fresh water and 1–5 years in the open ocean and generally mature at ages 2–7 and around 500–1100 mm in length (Busby et al. 1996; Kuzishchin et al. 2007; Quinn and Myers 2004). Anadromous estuarine and half-pounder life histories spend 1–3 years in fresh water and only 1–3 months in estuaries or nearshore areas, respectively, and tend to mature at slightly younger ages and much smaller sizes (250–400 mm in length; Kesner and Barnhart 1972; Kuzishchin et al. 2007; Quinn and Myers 2004; Satterthwaite 1988; Savvaitova et al. 2002). Residents are typically smaller and younger at maturation than their fully anadromous counterparts, often maturing for the first time at 2–4 years of age and 100–350 mm in length, but, as with anadromy, there is a wide range in size and age at maturation (Behnke 2002; Kuzishchin et al. 2007; Schroeder and Smith 1989). Some residents, most commonly males (e.g., McMillan et al. 2007), may mature as early as age 1 at very small sizes, whereas others may not mature until ages 5 or 6 at sizes exceeding 800 mm in length (Pavlov et al. 2008; Russell 1977; Savvaitova et al. 2003; Schroeder and Smith 1989). Lastly, some residents that mature in fresh water undergo the smolt transformation later in life (Shapovalov and Taft 1954), while some anadromous fish may remain in fresh water as residents after spawning (Null et al. 2013).

The prevalence of these life history patterns varies between the sexes and among populations, reflecting differences in fitness trade-offs between males and females and their environments (Sloat et al. 2014). Thus, we consider the processes and patterns in anadromy and residency within the context of sex when separate data are available for males versus females.

The extent of genetic influence and plasticity

Life histories in salmonines are partly, and sometimes strongly, shaped by genetic and maternal influences (Carlson and Seamons 2008). An important question for *O. mykiss*, then, is the extent to which life histories are heritable and how much room is left for plasticity (i.e., environmental influences). We reviewed several studies that examined genetic and maternal influence on anadromy and residency in *O. mykiss* (Table 2). Neave (1944) presented the first evidence of a genetic basis for *O. mykiss* life histories using common garden and transplant experiments with sympatric steelhead and rainbow trout in the Cowichan River, British Columbia, Canada. After marking and releasing the progeny of steelhead and rainbow trout reared from eggs under common hatchery conditions for 8–12 months, Neave (1944) concluded that life histories were heritable after a greater proportion of rainbow trout offspring were recaptured in the river over the next several years. Whether the lower recapture rate of steelhead progeny reflected differential freshwater survival after release or a higher rate of smolt transformation could not be determined, but Neave (1944) also observed heritable differences between steelhead and

Table 2. Topics and major findings of *O. mykiss* studies that examined processes and patterns in anadromy and residency in relation to genetic and maternal effects, individual condition, and size at maturation.

Topic	Finding	Study location and reference
Heritability	First evidence of genetic basis for anadromy and residency — transplant experiment found residents more likely to produce residents and heritable differences in meristic traits.	British Columbia; Neave 1944
	No difference in growth between maturing males and smolts; heritability estimates were moderate to strong (h^2 = 0.44–0.56) for anadromy, residency, and growth-related traits.	Alaska; Thrower et al. 2004
	Anadromous × anadromous matings produced most smolts, while resident × resident matings produced the fewest.	Oregon; Ruzycki et al. 2009
	Strong maternal effects: offspring of anadromous origin made up 63% of the juveniles below barriers to anadromy and 97% of the outmigrating smolts.	California; Hayes et al. 2012
	Genomic regions linked to early maturation, but regions linked to maturation differed between males and females, suggesting sex-specific variation in maturation timing.	Commercial hatchery fish; Haidle et al. 2008
	One locus linked to multiple traits and physiological processes regulating smoltification, suggesting potential for common genetic component to smoltification.	Washington State; Nichols et al. 2008
	Anadromous × anadromous matings produced the most smolts, while resident × resident matings produced the fewest smolts.	Oregon; Ruzycki et al. 2009
	Two quantitative trait loci (QTL) affected smoltification processes, indicating that a few QTL have a strong effect on smoltification and migration.	Washington and Idaho; Le Bras et al. 2011
	Genomic regions linked to embryonic development and breeding timing under differential selection between resident and anadromous individuals.	California; Martínez et al. 2011
	Reinforced QTL in previous studies and identification of several additional genetic regions, indicating a more complex basis to smoltification.	Washington and Idaho; Hecht et al. 2013
	Genes linked to major physiological processes, including metabolism and digestion, differentially expressed in resident and anadromous individuals.	Oregon; Garrett 2013
	Genetic basis of migration linked to several regions of the genome.	Alaska and Oregon; Hale et al. 2013
	Broad sense heritability for growth (H^2 = 0.40–0.60), condition factor (H^2 = 0.07–0.59), and smoltification (H^2 = 0.69 and 0.77) were high, with approximately half or more of the variation in these traits explained by genetic variation.	Washington; Doctor et al. 2014
Maternal effects	Strong maternal control in one population — anadromous mothers only produced anadromous offspring — and lesser maternal control in another population.	Oregon and British Columbia; Zimmerman and Reeves 2000
	Anadromous mother × resident male matings produced significantly more smolts than matings with resident mothers and anadromous males.	Oregon; Ruzycki et al. 2009
	Offspring of anadromous mothers were larger and grew faster than resident offspring; larger offspring more likely to become anadromous than smaller offspring.	Argentina; Liberoff et al. 2014*a*
	Strong maternal control over life histories in offspring from anadromous and resident parents; greater influence for females.	Washington; Berejikian et al. 2014
Individual condition	Early-maturing resident males had higher lipid content that nonmaturing males in late summer, approximately 9 months in advance of spawning.	Kamchatka Peninsula; Pavlov et al. 2001*b*
	Anadromous individuals were larger and had higher lipid content than residents, but lipid levels were substantially higher than reported in other studies.	Kamchatka; Pavlov et al. 2007, 2010*a*,*b*
	Faster-growing fish predicted to become anadromous; residency predicted to increase with maximum size attainable in fresh water, freshwater survival, and when migration survival decreased.	California; Satterthwaite et al. 2009, 2010, 2012
	In laboratory experiment, future smolts had consistently greater growth than non-smolts, but condition factor of smolts shifted from being greater than to less than that of non-smolts as the time of smolt transformation approached.	California; Beakes et al. 2010
	Hatchery steelhead smolts had lower condition factor but were longer than residuals (residents) at time of release.	Washington; Hanson et al. 2011
	Early male maturation in fresh water positively correlated with size and lipid content 9 months prior to the spawning season	Oregon; McMillan et al. 2012
	Females with faster growth and higher lipids matured as residents, while males with faster growth matured as residents; residents had lower metabolic costs.	Oregon; Sloat and Reeves 2014
	Size had positive effect on probability of residency; males had different maturation probabilities than females for a given age and size.	Washington; Berejikian et al. 2014

Table 2 (*concluded*).

Topic	Finding	Study location and reference
Size and age at maturation	Resident and anadromous females overlapped in size and age at maturation, and resident female lifetime egg production was similar to that of anadromous female because of greater iteroparity.	Oregon; Schroeder and Smith 1989
	Resident and anadromous females overlapped in size and age at maturation, but 80% of resident females spawned twice, so lifetime egg production was similar to anadromous females, most of which spawned only once.	Kamchatka; Kuzishchin et al. 2007; Pavlov et al. 2008; Savvaitova et al. 1997
	Resident males matured earlier in life, and at presumably smaller sizes, than resident females	Oregon; Christie et al. 2011

Note: Some studies are listed more than once with different descriptions if their results contributed to multiple topics.

rainbow trout progeny in meristic traits, suggesting some level of reproductive isolation between life histories.

The importance of heritable effects has also been documented more recently. Like Neave (1944), Ruzycki et al. (2009) produced various crosses of anadromous and resident *O. mykiss*, including crosses of different sexes, and found that anadromous × anadromous matings produced the most smolts and resident × resident matings produced the fewest (Table 2). Similarly, Hayes et al. (2012) found that the propensity for anadromy was influenced by anadromous genetic ancestry in *O. mykiss* smolts captured in coastal California (Table 2). Individuals with anadromous ancestry made up approximately 63% of the juvenile population in reaches below an anadromous barrier, but comprised 97% of the outmigrating smolts (Hayes et al. 2012), though nongenetic maternal factors may also be influential.

The apparent genetic contribution to *O. mykiss* life histories could partly be related to maternal influences. In the Deschutes River, Oregon, Zimmerman and Reeves (2000) determined through otolith microchemistry that all anadromous adults had anadromous mothers and resident adults had only resident mothers, and field observations indicated there was temporal and spatial isolation during mating (Table 2). Ruzycki et al. (2009) also documented that more smolts were produced by anadromous mothers than resident mothers, as did Liberoff et al. (2014*a*). Offspring of anadromous mothers were more likely to become anadromous because they grew faster and achieved a larger size than resident offspring in an introduced population of *O. mykiss* in Argentina (Table 2; Liberoff et al. 2014*a*). Lastly, Berejikian et al. (2014), working in coastal streams in Washington State, also reported a strong maternal effect. Only 2% of age-1 and age-2 females from anadromous mothers matured in fresh water (i.e., were resident) compared with 33%–53% for offspring from resident mothers (Table 2).

Research on the extent of heritability (the proportion of phenotypic variance explained by genetic factors; Hazel et al. 1990; Roff 1997) is limited but shows moderate to strong genetic influence on *O. mykiss* life histories. For example, Thrower et al. (2004) bred pure and reciprocally crossed lines of anadromous and resident *O. mykiss* from Alaska and determined narrow-sense heritabilities for smolt transformation and freshwater maturation after 2 years of rearing in a common environment (Table 2). The crosses came from parapatric populations separated by a barrier waterfall, with the upstream resident population originating from a transplant of juvenile fish from below the falls that occurred approximately 70 years prior to the study. Heritability estimates for freshwater maturation and smolting were between 0.44–0.51 and 0.45–0.56, respectively, and are similar to field-derived estimates for partially migratory brook trout (*Salvelinus fontinalis*) life histories (h^2 = 0.52–0.56; Thériault et al. 2007). In another common garden experiment, Doctor et al. (2014) transplanted two Washington State populations of anadromous *O. mykiss* from relatively cold and warm thermal regimes (Table 2). They examined growth rate, condition factor, and life history (smolting or freshwater maturation) and found a genotype–temperature interaction, with fish in warmer temperatures smolting at earlier ages than fish in cooler ones because of differences in growth. Despite the strong environmental influence, they also reported broad-sense estimates of heritability for smolting (H^2 = 0.69 and 0.77) that were comparable to the narrow-sense estimates by Thrower et al. (2004).

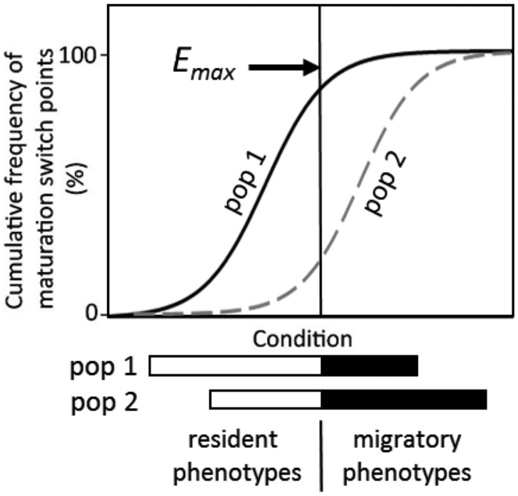
Although there is clearly a genetic component to anadromy and residency, the data also indicate that fish displaying each life history pattern can give rise to the other. For example, Christie et al. (2011) demonstrated that resident fish contributed approximately 40% of the genes to Hood River, Oregon, steelhead populations. In the study by Thrower et al. (2004), progeny from all possible combinations of anadromous and resident crosses exhibited similar mean rates of freshwater maturation. Offspring from the above-waterfall resident population described earlier also produced significant numbers of smolts and returning anadromous adults despite over 70 years of complete selection against migration (see also Hayes et al. 2012; Thrower and Joyce 2004). Likewise, freshwater maturation persists in many, if not all, hatchery steelhead trout stocks after decades of selectively breeding only anadromous adults (Christie et al. 2011; Sharpe et al. 2007; Sloat and Reeves 2014). Otolith microchemistry revealed that anadromous kelts in the Yakima River basin, Washington, had resident mothers 7% and 20% of the time in each of 2 years of study (Courter et al. 2013). Similar observations of residents producing anadromous offspring have been documented in other populations (Zimmerman et al. 2009; Zimmerman and Reeves 2000), in addition to female steelhead producing resident offspring (Zimmerman et al. 2003). Interchange between forms was also observed in the Santa Cruz River, Argentina, where steelhead apparently evolved from resident trout (Pascual et al. 2001; Riva-Rossi et al. 2007). Perhaps not surprisingly, molecular analysis has seldom revealed genetic divergence between anadromous and resident individuals where fish displaying these life histories patterns are sympatric (Docker and Heath 2003; McPhee et al. 2007; Olsen et al. 2006), consistent with evidence for considerable interbreeding between life histories from parentage analysis (Christie et al. 2011; Seamons et al. 2004) and direct observation (McMillan et al. 2007).

The studies summarized above provide evidence of a heritable basis for *O. mykiss* life histories, but also demonstrate that individuals in partially migratory populations are not precluded by their parentage from expressing either anadromy or residency. The ability of offspring to express either life history pattern suggests there is substantial developmental plasticity in *O. mykiss* and that the traits underlying anadromy and residency are partly labile and sensitive to environmental influences (Sloat et al. 2014). In the following section, we explore the influence of genetic and environment interactions on *O. mykiss* life histories to illustrate how anadromy and residency can be both heritable and strongly shaped by environment.

Conditional strategy theory

Anadromy and residency in salmonines are most commonly explained as alternative tactics within a single conditional strategy (Dodson et al. 2013; Hutchings and Myers 1994; Sloat et al. 2014). The evolutionary goal of a conditional strategy is to maximize fitness by using proximate cues to adopt the most appropriate life history from among several alternatives. The theory posits

Fig. 2. An example of two populations (or sexes) with different reaction norm cumulative frequency distributions. Population 1 (pop 1: black line) has evolved lower conditional thresholds for freshwater maturation than population 2 (pop 2: dashed grey line). In a freshwater habitat with an upper limit to the conditional state individuals may achieve ($E_{\max}$: black vertical line), a higher proportion of individuals in population 1 would surpass the threshold for freshwater maturation than in population 2 (horizontal bars below *x* axis).



that all individuals within a population are capable of expressing the full range of alternative tactics (in this case, residency or anadromy; Gross 1996; Hazel et al. 1990). The expression of a particular tactic occurs if an individual's condition surpasses a genetically based threshold that triggers one of several alternative developmental pathways (e.g., smolt, mature, wait; Satterthwaite et al. 2009). In salmonines, the processes of maturation and smolt transformation have been linked to individual size, growth rate, and whole body lipid content at particular times of the year (i.e., "decision windows"; Beakes et al. 2010). Body size, growth, and energy content directly influence fitness components such as survival to reproduction and fecundity, and they may provide cues to individuals about whether to exploit opportunities for reproduction given their recent performance in a particular environment (Dodson et al. 2013; Sloat et al. 2014; Thorpe et al. 1998).

The genetically based threshold that triggers the adoption of a particular tactic can be depicted as a step function that is unique to each genotype (Hazel et al. 1990; Sloat et al. 2014 Fig. 1*a*). These functions, known as reaction norms (Hutchings 2011), depict the minimum condition (e.g., size, growth, or lipid content) at which a genotype commits to a particular tactic. Individual reaction norms reflect heritable genetic variation, so their distribution among individuals within a population can be shaped by local selective pressures (Debes et al. 2014; Hazel et al. 1990; Piché et al. 2008). For example, a combination of poor freshwater growth opportunities and a fitness advantage of large size at reproduction should result in directional selection for higher conditional thresholds for freshwater maturation (Sloat et al. 2014). Similarly, females should evolve higher conditional thresholds for freshwater maturation than males given that their reproductive success tends to be more size-dependent (Hendry et al. 2004; Jonsson and Jonsson 1993). Consequently, the distribution of reaction norms may vary among populations and between sexes depending on the relative fitness of alternative tactics in a given environment over time (Fig. 2; Dodson et al. 2013; Sloat et al. 2014).

Environmental variation strongly influences juvenile growth and energy storage, and therefore it plays a major proximate role in the expression of anadromy and residency (e.g., Doctor et al. 2014; Sloat and Reeves 2014). Environmental factors such as rearing temperature, food supply, and competition (reviewed in more detail below) constrain the maximum potential condition that individuals may achieve in fresh water. Consequently, the frequency of anadromy and residency within a given cohort is hypothesized to be controlled by the distribution of individual reaction norms relative to the level of individual condition that could be achieved during freshwater rearing (Fig. 2; Sloat et al. 2014). Thus, the conditional strategy framework incorporates a genetic basis for life histories that operates through heritable reaction norms, but also incorporates the adaptive plasticity of individuals to adjust their life histories according to proximate environmental influences (Hazel et al. 1990; Sloat et al. 2014).

Gene expression influencing *O. mykiss* anadromy and residency

Gene expression studies can improve our understanding of anadromy and residency by providing mechanistic insight into traits (e.g., growth, metabolism, and smolt transformation) that are most likely to influence salmonine life histories (Hale et al. 2013; Hecht et al. 2013). Such studies can also provide information about genomic regions and markers that could be used to determine whether there are consistent differences among individuals displaying alternative life histories (Nichols et al. 2008). We found a limited, but emerging, body of research examining gene expression for *O. mykiss* living in the wild, so we also used research from domesticated stocks and other salmonine species.

The studies we reviewed indicated a specific epigenetic basis for several traits related to life histories in *O. mykiss*, with smolt transformation perhaps being the most obvious. For example, Nichols et al. (2008) analyzed quantitative trait loci (QTL) in clonal crosses of captive anadromous and resident *O. mykiss* and found that one locus in particular was associated with multiple traits and physiological processes regulating the smolt transformation process (Table 2). Similarly, Le Bras et al. (2011) identified two QTL affecting blood plasma chloride and sodium concentrations, which are important to osmoregulation and smoltification (Table 2). Hecht et al. (2013) corroborated that the QTL results identified additional genomic regions linked to smoltification, suggesting a complex polygenic basis for saltwater transformation in *O. mykiss* where several loci of small effect are distributed throughout the genome (Table 2). These studies demonstrate that the epigenetic basis of migration in *O. mykiss* is associated with many different regions of the genome, with some of those regions shared among populations and others unique to individual populations (Table 2).

Differential expression of genes associated with physiological traits such as metabolism and food conversion efficiency may also influence salmonine life histories. Individuals expressing marine and freshwater migratory phenotypes often have higher metabolic expenditures as juveniles in a variety of salmonine species (e.g., Forseth et al. 1999; Morinville and Rasmussen 2003), including *O. mykiss* (Sloat and Reeves 2014). Garrett (2013) documented differential expression of genomic markers for proteasome activity, metabolism, and digestion between resident and anadromous *O. mykiss* (Table 2). Anadromy, and migration in general, may be partly controlled by individual variation in metabolic costs, with individuals that have greater costs being more likely to migrate until they locate an environment providing adequate conditions (e.g., food supply) for growth and maturation (Forseth et al. 1999; Morinville and Rasmussen 2003; Sloat et al. 2014).

In addition to variation in the expression of genes related to smoltification and metabolism, anadromous and resident fish have epigenetic differences in spawn timing and developmental rate. For example, Martínez et al. (2011) documented genomic regions linked to embryonic development and spawn timing that were under differential selection within an *O. mykiss* population of both resident and anadromous individuals (Table 2). Such differ-

Table 3. Summary of predicted associations for some measures of individual condition with *O. mykiss* life histories, for males and females, and the rationale for how individual condition appears to influence the extent of residency.

Measures of individual condition	Life history association Male	 Female	Rationale
Faster or slower growth	A or R	A or R	Associations can vary in relation to sex, population, and environment.
Slower growth and lower lipid content	A	A	Residency less likely because slower growth increases risk of mortality with older age at maturity and lipid levels are inadequate for sexual development.
Faster growth and higher lipid content	R	A or R	Residency more likely for males as faster growth decreases risk of mortality with younger age at maturity and lipid levels can be adequate for sexual development; for females, associations depending on maximum freshwater size.
Slower growth, lower lipid content, and smaller maximum freshwater size	A	A	Residency less likely because lower lipids inhibit maturation, slow growth increases age at maturity and increases risk of mortality, and a smaller maximum size reduces fecundity.
Faster growth, higher lipid content, larger maximum freshwater size	R	R	Residency more likely because higher lipid stores provide surplus energy for maturation, fast growth decreases age at maturity and risk of mortality, and a larger maximum size increases fecundity.

Note: Maximum freshwater size = maximum size achievable in fresh water. A, higher probability of anadromy; R, higher probability of residency; A or R, response is variable and depends on environment that population is found in.

ences may also extend to males and females. Haidle et al. (2008) examined a highly domesticated stock of *O. mykiss* and discovered genomic regions linked to early maturation and individual condition (Table 2). Those regions differed between males and females, suggesting sex-specific variation in maturation timing (Haidle et al. 2008), consistent with the observation that males often mature at younger ages and smaller sizes than females (Pavlov et al. 2008). Although the studies discussed do not necessarily demonstrate cause and effect, they provide evidence of individual variability in gene expression related to traits such as smoltification and metabolism that are directly correlated with anadromy and residency.

Individual condition influencing *O. mykiss* anadromy and residency

Growth, size, and lipid content

As expected, based on the conditional strategy hypothesis and research on other salmonines (Dodson et al. 2013; Jonsson and Jonsson 1993; Rikardsen et al. 2004; Thorpe et al. 1998), all studies we reviewed on *O. mykiss* suggested a proximate influence of individual condition on the expression of anadromy and residency. The specific effects of size and growth on *O. mykiss* life history expression were variable, however, sometimes inconclusive, and depended on population, sex, and other factors (Tables 2 and 3).

Some studies suggested a positive association between early juvenile growth and anadromy. Satterthwaite et al. (2009, 2010, 2012) used state-dependent models to simulate the effects of growth and other parameters on female life history patterns in three *O. mykiss* populations in coastal and central California (Table 2). They predicted that the early emerging and fastest-growing females would smolt at age 1 or age 2 and that only the latest-emerging and slowest-growing females would become residents, which generally matched empirical observations from these populations (Sogard et al. 2012). In addition, Liberoff et al. (2014*a*) and Pavlov et al. (2007, 2010*a*, 2010*b*) also reported that larger individuals became anadromous, but these studies did not differentiate between sexes (Table 2).

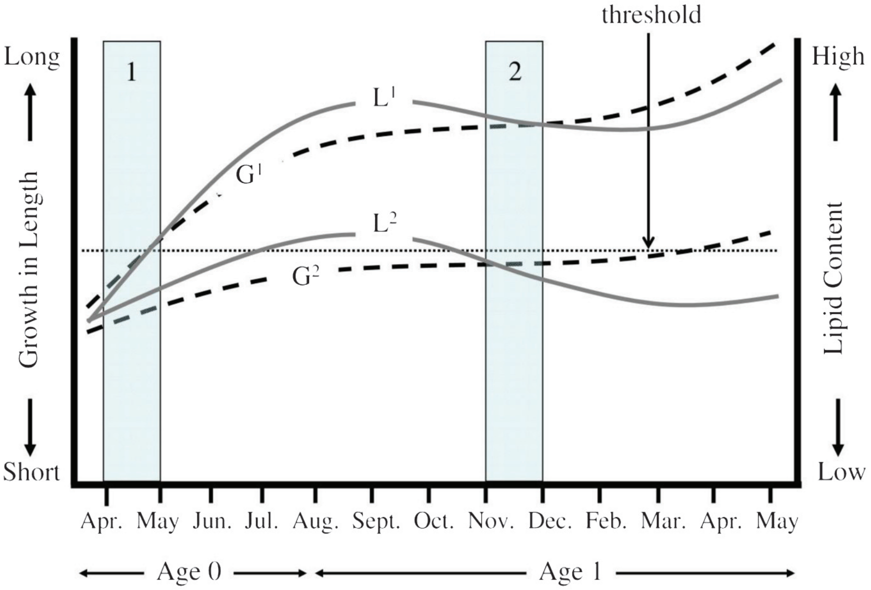
Other studies reported different associations between individual condition and residency. McMillan et al. (2012) found, for a population of *O. mykiss* in interior Oregon, that males maturing at age 1+ were significantly longer than nonmaturing males (Table 2). They did not find any age-1+ females maturing as residents. A common garden experiment by Sloat and Reeves (2014) in Oregon revealed that maturing (i.e., resident) female and male *O. mykiss* grew significantly faster than immature fish at age 1+ (Table 2). In contrast, Thrower et al. (2004) reported no overall difference in growth between fish that became smolts and those that matured as residents for a laboratory-reared population from Alaska (Table 2). The effect of growth did vary among families, however, including some positive associations between growth and male residency and vice-versa for anadromy (Thrower et al. 2004).

The different influences of growth on *O. mykiss* life history could be influenced by a fish's sex (Table 3). For instance, both McMillan et al. (2012) and Sloat and Reeves (2014) found that male *O. mykiss* that matured in fresh water were larger than nonmaturing males. This is generally consistent with what has been documented in Atlantic salmon, where faster growth and larger size early in life are often (e.g., Aubin-Horth et al. 2005, 2006), but not always (e.g., Bacon et al. 2005), linked to male residency. On the other hand, Satterthwaite et al. (2009, 2010) constructed their model only for female *O. mykiss*, which appear to express freshwater residency at much lower rates than males (Berejikian et al. 2014; Rundio et al. 2012; Sloat and Reeves 2014). There is also some evidence of different reaction norms between males and females, resulting in varying influences of growth and size (Doctor et al. 2014; Sloat et al. 2014). Berejikian et al. (2014) found that male maturation in fresh water was positively correlated with body size, and they matured at younger ages and smaller sizes more commonly than females, indicating different reaction norms (Table 2). Reaction norms also varied among males based on maternal origin, with males from resident mothers maturing at smaller sizes than those from anadromous mothers (Berejikian et al. 2014).

Not accounting for sex can make it difficult to evaluate some studies' reports of effects of growth on life history. McMillan (2009) would have found no difference in size between nonmaturing and maturing *O. mykiss* unless males and females were examined separately. This suggests that the findings of Liberoff et al. (2014*a*) and Pavlov et al. (2007, 2010*a*, 2010*b*) may have been different if sex was considered. However, this may not necessarily be the case; Thériault and Dodson (2003) looked only at males and reported little if any difference in growth between resident and anadromous fish in a population of brook char. Regardless of the correlations between growth and size with anadromy or residency, studies on *O. mykiss* indicate that individual condition early in life does influence life history patterns (Table 3).

Although measures of growth and body size have been traditionally used to explain life history expression, they may not fully

Fig. 3. Salmonines are posited to be sensitive to measures of individual condition early in life several months prior to expression of the life history tactic, such as during windows 1 and 2 (shaded vertical bars), which are based on developmental windows proposed by Satterthwaite et al. (2009). Here individuals experience different potential trajectories in growth (G^1 and G^2) and lipid content (L^1 and L^2). In this conceptual model, fish experiencing the greatest growth G^1 and lipid storage L^1 would adopt one life history form because they exceed the genetic threshold during both windows 1 and 2, while at the other extreme individuals experiencing slowest growth (G^2) and lowest lipid levels (L^2) did not exceed the threshold and instead wait to adopt a life history pattern the following year.



reveal the mechanisms involved. Research on other salmonines suggests that lipid content may better predict physiological opportunities for sexual development (Rikardsen and Elliott 2000; Rikardsen et al. 2004; Thorpe et al. 1998). While growth may partly stimulate hormones responsible for initiating maturation, lipids are the major source of energy for sexual development (Sargent et al. 1989; Tocher 2003), and low levels of lipids can inhibit maturation in salmonines regardless of growth (Rowe et al. 1991; Simpson 1992).

There is evidence in *O. mykiss* that higher lipid levels increase the tendency to be a resident. McMillan et al. (2012) found that resident males in Oregon had higher lipid levels than nonmaturing males, as did Pavlov et al. (2001*b*) for a population on the Kamchatka Peninsula (Table 2). Sloat and Reeves (2014) also found that resident females were fatter than nonmaturing females, but maturing males were not fatter than immature males (Table 2). They noted the latter result was probably due to mistimed sampling, as fish were already mature or in an advanced state of maturation when lipid levels were measured. Earlier sampling may have revealed higher lipids in maturing males because a substantial proportion of lipids had to be metabolized for sexual development (Sargent et al. 1989). This has been found for Atlantic salmon (Simpson 1992), though it is important to note that lipids are also metabolized when individuals undergo the smoltification process (Farmer et al. 1978). Regardless, given that growth and size are not necessarily correlated with lipids (McMillan et al. 2012; Sutton et al. 2000), studies that only consider measures of growth or body size may not fully elucidate how individual condition can influence life history patterns (Table 3; Sloat et al. 2014; Sloat and Reeves 2014).

We found one study, however, that reported a different correlation between lipid content and residency, likely because lipid content was already extremely high. Migratory smolts from the Utkholok River of the Kamchatka Peninsula, which is dominated by anadromous fish, had higher lipid levels in the autumn than future residents (Table 2; Pavlov et al. 2007, 2010*a*, 2010*b*). Sexes were not differentiated. Lipid level ranges were 13%–14% and 22%–30% in the low and high lipid level groups, respectively, which were markedly higher than the 1%–10% reported in the other Russian study (Pavlov et al. 2001*b*) and three studies on Oregon *O. mykiss* (Kammerer and Heppell 2013; McMillan et al. 2012; Sloat and Reeves 2014). Pavlov et al. (2007, 2010*a*, 2010*b*) indicated that lipid levels were high because the fish were gorging on salmon eggs. Consequently, in this case lipids were presumably no longer limiting to maturation. In such cases, asymptotic size (Satterthwaite et al. 2009) or growth may instead be limiting (e.g., Chinook salmon (*Oncorhynchus tshawytscha*): Larsen et al. 2006; Table 3). Such contradictions raise questions about whether any measure of individual condition has a consistent directional influence on anadromy and residency in *O. mykiss* across sexes and populations (Table 3).

Despite the varying influences of individual condition, all studies reported that their effects were present at least 9–10 months before the life history form was expressed (Table 2; McMillan et al. 2012; Pavlov et al. 2007, 2010*a*, 2010*b*; Sloat 2013). This supports the theoretical expectation that there may be particular periods when salmonines are most sensitive to hormonal cues correlated with individual condition, maturation, and smolt transformation (e.g., Gross and Repka 1998; Thorpe et al. 1998). For *O. mykiss*, the models of Satterthwaite et al. (2009, 2010) predicted the window for initiation of maturation to be during April, with a permissive window in November (Fig. 3), and laboratory work on smolts and nonsmolts by Beakes et al. (2010) suggested that differences in condition were also occurring a year in advance of life history expression. Small maturing male *O. mykiss* in McMillan et al. (2012) and Pavlov et al. (2001*b*) and males and females in Sloat and Reeves (2014) were at a moderate to late stage of sexual development in late summer. Hence, it is plausible that maturation may have begun during the previous spring, as proposed by Satterthwaite et al. (2009).

The timing of individual condition measurements has implications not only for life history expression, but also for futures studies on the topic. Laboratory experiments on Atlantic salmon (Simpson 1992) and Chinook salmon (Silverstein et al. 1998) indicated that maturing fish may experience reduced growth and lipid content as they commit energy reserves to maturation, while the future anadromous members of their cohort continue growing in preparation for smolting. This has also been shown for *O. mykiss*. Hanson et al. (2011) found that steelhead smolts released from a hatchery that did not migrate had higher condition factors but were shorter than smolts at the time of release (Table 2). This is relevant because Beakes et al. (2010) found in 1 of 2 years that future *O. mykiss* smolts had higher condition factors than future non-smolts almost a year prior to smolting, but that by November–December non-smolts had greater condition factors (Table 2), perhaps because smolts became more fusiform in shape as time of smolting approached (Jonsson 1985). Accordingly, sampling fish closer to spawning or smolting may miss differences in body size, growth, or lipid content that were present earlier in life, during the decision windows, and were important to life history expression (e.g., Sloat 2013).

Size at maturation and iteroparity

In addition to proximate influences of individual condition in early life, there may also be ultimate effects on fitness later in life via size at maturation and rate of iteroparity. For example, if females can acquire ample lipids and achieve a large size in fresh water (i.e., approximate size of an anadromous female) to reduce potentially large differences in fecundity, the need for an ocean migration is eliminated (Table 3; Sloat et al. 2014). Similarly, a higher rate of iteroparity among residents may compensate for an otherwise reduced size at reproduction (e.g., Schroeder and Smith 1989).

Evidence suggests that a large attainable size in fresh water and iteroparity are indeed important to increased residency in *O. mykiss*. For example, models by Satterthwaite et al. (2010) predicted that a greater asymptotic size in fresh water would have increased residency in an *O. mykiss* population that was predominately anadromous (Table 2; Sogard et al. 2012). They also predicted that the effects of growth, faster or slower, on life histories would vary depending on the size at maturity.

Empirical data on size at maturation and iteroparity generally support the hypotheses and model predictions by Satterthwaite et al. (2009; 2010; Table 2). For example, the Deschutes River, Oregon, is dominated by resident *O. mykiss* in abundance and biomass, yet it also has a substantial anadromous component (Table 2; Schroeder and Smith 1989; Zimmerman and Ratliff 2003). Most female residents spawned for the first time at ages 3–4 at a mean length of 300–330 mm, though some reached 490–580 mm, with an mean fecundity of 1400 eggs (Schroeder and Smith 1989). Most anadromous individuals migrated to the ocean at ages 1–2, and females reached first maturity at a mean age of 4 years and a mean size of 610 mm (range: 490–710 mm) carrying a mean of 3500 eggs (Howell et al. 1985). The rapid growth in fresh water apparently led to a large attainable size at maturation for resident females at the same age as or at a younger age than anadromous females, and while resident females were generally smaller, 80% spawned a second time (Schroeder and Smith 1989). The high level of iteroparity effectively doubled the lifetime egg production of residents so that it was very similar to that of anadromous females (<5% of which spawned a second time; Howell et al. 1985).

Howell et al. (1985) did not provide data on egg size, but it tends to be smaller in residents than in anadromous females (Gross 1987). However, Gross (1987) indicated that resident and anadromous *O. mykiss* displayed the same size eggs, which was not typical for other salmonids displaying anadromous and resident life histories. Kuzishchin et al. (2007) also reported similar egg diameters for resident and anadromous females in one Russian population of *O. mykiss*. Larger eggs can be beneficial to growth early in life (Einum and Fleming 1999; Fleming and Reynolds 2004), but in *O. mykiss* it appears that it cannot necessarily be assumed that anadromous life histories produce larger eggs than residents.

There is also a wealth of data for *O. mykiss* populations on the Kamchatka Peninsula, where female residents attain large sizes and are more numerous than anadromous individuals in some watersheds (Kuzishchin et al. 2007; Pavlov et al. 2001*a*, 2001*b*, 2008; Savvaitova et al. 1997; Table 2). In the Kol River, for example, residency predominates and residents overlap in age and size at first maturation with anadromous fish (resident age and size at first maturation: 3–5 years and 375–605 mm (mean = 501 mm) versus anadromous age and size at first maturation: 4–6 years and 594–854 mm (mean = 735 mm); Kuzishchin et al. 2007; Pavlov et al. 2008). A similar pattern was observed in the Utkholok River (resident age and length at first maturation: 3–5 years and 310–545 mm versus anadromous age and length at first maturation: 3–5 years and 550–950 mm; Savvaitova et al. 1997). Mean fecundity of resident females was substantially less (3065 eggs) than that for larger anadromous females (10 638 eggs), but was similar to that of smaller estuarine (3102 eggs) and river–estuarine (3115 eggs) anadromous life histories (Kuzishchin et al. 2007). As in the Deschutes River, however, 80% of the residents were repeat spawners and some spawned up to five times, whereas most anadromous fish spawned only once (Kuzishchin et al. 2007). Consequently, lifetime fecundity of resident females that spawn multiple times could approach or even exceed that of anadromous females that are less likely to spawn multiple times (Kuzishchin et al. 2007; Savvaitova et al. 1997), indicating that egg production differences are less than they would appear to be without considering repeat spawning (Pavlov et al. 2001*b*, 2007, 2008). Similar patterns in size at maturation have been documented in northern Alaska, where resident *O. mykiss* also attain very large sizes (300–800+ mm) and predominate over anadromous individuals or are the only form present (McHenry et al. 1975; Quinn and Myers 2004; Russell 1974, 1977).

The 80% rate of repeat spawning for resident females in the Deschutes River and Kamchatka Peninsula was double the estimate of 41% from Shapovalov and Taft (1954), indicating the potential for a wide range of iteroparity. This could be another reason, in addition to lipid content, that the Satterthwaite et al. (2010) model predictions underestimated the extent of residency in one of the California populations where both males and females were frequently resident (Sogard et al. 2012). Regardless, the studies we reviewed suggest that female residency is likely to be increasingly favored relative to anadromy in populations where resident individuals experience a high level of iteroparity in addition to fast growth, higher lipids, and a large size at maturation in fresh water (Table 3).

Although apparently important for resident females, asymptotic size may be less important for males (Tables 2 and 3). A significant portion of males were reported to mature at smaller sizes and younger ages than females in several studies (Christie et al. 2011; Kuzishchin et al. 2007; Pavlov et al. 2008; Schroeder and Smith 1989; Table 2). Despite being smaller than anadromous males, resident males can sire a large proportion of offspring by mating with anadromous females (Christie et al. 2011; Seamons et al. 2004). The reproductive success of smaller males found by these parentage studies aligns with observations by McMillan et al. (2007) and reports by Kostow (2003) of small resident males sneaking matings with larger anadromous females.

A higher frequency of early maturation at a small size for *O. mykiss* males and the potential reproductive success of these small resident males imply that the importance of size at maturation differs between sexes. It is hypothesized that females are less plastic than males because of the importance of body size, and there is some indication that the threshold size at which individuals mature is higher for females than males (Morita and Nagasawa 2010). Indeed, the model of Satterthwaite et al. (2009, 2010) predicted that the effects of growth depended on asymptotic size, with faster-growing *O. mykiss* likely to become anadromous when asymptotic size was small and faster-growing individuals likely to become residents where asymptotic size doubled. This is not to suggest that size at maturation and iteroparity, and their influence on fecundity, are the only factors driving female life history expression. For example, small size at maturation for females may be favored in smaller streams that limit access by larger anadromous individuals, as we discuss later. Still, the data we reviewed suggest that females are more likely to become anadromous regardless of growth or size early in life unless they can increase lifetime egg production to a point where it is equal, or nearly equal, to that of anadromy.

Environmental factors influencing *O. mykiss* anadromy and residency

Water temperature

Water temperature is widely considered a major factor shaping salmonine life history patterns (Brannon et al. 2004). This may be particularly relevant for *O. mykiss* because their distribution incorporates a wider range of thermal habitats than most Pacific salmonines (Kammerer and Heppell 2013; Richter and Kolmes 2005; Sloat and Osterback 2013). Water temperature has direct effects on metabolism, growth (Brett 1952, 1979), and lipid content (Feldhaus 2006; Kammerer and Heppell 2013), which influence the expression of anadromy and residency (McMillan et al. 2012; Sloat 2013). Thermal regimes that reduce opportunities for obtaining a large size and high lipid levels in fresh water may therefore increase the likelihood of anadromy (Fig. 4; Sloat et al. 2014). Later in life, water temperature could also influence residency and anadromy through effects on spawn timing and subsequent emergence (Pavlov et al. 2001*a*; Satterthwaite et al. 2009) and the timing of returning adults (High et al. 2006; Robards and Quinn 2002; Waples et al. 2008).

In two California *O. mykiss* populations, anadromy was the predominant, if not the sole, life history in a warm stream that frequently exceeded 20 °C during summer (Table 4; Sogard et al. 2012). In contrast, residents were abundant in a cool stream where summer temperatures typically fell within the optimal range for growth (Table 4; Sogard et al. 2012). Model predictions also indicated that large changes in water temperature would be needed to shift the life history balance (Table 4; Satterthwaite et al. 2010). Cooler water has been correlated with an increased prevalence of residents elsewhere, including *O. mykiss* populations on the Kamchatka Peninsula (Augerot and Foley 2005), western Washington State (Berejikian et al. 2013), and central Washington State (Courter et al. 2009) and Oregon (Table 4; McMillan 2009). On the other hand, modeled predictions by Benjamin et al. (2013) suggested that warming of temperatures into the optimum range for growth would increase the prevalence of resident fish in a Washington State population of *O. mykiss* living in relatively cool streams where summer temperatures rarely exceeded 15 °C (Table 4; Rieman et al. 2007). Thus, while colder temperatures may provide more favorable conditions for residency, the effects may be relative within a given environment.

A correlation between residency and cooler water temperatures appears related to trade-offs in energy allocation (Table 4). For wild *O. mykiss*, McMillan et al. (2012) found that both faster growth and higher lipid levels were positively correlated with resident male maturation. However, fish grew longer in warmer streams, but lipid levels were significantly higher in fish from cooler streams than warmer ones (Table 4). As a result, males matured as residents at smaller sizes but with higher lipid levels in cooler streams than in warmer streams (Fig. 5). In a laboratory experiment, Sloat and Reeves (2014) reared *O. mykiss* in cool (6–13 °C) and warm (6–18 °C) thermal regimes and found that significantly more females and males matured in fresh water in the cool regime (Table 4). As in McMillan et al. (2012), growth in length was greater in the warm regime and lipid content was higher in the cool regime. An experiment by Doctor et al. (2014) also found greater growth of *O. mykiss* in warmer treatments (6–13 °C) than colder ones (5–11 °C), but the only resident maturing males were documented in the warmer treatment (10 of 394 fish; Table 4). These results make sense if we consider the context of the temperature differences. It is the combination of absolute temperature and variation in temperature that act jointly on the expression of anadromy and residency. Mean monthly temperatures in McMillan et al. (2012) ranged from 0 to 13 °C and from 1 to 17 °C in the cold and warm streams, respectively, and those in Sloat and Reeves (2014) were similar, though slightly warmer. Responses by fish were fairly similar in each study. The warmer temperatures in Doctor et al. (2014) were nearly identical to the cold treatment in the experiment by Sloat and Reeves (2014), but the spread between the warm and cold treatments was much less. Such comparisons further highlight the importance of considering the temperature in a given system and the optimal value when determining the influence of nominally "cold" and "warm" temperatures on *O. mykiss* life histories.

The hypothesis that colder thermal regimes may foster residency via increases in lipid content has implications for research and management. Growth and size are the most commonly used variables in explaining life history patterns in salmonines, but growth is only one of several competing pathways through which energy is allocated (Sloat and Reeves 2014). Consequently, the predictions of models that were based only on somatic growth and examined the effects of altered thermal regimes on residency and anadromy (e.g., Benjamin et al. 2013; Satterthwaite et al. 2010) may have differed if lipids had been considered (e.g., Fig. 5; Sloat and Reeves 2014). Such comparisons further highlight the importance of considering the actual thermal regime of a given system when determining the influence of nominally "cold" and "warm" temperatures on *O. mykiss* life histories. Further tests could provide important insight into the extent that cooler thermal regimes favor residency through energy allocation towards lipids and help determine the extent to which management actions can alter life histories through restoration of thermal regimes.

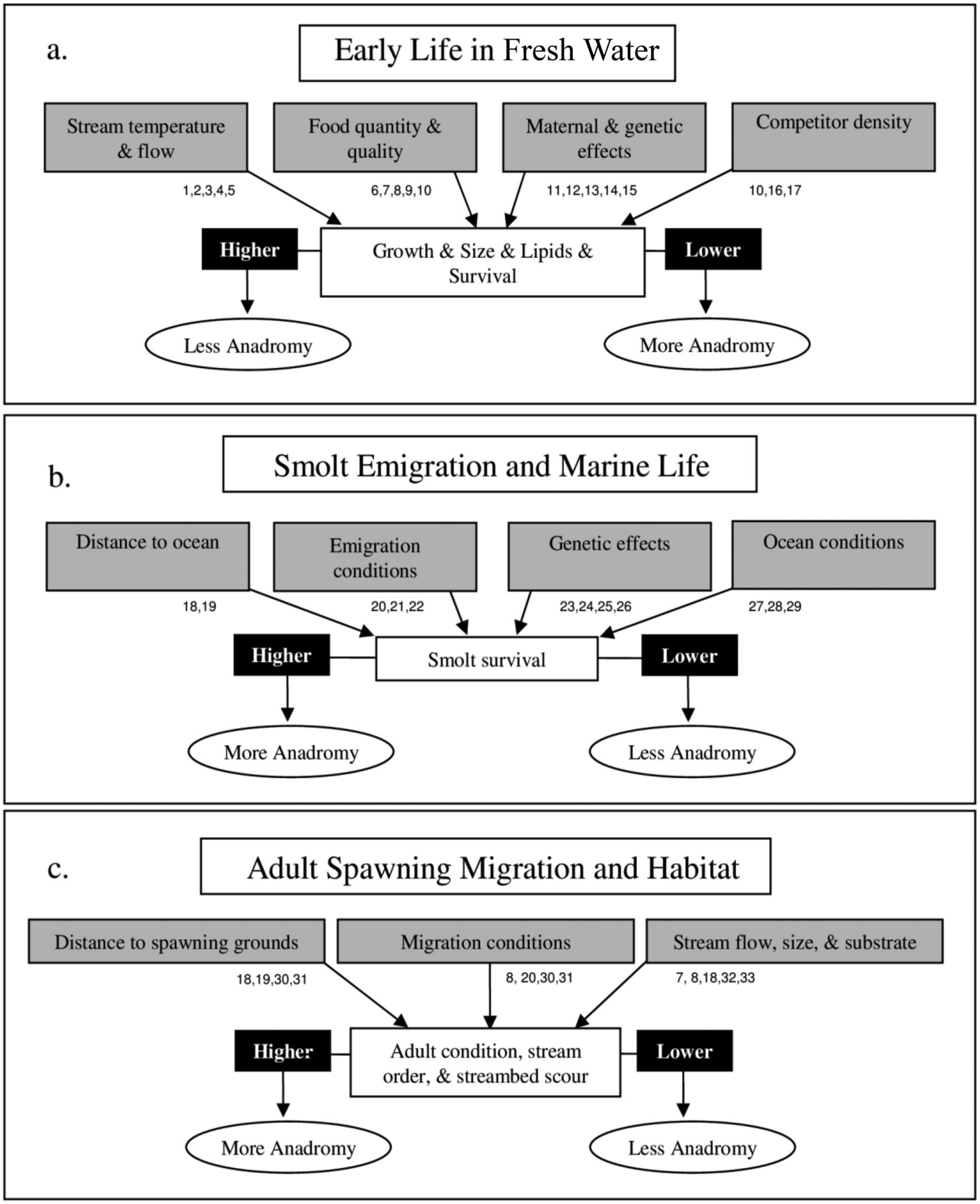
Water temperature may be linked to changes in residency and anadromy in other ways, such as through embryonic development. Pavlov et al. (2001*a*) found, in mixed resident–anadromous *O. mykiss* populations on the Kamchatka Peninsula, that residents spawned in smaller tundra streams that warmed quickly during the spring and led to earlier emergence (Table 4). The earlier emergence effectively lengthened opportunities for development in a cold environment with short growing seasons. A longer period for growth due to earlier emergence was also predicted to increase the chances of residency in the coastal California *O. mykiss* modeled by Satterthwaite et al. (2009), though it may also select for an earlier age at smolting, particularly in females, in Washington State populations where anadromy predominates (Berejikian et al. 2014).

Temperature of a fish's migration corridor can also influence the benefits of anadromy. For example, in the Columbia River basin, anadromous *O. mykiss* commonly rely on cold-water refuges to withstand elevated summer temperatures (High et al. 2006). Additionally, the timing of anadromous fish entry into fresh water has changed substantially over the past several decades in response to changing temperature and flow regimes (Robards and Quinn 2002). Continued increases in migratory habitat water temperatures could eventually reduce the fitness of anadromous *O. mykiss*, favoring residency (Benjamin et al. 2013; Waples et al. 2008), at least to the extent permitted by other factors. Future water flow and temperature regulation should consider these effects to optimize conditions to maintain diversity for the species.

Food supply

Food supply is often limiting in nature and strongly affects growth, body size, lipid stores, and survival (Fig. 4; Grant et al. 1998; Pavlov et al. 2007, 2010*a*, 2010*b*; Railsback and Rose 1999). If migration is partly a function of opportunities for growth, development, and survival (Rounsefell 1958), then the frequency of

Fig. 4. Conceptual diagram depicting the ways that environmental and genetic factors (grey rectangles) can influence the frequency of anadromy (white ovals) in *O. mykiss* through effects on (*a*) individual condition and survival early in life, (*b*) smolt survival during emigration and marine life, and (*c*) adult fitness and survival and extent of stream bed scour during the return migration and spawning. Numbers below grey boxes correspond to the following references: 1. Harvey et al. 2006, 2. McMillan et al. 2012, 3. Sogard et al. 2012, 4. Sloat and Reeves 2014, 5. Railsback and Rose 1999, 6. Schwanke and Hubert 2003, 7. Pavlov et al. 2001*b*, 8. Pavlov et al. 2008, 9. Benjamin et al. 2013, 10. Holm et al. 1990, 11. Thrower et al. 2004, 12. Martínez et al. 2011, 13. Hayes et al. 2012, 14. Doctor et al. 2014, 15. Berejikian et al. 2014, 16. Keeley 2001, 17. Imre et al. 2004, 18. Mills et al. 2012, 19. Ohms et al. 2014, 20. Waples et al. 2008, 21. Courter et al. 2009, 22. Satterthwaite et al. 2010, 23. Nichols et al. 2008, 24. Le Bras et al. 2011, 25. Hecht et al. 2013, 26. Hale et al. 2013, 27. Savvaitova et al. 2003, 28. Satterthwaite et al. 2009, 29. Moore et al. 2010, 30. Robards and Quinn 2002, 31. High et al. 2006, 32. McPhee et al. 2014, 33. Zimmerman and Reeves 2000.



anadromy should partially depend on the availability and quality (e.g., lipid content) of food in fresh water, with the frequency of anadromy predicted to increase as freshwater productivity decreases and marine productivity increases (Fig. 4; Gross et al. 1988).

Tests of the food availability hypothesis are limited (Gross et al. 1988) for all salmonines, but the results suggest that it is likely an important factor driving residency or anadromy. Nordeng (1983) reared crosses of anadromous and resident Arctic char (*Salvelinus alpinus*) offspring under different ration levels and found that in-

Table 4. Topics and major findings of *O. mykiss* studies that examined processes and patterns in anadromy and residency in relation to environmental factors influencing individual condition and size and age at maturation.

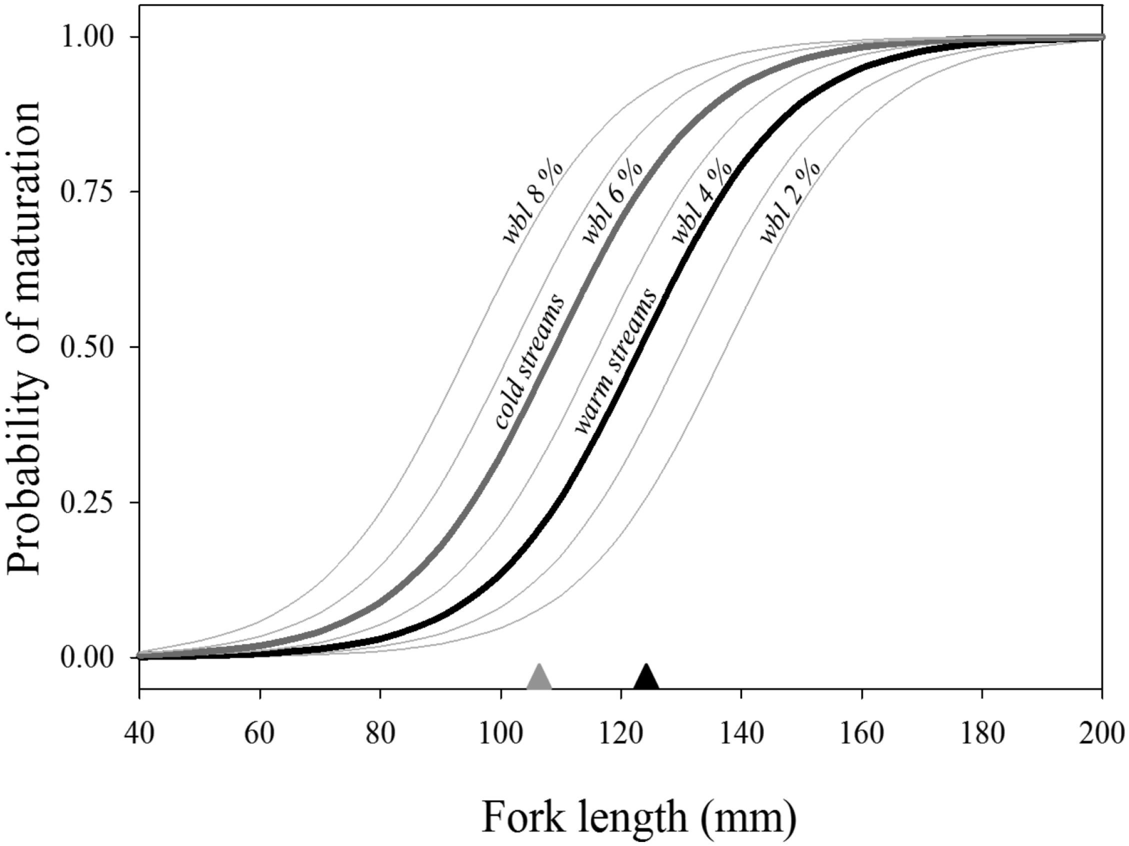
Topic	Finding	Study location and reference
Water temperature and food	Decreased summer water temperatures and increased food supply were not predicted to influence extent of anadromy and residency in streams with high summer temperatures.	California; Satterthwaite et al. 2010
	Increased water temperature predicted to increase residency; less food predicted to reduce growth and increase anadromy; more food predicted to increase growth and residency.	Washington; Benjamin et al. 2013
Water temperature	Water temperature induced different responses in growth and lipid content: higher lipids in colder temperatures, greater growth in warmer temperatures, and higher rates of resident maturation in colder temperatures.	Oregon; McMillan et al. 2012; Sloat and Reeves 2014
	Anadromy predominated in a warmer stream with stressful temperatures, while residency was common in a cooler stream without stressful temperatures.	California; Sogard et al. 2012
	Greater growth and mass in the warmer temperatures than colder ones; male resident maturation only observed in the warmer temperatures.	Washington; Doctor et al. 2014
Food	Ratio of anadromy and residency explained by amount of feeding and spawning habitat, food supply, stream size, and water temperature.	Kamchatka; Pavlov et al. 2001*a*, 2008; Savvaitova et al. 2007
	Populations dominated by residents that could undertake extensive migrations within rivers and lakes where they grow to large sizes by feeding on marine-derived nutrients provided by sockeye salmon.	Alaska; Russell 1974, 1977; Schwanke and Hubert 2003
Stream flow and temperature	Residents spawned mostly in small tundra streams that warmed quickly and led to earlier emergence, which increased growth potential in otherwise cold, short growing seasons.	Kamchatka; Pavlov et al. 2001*a*
	Anadromy most common in streams with greatest variability in flow; residents were most abundant in the river section with the most stable flows.	Washington; Pearsons et al. 2008
	Residency favored in streams with sustained, higher flows and cooler water temperatures during summer, though cost of migration also had a strong effect.	Washington; Courter et al. 2009
	Resident offspring increased with extent of residents upstream of barriers, higher stream flows, and cooler water temperatures, as opposed to ocean survival.	Washington; Berejikian et al. 2013
Density dependence	Introduction of anadromous offspring to a formerly resident population increased juvenile density, reduced variation in size, and decreased the proportion of residents.	Idaho; Bjornn 1978
Overfishing and density dependence	Overfishing depleted anadromy and residency subsequently increased, followed by return to previous levels of anadromy when fishing was curtailed.	Kamchatka; Savvaitova et al. 1997, 2002
Spawning habitat	Smaller, resident females excavate redds in smaller substrate and different microhabitats than larger, anadromous females.	Oregon; Zimmerman and Reeves 2000
Cost of migration	More females became smolts than males, but no association between migration distance and degree of female bias in smolts.	Washington, Oregon, Idaho; Ohms et al. 2014
Elevation and stream gradient	Hypothesized that cost of migration was responsible for increasing frequency of residents at higher elevations and in steeper tributaries.	Washington; Narum et al. 2008
Stream size and flow	Probability of female anadromy increased with increasing stream flow and size; cost of migration had little effect on life history expression.	Oregon; Mills et al. 2012
Stream size and geomorphology	Frequency of anadromy decreased with increasing basin size, but was not related to number of channel breaks and tributary junctions in each mainstem river.	Kamchatka, Canada, USA; McPhee et al. 2014
Stream habitat	Proportion of anadromous individuals was greater in areas with deeper channels and larger substrate.	Argentina; Liberoff et al. 2014*b*
Distance upstream and sex bias	Residents were more common farther upstream in the stream network and appeared male-biased, while anadromy appeared female-biased.	Washington; McMillan et al. 2007

Note: Some studies are listed more than once with different descriptions if their results contributed to multiple topics.

creasing the amount of food significantly increased the proportion of residents. Similarly, Olsson et al. (2006) found that their rates of anadromy increased with decreasing food supplies in captive brown trout (*Salmo trutta*). In nature, O'Neal and Stanford (2011) found that resident brown trout dominated in smaller streams where invertebrate biomass was two to three times higher than in larger streams, which supported a mix of anadromous and resident individuals or were dominated by anadromous fish.

Evidence is more scant for *O. mykiss*. While not focused on naturally living individuals, experimentally reducing food rations did decrease the rate of residency in hatchery steelhead trout (Tipping and Byrne 1996). In addition, two different models partly focused on food and anadromy in *O. mykiss* suggested that food supply and its interaction with other variables was important to life history expression (Table 4). For instance, the model by Satterthwaite et al. (2010) predicted that increasing food availability (total biomass of drift) would not lead to increased female residency in interior California streams. The authors hypothesized that freshwater growing conditions were insufficient to counter the fecundity advantage offered by anadromy (Table 4). However, it is likely that continued increases in food supply in Satterthwaite et al. (2010) would have eventually, by improving the freshwater environment, resulted in a higher predicted fre-

Fig. 5. Probability of age-1+ male *O. mykiss* maturation in relation to fork length and percent whole-body lipid (wbl) in relation to relatively warm and cold streams (redrawn from McMillan et al. 2012). Individual lines represent the relationship between fork length and probability of maturation for levels of wbl from 2% to 8%. Mean percent whole-body lipid for cold streams (dark grey line) and warm streams (black line) are represented by thick lines. Fork lengths corresponding with a probability of maturation of 0.5 for cold and warm streams are represented by dark grey and black triangles on the *x* axis (cold = 109 mm; warm = 123 mm). For every 1% increase in wbl there is a 7 mm decrease in the fork length with a probability of maturation of 0.5.



quency of residents. On the other hand, a model by Benjamin et al. (2013) indicated that growth improved with increasing food supply in a Washington State stream, as did female residency (Table 4). In this case, water temperatures were much colder (mean summer water temperature = 13 °C). In the California streams modeled by Satterthwaite et al. (2010), however, they were so warm (mean summer water temperature = 18–19 °C; Sogard et al. 2012) that it would require even greater levels of food to offset energetic demands that increase with water temperature and metabolic costs. Whatever the reason, the differences suggest that "more" or "less" food is context-dependent for each population and environment.

Empirical spatial patterns in anadromy and residency of *O. mykiss* also suggest that food supply may play a critical role in shaping life history patterns (Fig. 4). As an example, anadromous *O. mykiss* are rare or absent throughout much of western and northern Alaska, and residents are abundant, particularly in rivers supporting large populations of sockeye salmon (*Oncorhynchus nerka*; Table 4; McHenry et al. 1975; Quinn and Myers 2004; Russell 1974, 1977). The annual pulse of marine-derived nutrients supplied by salmon eggs and flesh, in addition to maggots, salmon fry, and smolts as food sources, greatly improves *O. mykiss* growth and may compensate for the short growing season (Bentley et al. 2012). The exceptional productivity allows residents to attain sizes comparable to their anadromous counterparts (e.g., >650 mm; Schwanke and Hubert 2003).

Residency in *O. mykiss* populations on the Kamchatka Peninsula is also thought to be related to food supply (Table 4; Savvaitova et al. 2007). There is tremendous spatial variation in the extent of anadromy and residency among Kamchatka populations, including several populations dominated by residents (Fig. 5; Pavlov et al. 2001*a*, 2007). As in Alaska, *O. mykiss* that feed on salmon eggs and flesh along with maggots grow faster and have higher lipid levels than individuals that feed mainly on aquatic insects (Pavlov et al. 2007, 2010*a*, 2010*b*). Residency is common in streams with high levels of salmon nutrients and an array of feeding habitats (Pavlov et al. 2001*a*, 2008; Savvaitova 1975) that allow individuals to mature at similar sizes and ages as fish undertaking an ocean migration (Kuzishchin et al. 2007).

Correlations between *O. mykiss* residency and the presence of spawning salmon in Alaska and the Kamchatka Peninsula are notable for two reasons. First, they imply that food quality may be as important as food quantity. Salmon eggs are two to three times as energy dense as benthic and terrestrial invertebrates (Armstrong et al. 2010; Cummins and Wuycheck 1971), allowing for higher levels of both growth and lipid accumulation (Pavlov et al. 2007, 2010*a*, 2010*b*). Second, the number of salmon returning to an individual spawning location can vary among years as a result of natural population dynamics (Bentley et al. 2012; Rogers and Schindler 2008). This suggests that in addition to spatial variability, there is the potential for temporal shifts in the prevalence of *O. mykiss* residents as a function of food supplied by spawning salmon (Savvaitova et al. 2007 and references therein), though there is very little evidence supporting such a hypothesis.

Stream flow

Stream flow is a fundamental aspect of stream habitat, influencing juvenile growth and survival, migration of emigrating juveniles and returning adults, and redd scour (Groot and Margolis 1991; Quinn 2005). *Oncorhynchus mykiss* rear and spawn in a broad range of ephemeral and perennial streams (Boughton et al. 2009; McMillan et al. 2013). Variation in annual flow regime, particularly summer low flows, may represent a population bottleneck for nonmigratory fishes (Courter et al. 2009). Larger residents require more space and tend to occupy faster and deeper water than smaller individuals, and streams that do not maintain sufficient flow are unlikely to support large, old, resident *O. mykiss* (Todd et al. 2008). As an example, by manipulating stream flow, Harvey et al. (2006) found that growth rates of *O. mykiss* were 8.5 times lower in reaches with reduced flow than in control reaches. This line of reasoning has led to the hypothesis that higher summer flows improve opportunities for feeding and development, thereby permitting the expression of larger and older freshwater residents (Fig. 4; Cramer et al. 2003; McMillan et al. 2007; Pearsons et al. 1993).

Empirical evidence supports a correlation between summer stream flows and *O. mykiss* life histories, at least in climates where summer flows are a limiting factor (Table 4). Courter et al. (2009) found a strong effect of stream flow on residency and anadromy in a population of *O. mykiss* in the Yakima River, a large tributary to the Columbia River in semiarid central Washington State. There are numerous relatively large residents in the Yakima River, in addition to numerous anadromous individuals. The model by Courter et al. (2009) predicted anadromy to predominate only in lower basin tributaries, where summer low flows were highly variable, and residency to predominate in locations with more stable flow regimes and higher summer flows. This prediction generally matched what was observed in the field (Pearsons et al. 2008).

Similar correlations between summer stream flows and residency have been documented elsewhere. Berejikian et al. (2013) found that higher summer stream flows were correlated with an increase in the proportion of female residents in several rivers in western Washington State (Table 4), though several other factors were also in play. The streams with greater flow also had lower temperatures and more abundant above-barrier resident populations (the source of residents in the study) than streams with lower flows (Berejikian et al. 2013). As previously discussed, resident *O. mykiss* predominate in the Deschutes River, Oregon, which has an exceptionally stable flow and temperature regime and relatively high summer flows (Zimmerman and Ratliff 2003). As in the Yakima River, residency is more common than anadromy in the more stable flows of the mainstem Deschutes River and several spring-fed tributaries draining the west side of the Cascade Mountains. While anadromous individuals spawn in the mainstem Deschutes River, they more commonly spawn and rear in tributaries on the east side of the river that are intermittent except in the wettest years. Residents are less common in these streams (Currens et al. 1990; Zimmerman and Ratliff 2003; Zimmerman and Reeves 2002). The patterns suggest that more stable and higher summer flows may provide better opportunities for growth and lipid accumulation, in addition to providing adequate space and depth for feeding and breeding of larger residents.

Influences of stream flow are not likely limited to summer, however. There may be mechanisms that shape the distribution of anadromous and resident adult spawners. For instance, Mills et al. (2012) found that female residency increased with decreasing mean annual discharge within a sub-basin of the interior Columbia River. Although anadromous *O. mykiss* spawn in smaller tributaries, the results of Mills et al. (2012) suggests there may be a point at which stream size begins to influence the fitness of female body size. Narum et al. (2008) also hypothesized that anadromous *O. mykiss* were essentially absent from the smallest and steepest streams because of their large size and the challenge of migrating upstream.

Smaller streams may also provide flow regimes and sediment characteristics that are better suited for spawning by smaller residents. Stream flow regimes shape female reproductive success through gravel size and scouring of eggs from redds (Montgomery et al. 1999). Resident females are typically much smaller than anadromous females and spawn in smaller substrate (Zimmerman and Reeves 2000) and dig shallower redds (Steen and Quinn 1999). The smaller substrate and shallower redds are more prone to mobilization and scour (Lapointe et al. 2000; Montgomery et al. 1999). Larger streams with a greater frequency of larger substrate and frequent scouring flows may thus select against spawning by smaller females (Table 4; Montgomery et al. 1999), such as residents. Of course, there is no explicit threshold for what constitutes a "small" or "large" stream. A more helpful construct may be "optimum size," but we could not find such tests or data for *O. mykiss*.

Density dependence

Density dependence can influence life history expression through at least two mechanisms. The first is through direct effects on growth and survival, mediated through competition for food and space (Grant and Imre 2005; Keeley 2001). Theoretically, increased competition for food resources decreases growth and size, in turn leading to a higher number of ocean migrants within a population (Hendry et al. 2004; Jonsson and Jonsson 1993; Fig. 4). We did not find any direct tests of density dependence on anadromy and residency in *O. mykiss*. However, a positive association between density and number of migrants was confirmed in an experiment on white-spotted char (*Salvelinus leucomaenis*) by Morita et al. (2000), and somewhat similar findings have been reported for brown trout (Olsson and Greenberg 2004; Olsson et al. 2006), Atlantic salmon (Gibson 1978; Prevost et al. 1992), and sockeye salmon (Krogius 1981). On the other hand, Aubin-Horth et al. (2006) and Baum et al. (2004) did not find a relationship between population-specific juvenile fish density and rates of anadromous migrations in Atlantic salmon.

Density of fish in a given population may be related to the life history expressed. Anadromous populations of *O. mykiss* on the Kamchatka Peninsula were dramatically reduced because of illegal fishing in the early 1990s (Table 4), which was correlated with an increased proportion of residents (Savvaitova et al. 1997, 2002). While the sample sizes were not large enough to determine if the actual prevalence of total residents increased or if the proportions of life histories simply shifted, the authors did document an increase in the prevalence of resident females that had previously only been anadromous. Once the illegal fishing was curtailed, populations began to recover to their former state and the proportion of anadromous individuals increased from the late 1990s to early 2000s. This implies there may be feedback loops with density dependence. Specifically, with higher numbers of anadromous adults, more offspring are produced, resulting in higher densities of juveniles during early life (Morita et al. 2000). The increased competition for food and space means fewer individuals may achieve the necessary conditional status to successfully mature and reproduce in fresh water, and thus more fish would need to emigrate to meet their developmental needs (Jonsson and Jonsson 1993). If this is the case, then anadromy may be self-reinforcing, not only through genetic controls but also by populating a stream to the point where competition for limited resources reduces opportunities for residency in fresh water.

The latter hypothesis was supported by Bjornn (1978), who studied the size and age distribution of juvenile *O. mykiss* in an Idaho, USA, stream that originally supported only residents of various sizes and ages. After anadromous *O. mykiss* were introduced, the population became dominated by age-1 and age-2 anadromous individuals (Table 4). Bjornn (1978) hypothesized this was due to increased competition for food and space. Although the effects of density dependence are not well studied, and variables other than density were not accounted for in these studies, the available results provide an additional piece of evidence indicating that juvenile density can influence anadromy and residency.

Density dependence can also influence life history indirectly through selection on traits, such as energy metabolism, that are correlated with anadromy. As discussed above, anadromous individuals may have higher metabolic costs than resident individuals (Morinville and Rasmussen 2003; Sloat and Reeves 2014). In a laboratory study on *O. mykiss*, intense competition for feeding territories favored fish with high standard metabolic rate (Sloat 2013). These fish are more likely to express anadromy and be more fecund than residents, resulting in higher densities of juvenile fish in fresh water. Sloat (2013) hypothesized that this in turn creates higher rates of competition, continuing a positive feedback loop that favors anadromy (Sloat 2013). In a subsequent experiment, Sloat and Reeves (2014) demonstrated that competitively dominant juveniles had higher mean metabolic rates and were indeed more likely to become anadromous.

Stream geomorphology and the role of lakes

There appear to be correlations between the prevalence of anadromy and residency and physical features of river drainages, including drainage size (McPhee et al. 2014), stream channel complexity (e.g., Pavlov et al. 2001*a*) and depth (Liberoff et al. 2014*b*), and the presence of lakes (e.g., Russell 1974). These habitat features likely influence and are correlated with several other parameters (e.g., food and temperature), so it is difficult to untangle the specific effects of any single factor. Nonetheless, they are relevant because they could potentially be used in conjunction with other variables to predict the extent of residency and anadromy among and within populations.

The extensive datasets on anadromy and residency on the Kamchatka Peninsula provide the best examples of possible correlations between life histories and physical stream features, though recent analyses indicates the story may be highly complex (Table 4). For example, examination of 12 *O. mykiss* populations in Russia found that anadromy predominated in smaller, confined rivers with simple channels compared with residency in drainages with an abundance of small tributaries and larger, longer mainstem rivers with broad floodplains (Pavlov et al. 2001*a*). The broad floodplains in the lower portions of the larger mainstem rivers branched (i.e., channel breaks) into numerous small to large channels that were littered with instream wood, had highly variable depth and water temperatures, and were rich in food, all of which were hypothesized to provide excellent feeding areas for small and large residents compared with the smaller confined rivers, which had less complexity and food resources (Fig. 6; Pavlov et al. 2001*a*, 2008). Indeed, such features (e.g., depth, food, temperature) were found to be important to the maintenance of residents in studies of other areas and populations (Bentley et al. 2012; McMillan et al. 2012; Todd et al. 2008).

However, a comparison of the ratio of anadromy to several stream channel physical metrics in 17 Kamchatkan *O. mykiss* populations, such as the number of tributary junctions and channel breaks, did not find any statistical relationship (McPhee et al. 2014). Instead, drainage area was the best predictor of anadromy, with the proportion of anadromous individuals being highest in small rivers (also partly reported by Pavlov et al. 2001*a*) and lowest in large rivers. It may be that the relationship was based more on the availability of small tributaries and smaller stream channels where residents prefer to spawn rather than the number of channel breaks, because anadromy tends to predominate in larger streams (Mills et al. 2012; Pavlov et al. 2001*a*). Alternatively, larger drainages may simply have more spawning salmon, and hence more food, along with more habitat, which may reduce density dependence for freshwater growth and provide greater opportunities for reproductive segregation of anadromous and resident *O. mykiss*. Most likely the balance of life history patterns is related to interconnected factors, such as water temperature and food supply, which were considered conceptually by Pavlov et al. (2001*a*) but not tested by McPhee et al. (2014; Fig. 6). Accordingly, the associations observed on the Kamchatka Peninsula may be more accurately explained by the ratio of spawning to feeding grounds, with residency increasing with higher rearing habitat productivity and decreased spawning habitat availability (Table 4; Pavlov et al. 2001*a*, 2008).

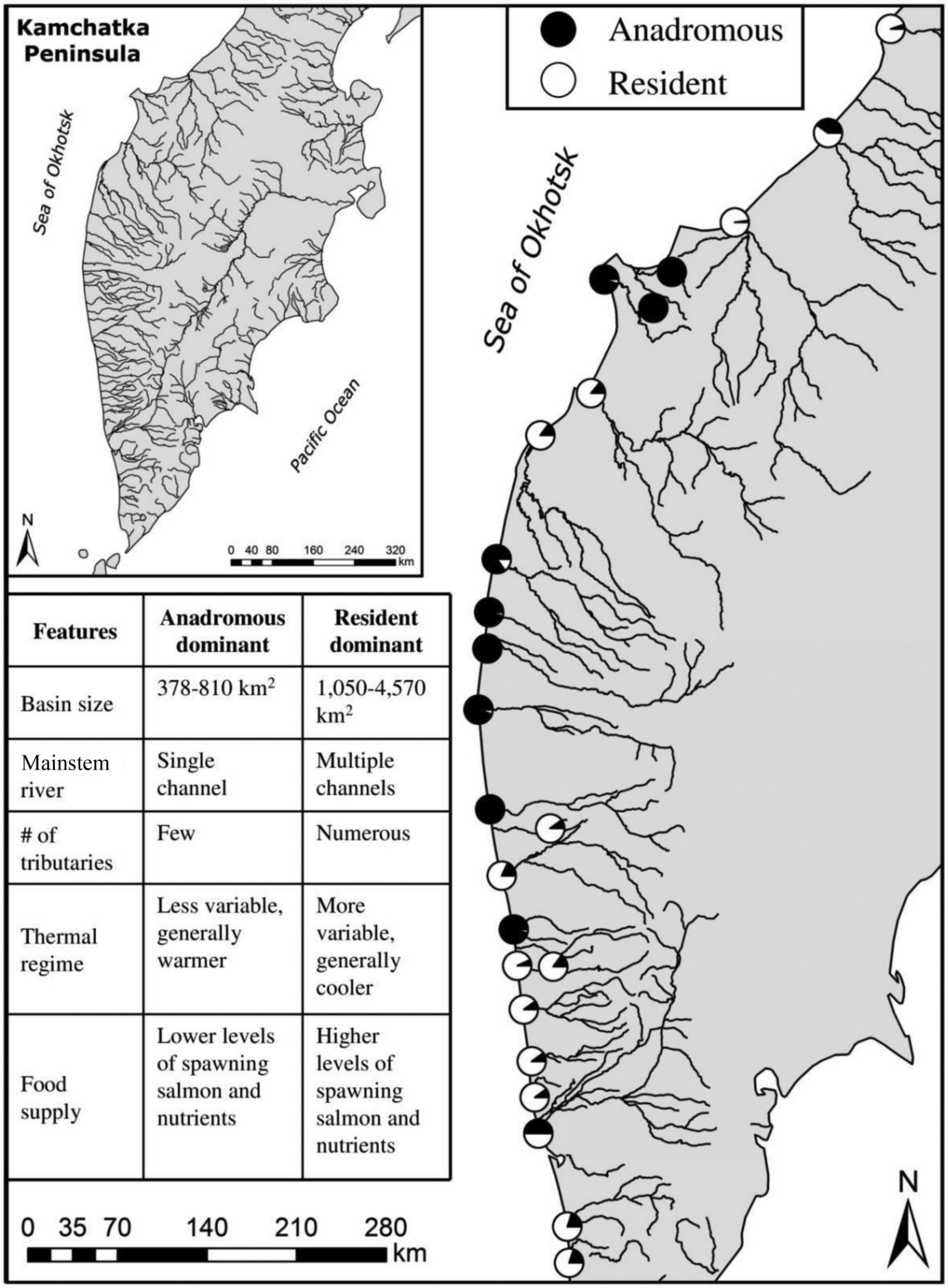
Lastly, there appears to be a correlation between the presence of large lakes and residency in *O. mykiss*. This influence may be indirect, through the migratory (e.g., smolt predation and reduced downstream migration rates) and foraging conditions (e.g., the presence of sockeye salmon nutrients) they create, or direct, through mechanisms such as water temperature and hydrology. Large lakes, particularly if they are productive, may increase growth opportunities for resident fish but also increase the mortality of anadromous individuals by supporting predators of smolts passing through (Jepsen et al. 1998; Olsson and Greenberg 2004). For example, resident *O. mykiss* in Alaska and interior British Columbia are commonly abundant and reach large sizes in river networks with lakes, and particularly so in lakes that support large populations of sockeye salmon (McHenry et al. 1975; Quinn and Myers 2004; Russell 1974, 1977; Table 4). The lakes are presumably not only important because they support sockeye salmon, which provide a critical food source to *O. mykiss*, but also because they have more diverse water temperatures than rivers that easily enable behavioral thermoregulation to maximize growth (e.g., Stewart and Bowlby 2009). In addition, lakes provide a winter refuge from the flows and cold temperatures that prevail in northern streams.

On the other hand, lake outflows have more attenuated flows and low sediment loads that may provide high-quality spawning habitat for anadromous *O. mykiss*. Hence, when resident and anadromous *O. mykiss* co-occur in the same watershed, large lakes can act as life history breakpoints, with residency more prominent above lakes and anadromy more prominent below. This has been documented in several drainages in British Columbia, including the Babine, Morice, Cowichan, and Thompson rivers (Beere 2004; Lough 1980; Narver 1969; Neave 1944). Such large lakes are less common in the USA. Resident *O. mykiss* are particularly abundant in the parts of the Columbia River basin with lakes, with residents also being more common above the lake and anadromous fish below (Washington Department of Fish and Wildlife, unpublished data).

Freshwater migration challenges

Migration cost is predicted to influence the prevalence and distribution of anadromy and residency through effects on survival (Hendry et al. 2004; Jonsson and Jonsson 1993; Sahashi and Morita 2013; Wood 1995). It is best measured as the cumulative survival of fish from and back to their natal streams, including ocean residency. However, because processes affecting freshwater migration and ocean survival differ, we evaluated them separately. Cost of freshwater migration is often described as a function of migration corridor characteristics from natal environment to the ocean and from the ocean back to the natal system, including stream channel gradient, distance (length and time), habitat types (e.g., lentic environments), natural (e.g., temporary estuary sand berms) and artificial (e.g., dams) blockages, water temperature, stream flow, and predators (Hendry et al. 2004; Waples et al. 2008). Romer et al. (2013) found that only 40%–50% of *O. mykiss* smolts survived downstream migration in a short coastal stream in Oregon. Juvenile salmonines passing through lakes and reservoirs (Jepsen et al. 1998; Olsson and Greenberg 2004) and larger rivers (Collis et al. 2001; Rieman et al. 1991) during their smolt migration

Fig. 6. Proportion of anadromous (black) and resident life histories (white) in several *O. mykiss* populations across the Kamchatka Peninsula, Russia, where the extent of life histories is strongly related to basin size, stream geomorphology characteristics, water temperature, and food supply in fresh water (some data from Pavlov et al. 2001*b*, 2008).



Features	Anadromous dominant	Resident dominant
Basin size	378-810 km^2	1,050-4,570 km^2
Mainstem river	Single channel	Multiple channels
# of tributaries	Few	Numerous
Thermal regime	Less variable, generally warmer	More variable, generally cooler
Food supply	Lower levels of spawning salmon and nutrients	Higher levels of spawning salmon and nutrients

can incur relatively high levels of mortality owing to predation by fish and birds. Additionally, juvenile salmonines often incur direct mortality during dam passage (Sandford et al. 2012; Zabel et al. 2008), and dams may influence the timing and speed of adult migration. Consistently higher rates of mortality during juvenile or adult migration, such as those caused by anthropogenic barriers and impediments, may therefore select against anadromy (Fig. 4).

Cost of migration had mixed impacts on anadromy and residency in *O. mykiss* in the studies we reviewed (Table 4). While migration distance is often considered an important factor affecting salmonine life history patterns (Hendry et al. 2004), we found only one study that directly assessed migration distance on anadromy across populations at varying distances from the ocean. In that study, Ohms et al. (2014) hypothesized that residency in male *O. mykiss* would be more common when migration distance was greater, in which case the sex ratios of outmigrating smolts should be female-biased (Table 4). However, analysis of data from eight North American *O. mykiss* populations with migration distances ranging from ~1 to 1200 km found no association between migration distance and the proportion of females among the anadromous individuals.

On the other hand, migration cost did influence life histories in one model, which indicated that emigration survival was one of the critical factors shaping the expression of anadromy (Table 4; Satterthwaite et al. 2010). Residency was predicted to increase as emigration survival decreased. Also in support of theoretical expectations, Narum et al. (2008) observed that *O. mykiss* at higher elevations in the Klickitat River, Washington State, were dominated by residents and hypothesized higher stream gradients and physical barriers created physical challenges that limited upstream migration of larger fish, and thus anadromy, to lower elevations (Table 4).

Inconsistent conclusions are expected considering the great variation in other factors driving anadromy and residency among neighboring populations with similar migration distances (McPhee et al. 2014; Pavlov et al. 2001*a*, 2008; Savvaitova et al. 2003). Additionally, the overall effects of migration distance may be less in *O. mykiss* because they are some of the strongest swimmers and highest leapers among salmonines, which is related to their fusiform shape, thicker caudal peduncle, and larger tail (Reiser et al. 2006). Additionally, migration cost in fresh water almost certainly covaries with other factors. For example, Narum et al. (2008) measured altitude as a surrogate for cost of migration, but altitude may be also inversely correlated with water temperature within a watershed. Cooler summers and winters may induce greater storage of lipids at the cost of decreased growth in length (e.g., McMillan et al. 2012; Sloat 2013), thereby potentially increasing the prevalence of residents, particularly for males (Sloat et al. 2014). Thus, the apparent influence of migration cost on anadromy in some cases may be more related to other factors that drive conditional status earlier in life, such as water temperature and flow regimes (e.g., Berejikian et al. 2013) or smaller streams impeding the access of larger anadromous adults (e.g., Mills et al. 2012). Finally, it is important to consider that migration cost may not be well represented by migration distance (Narum et al. 2008). Overall, it appears that the effects of freshwater migration cost can be variable, and more research is needed to resolve why theoretical expectations about migration distance do not necessarily match empirical findings for *O. mykiss* (Ohms et al. 2014).

In the southern portion of their range, the expression of anadromy in *O. mykiss* may not be a question of cost of migration, but whether or not fish can even access the ocean at all as smolts and then return to fresh water as adults. The semiarid climate of central and southern California produces low stream flows that are occasionally punctuated by flood events (Schonher and Nicholson 1989). Under these conditions, seasonally dry stream reaches and lagoon sandbar formations limit the frequency and duration of connectivity to the ocean (Schwartz and Orme 2005). Extended periods (e.g., years) of little or no access to the ocean require many *O. mykiss* populations to be sustained by freshwater reproduction until a return to conditions that facilitate migration of anadromous fish (Bell et al. 2011). Presumably, in these small coastal streams with sporadic ocean access, the life history form composition of *O. mykiss* populations is skewed towards residency, but little data on rates of residency and anadromy are available (Busby et al. 1996).

Ocean conditions

The ocean conveys benefits of food and growth that are generally unmatched in fresh water, but going to the ocean comes with the risk of higher mortality (Groot and Margolis 1991; Quinn 2005). It is thus predicted that shifts in marine survival should influence the extent of anadromy (Gross et al. 1988). Accordingly, consistent selection against anadromy based on decreased ocean survival (including fishing) could increase the prevalence of residents, at least to the extent that the freshwater habitat is capable of producing fish that are large and fecund enough to successfully reproduce therein, and vice-versa during periods of good ocean productivity (Fig. 4). This is a difficult hypothesis to test, however, because most research is conducted over short periods (a few years), and selection for or against anadromy and residency is likely occurring over longer periods (decades to centuries).

The studies we reviewed suggest varying effects of marine survival on anadromy and residency in *O. mykiss* (Table 4). In support of expectations, Savvaitova et al. (1997, 2002) examined the relationship between the prevalence of anadromous *O. mykiss* in Kamchatka populations and fishing rates at sea, a form of selection against anadromy in the marine environment (Table 4). They found that anadromy decreased and the prevalence of resident females increased during periods of high (illegal) fishing rates and then anadromy increased when the fishing was curtailed. It is also possible the changes may or may not have been associated with changes in freshwater density (see Density dependence subsection). Additionally, model projections by Satterthwaite et al. (2009) indicated that small decreases in ocean survival could increase the extent of residents, and when ocean survival rates were cut in half, all fish were expected to follow a resident life history trajectory.

These results suggest that the degree of anadromy is highly sensitive to the expected benefits derived from expressing anadromy (mediated by ocean survival). In their follow-up paper, Satterthwaite et al. (2010) applied the same model to two other populations of California *O. mykiss* and also concluded that dramatic reductions in survival during emigration and in the ocean would increase the prevalence of residents, but the extent of reductions differed extensively between the two populations. For example, reduction in emigrant survival of approximately 30%–50% was predicted to increase prevalence of residents in a resident-dominant Mokelumne River, while the anadromous-dominant American River was predicted to only favor residents if the emigrant survival decreased by approximately 75%–80% (Satterthwaite et al. 2010). The difference between the populations is likely related to growth in fresh water and survival of smolts because anadromy is a relatively low-risk strategy in the American River, where smolts grow fast and achieve fairly large sizes at smolt transformation, but is more costly in the Mokelumne River, where growth is reduced and smolts are smaller (Satterthwaite et al. 2010; Sogard et al. 2012). This again highlights the complexity of trying to untangle freshwater versus marine effects.

While we found evidence that temporal shifts in marine survival can influence anadromy and residency, spatially there was more variation in the patterns. As discussed previously, there are populations with a consistently high prevalence of residents (e.g., Alaska (Quinn and Myers 2004), Kamchatka Peninsula (Pavlov et al. 2008), Deschutes River (Zimmerman and Ratliff 2003), Cowichan River (Neave 1944), and upper Babine and Morice rivers (Narver 1969; Lough 1980; Beere 2004)) and others that are mostly (McMillan et al. 2007) or almost entirely anadromous (Sogard et al. 2012). Additionally, Berejikian et al. (2013) examined the proportion of anadromous *O. mykiss* offspring with anadromous and resident mothers in eight streams in Puget Sound, Washington State, with similar run timings (Table 4; Berejikian et al. 2008). They found that freshwater habitat and the presence of resident *O. mykiss* above barriers best explained the proportion of residents, rather than marine survival rates immediately after saltwater entry. The variability in anadromy and residency among closely neighboring populations suggests that the initial effects of freshwater growth and survival, in addition to upstream sources of residents, can sometimes be the more important mechanism than marine survival, particularly when freshwater growing conditions are exceptional (Pavlov et al. 2001*a*, 2008).

Marine conditions may limit *O. mykiss* migration in some places, however. In the ocean, *O. mykiss* are most often found in the range of sea surface temperatures (5–15 °C) that maximize growth potential (Atcheson et al. 2012; Welch et al. 1998). The cooler ocean temperatures in some parts of Alaska, such as north of the Aleutian Islands where steelhead are rare, may select against anadromy. Accordingly, residency in those populations may be influenced by both freshwater opportunities for growth and reduced opportunities for ocean rearing.

Conclusions and next steps

Research on the expression of anadromy and residency in partially migratory *O. mykiss* has shed light on an issue of ecological and conservation importance. The studies we reviewed provide support for the conditional strategy as a theoretical framework for explaining life history expression and understanding how such life history patterns differ between males and females and within and among populations (Table 3). Although much uncertainty remains regarding the patterns and processes underlying anadromy and residency in *O. mykiss*, a number of important conclusions can be drawn, and they can be conceptualized as the three processes contributing to migration (Fig. 1).

Genetic influences

We found evidence of a genetic component to residency and anadromy in *O. mykiss*. However, few studies explicitly examined the extent of heritability associated with anadromy and residency in *O. mykiss* (Table 2). For instance, several studies estimated the proportion of anadromous offspring produced by anadromous and resident parents (Berejikian et al. 2013; Christie et al. 2011; Courter et al. 2013; Hayes et al. 2012; Ruzycki et al. 2009; Seamons et al. 2004). On the other hand, only two studies estimated heritability within the context of anadromy and residency ($h^2 = 0.44$–0.56 and $H^2 = 0.69$–0.77, respectively) (Doctor et al. 2014; Thrower et al. 2004). Although the studies provide evidence of a heritable component to *O. mykiss* life histories and for traits related to individual condition (e.g., body growth), they also demonstrate that individuals are not necessarily precluded by parentage from expressing alternative life histories (e.g., Christie et al. 2011; Courter et al. 2013; Zimmerman and Reeves 2000).

While a genetic component to *O. mykiss* life histories certainly exists, the specific differences in gene expression among individuals are just beginning to be understood (Table 2; Hecht et al. 2013; Nichols et al. 2008). Nonetheless, differences in gene expression for two traits seem particularly promising for understanding anadromy and residency. First, gene expression related to smolt transformation appears to be different between anadromous and resident individuals (Nichols et al. 2008). Second, there appear to be genetic differences in metabolism, with anadromous individuals having higher metabolic costs than residents (Sloat and Reeves 2014). Greater metabolic costs can lead to lower energy conversion rates, lower lipid storage, and higher rates of anadromy in other salmonine species (Morinville and Rasmussen 2003; Rikardsen and Elliott 2000).

Based on these findings, we suggest three next steps to improve knowledge. First, additional estimates of heritability are needed for life history patterns and for traits linked to individual condition, such as growth, lipid content, and condition factor. This would help determine the genetic and environmental basis for anadromy and residency and the extent to which heritability varies among and within populations (e.g., Thrower et al. 2004). Second, further genomic analysis would help identify specific regions associated with physiological capacity for smolt transformation and metabolism, because whether or not certain fish inherent a greater disposition for smolting may partly explain why some individuals smolt with greater success than others. Lastly, it would be helpful to further examine standard metabolic rate and how it influences social status, growth, and energy allocation relative to anadromy and residency (e.g., Sloat and Reeves 2014). Intrinsically higher metabolic costs could explain why some individuals migrate to food-rich environments (Forseth et al. 1999; Morinville and Rasmussen 2003) and represents a potential genetic basis for selection of particular life histories across environmental gradients (Álvarez et al. 2006).

Influence of individual condition

We found several studies or models on *O. mykiss* that demonstrated or predicted, consistent with observations in the field, a proximate influence of individual condition early in life on anadromy and residency (Table 2 and Fig. 3; McMillan et al. 2012; Satterthwaite et al. 2009, 2010; Sloat and Reeves 2014), consistent with work on other salmonine species. While the effects of somatic size and growth on life history expression were variable, higher levels of lipids generally increased the probability of residency (Table 3), suggesting it may provide a more consistent predictor of freshwater maturation (e.g., Rowe and Thorpe 1990). Second, the varying associations with somatic size and growth are partly related to sex and the asymptotic size attainable in fresh water (Table 3). For example, some studies reported that fast growth and high lipid content lead to early maturation in fresh water in males (e.g., McMillan et al. 2012) and females (e.g., Sloat and Reeves 2014). However, the models of Satterthwaite et al. (2009), 2010), using only growth, predict opposite results for females. Third, differences in conditional status are observed well in advance of life history expression, but the specific timing of life history decision windows is still speculative for *O. mykiss* (Fig. 3; Beakes et al. 2010; McMillan et al. 2012; Sloat and Reeves 2014).

These patterns highlight the need to parse out the relative effects of proximate factors such as somatic growth, size, and lipid content from the ultimate effects of asymptotic size and iteroparity on residency and anadromy (Table 3). Studies to date have typically focused on one sex or the other (e.g., McMillan et al. 2012; Satterthwaite et al. 2009), growth alone (Thrower et al. 2004), growth and asymptotic size but not lipid content (Satterthwaite et al. 2009, 2010), or growth and lipid content but not asymptotic size (McMillan et al. 2012). Sloat and Reeves (2014) indicated asymptotic size was one of the best predictors. Future research could further determine whether lipid content is indeed a better predictor of freshwater maturation and if associations between faster growth and freshwater maturation are shaped by a greater asymptotic size in fresh water (hence, larger size at maturation). There is also evidence that females have higher thresholds for maturation than males in other salmonines (Morita and Nagasawa 2010). The same appears to be true in *O. mykiss* because anadromous and resident males mature more commonly at younger ages and smaller sizes than their female cohorts (Busby et al. 1996; Pavlov et al. 2008; Savvaitova et al. 2003). Nonetheless, models of differing sex-based thresholds are limited for *O. mykiss* (Berejikian et al. 2014; Sloat and Reeves 2014). Lastly, the effects of individual condition may differ among populations because of local selection pressures (Beakes et al. 2010), but data on this topic are mostly limited to inferences about anadromy (Doctor et al. 2014). A next step, then, is to combine individual condition measurements from *O. mykiss* living in nature with further experimentation on fish under common garden settings (e.g., Beakes et al. 2010; Sloat and Reeves 2014).

We also suggest the need to determine whether individuals are more responsive to the effects of individual condition during specific time periods in their life. We know that *O. mykiss* are sensitive to their conditional status long in advance of smolt transformation or spawning (Fig. 3; McMillan et al. 2012; Sloat and Reeves 2014), and it has been proposed that they enter one developmental window in the spring and again in the fall each year (Satterthwaite et al. 2009). However, while Beakes et al. (2010) did measure condition factor of smolts and non-smolts over time, no study has systematically tested for differences in growth and lipid content over successive months early in life for maturing and nonmaturing individuals, as was done for Atlantic salmon by Simpson (1992). Such tests are needed and could be coupled with measures of hormone levels (e.g., Okuzawa 2002; Taranger et al. 2010) to determine the periods in life when *O. mykiss* are sensitive to changes in individual condition and how each measure of condition drives hormonal shifts triggering the onset of reproductive development.

Influence of environmental factors

The prevalence of anadromy and residency among and within populations of *O. mykiss* appears related to diverse environmental factors in fresh water and at sea (Table 4 and Fig. 4), but direct tests of mechanisms were few. Among those, water temperature, stream flow, and food supply in fresh water (Bentley et al. 2012; Courter et al. 2009; Savvaitova et al. 2007; Sloat and Reeves 2014) and marine survival (Satterthwaite et al. 2009, 2010; Savvaitova et al. 2002) appear to exert strong influences on life history patterns. The frequency of residents within populations was highest in watersheds with cooler temperatures, higher summer flows, an abundance of food, and adequate spawning habitat for smaller females. Such conditions appear to maximize opportunities for development and survival in fresh water, thereby reducing the advantage of an ocean migration. We also found stream or river size and lake presence effects, with residency being more common in watersheds with numerous small tributaries and those that contained large lakes. Although the results are revealing, the overall mechanisms behind the patterns remain poorly understood, because the data are often limited to a few geographic areas, and some key ecological factors (e.g., food supply) have not been tested empirically.

We propose four lines of future investigation, beginning with early life in fresh water. First, it seems important to more clearly understand the effects of water temperature. There is correlative (Sogard et al. 2012) and experimental evidence (Sloat and Reeves 2014) that temperature influences residency through effects on energy allocation, with cooler temperatures allowing for greater accumulation of lipids that are limiting to maturation (McMillan et al. 2012; Sloat and Reeves 2014). Water temperature may also help explain why residents were more common in streams with high summer flows (Courter et al. 2009) and at higher elevations within a river network (Cramer et al. 2003; Narum et al. 2006), all of which are often interconnected. Data on water temperature in relation to stream flow and altitude could answer the following questions: What are the effects of higher summer flows and cooler temperatures on growth and lipid storage and, in turn, residency and anadromy? Does water temperature provide a better indicator of the spatial extent of residency than stream flow because of its effects on lipid storage? Are residents more common at higher altitudes because of cooler water temperatures or the challenge of migrating further upstream, or both? A critical component of such research is obtaining a large number of firm estimates on the proportion of resident and anadromous *O. mykiss*, especially if they spawn a range of environments. Such data could be used to answer explicit questions and predict how *O. mykiss* life histories may respond to restoration actions influencing water temperature, stream flow, dam removal, and future climatic changes.

Next, while there were no direct tests of food on the frequency of anadromy and residency, the prevalence of residents seems to be highest and their body size largest in exceptionally food-rich river systems where spawning salmon are abundant, such as the Kamchatka Peninsula (Pavlov et al. 2008) and southwestern Alaska (Quinn and Myers 2004). As with all environmental factors, however, the effects of food supply are likely interconnected with other variables such as water temperature and ocean conditions. Data on food supply and life histories could also be used to further evaluate patterns documented on the Kamchatka Peninsula, where rivers with abundant food and relatively little spawning habitat are dominated by residents (Pavlov et al. 2001*a*, 2008). If spatial patterns in food abundance and life histories are present in Russia, then perhaps the frequency of residency has declined over time in response to a decreasing abundance of other salmonines that formerly provided energy-rich nutrients. Testing this hypothesis would not only provide insight into the role of food during juvenile ontogeny, but also how the balance between feeding and spawning habitat influences life history expression across life stages.

Third, there is a need to more explicitly test the effects of freshwater migration cost and marine survival on anadromy. Theoretically, migration cost should influence such expression (Hendry et al. 2004; Jonsson and Jonsson 1993). However, most existing studies (which are limited in number) use migration distance or elevation gain as a proxy for rigor (rather than measuring survival or energy costs empirically), which does not necessarily appear to strongly regulate the balance of life histories in *O. mykiss* (e.g., Ohms et al. 2014). Additionally, existing studies, models, and observations relating migration cost and marine mortality to *O. mykiss* life history patterns have found varying results, perhaps because of the species' strong swimming abilities or because distance is not an adequate covariate for cost of migration. Research that helps resolve this topic would provide insight into how anthropogenic impacts, particularly those impacting the survival of migrants, affect *O. mykiss* life histories.

Lastly, it would be interesting to evaluate whether declines in anadromy over long and short time periods are associated with an increase in residency, as documented by Savvaitova et al. (2002), and what those implications are for future environmental change. For example, recent models predict decreased emigration survival by smolts could alter the proportion of anadromy and, therefore, potentially residency (Courter et al. 2009; Satterthwaite et al. 2009, 2010). Although reductions in anadromy will shift the proportion of a population towards residency, it cannot necessarily be assumed that reductions in anadromy result in an equal and actual increase in the prevalence of residents because not all freshwater habitats are equally capable of growing and maintaining large residents (Todd et al. 2008). This suggests that declines in anadromy may not have the same effect on residents in all populations. Such information could improve predictions about how populations will respond to environmental variability and climate change and what factors are most relevant to sustaining residents if the anadromous component declines.

Complementary effects and explanations

In this review, we considered the conditional strategy and environmental explanations for anadromy and residency in *O. mykiss*. However, there are also other mechanisms that could have and perhaps did contribute to the patterns we reviewed. For example, females may prefer to spawn with larger males and larger males with larger females (Fleming 1996; Neff and Pitcher 2005; Rosengrave et al. 2008), which could reduce interactions between the two life histories. Despite potential preferences, anadromous female *O. mykiss* interact and mate with small resident males on the spawning grounds (Kostow 2003; McMillan et al. 2007), and resident males successfully produce offspring with larger anadromous females (Christie et al. 2011; Seamons et al. 2004). This is one reason why anadromous and resident *O. mykiss* appear to commonly represent a single panmictic population (McPhee et al. 2007). While female *O. mykiss* seem to accept resident males as mates, the mating success of small and large males may be frequency dependent (Gross 1991). In such instances, the fitness of a given life history form can decrease as their frequency in the population increases past a certain point (Gross 1991; Hutchings and Myers 1994). Testing hypotheses about mate choice and male life history frequencies in *O. mykiss* could elucidate the extent to which those factors influence the prevalence of residency and anadromy.

Limitations and implications

While we covered a number of topics on *O. mykiss*, there were limitations that could be addressed to improve knowledge of anadromy and residency. For example, many of our conclusions were drawn from only a few studies, models, or technical reports and, in some cases, research on other partially migratory salmonine species. This was due to a general lack of data on the conditional status and demographics of resident *O. mykiss*, which made it difficult to evaluate the relative effects of individual condition and environment on population-scale life history patterns. Assessing environmental effects on sympatric resident and anadromous populations is challenging because of the great temporal variation in demographics over annual and decadal time scales (Ardren and Kapuscinski 2003; Savvaitova et al. 2002; Shapovalov and Taft 1954; Ward and Slaney 1988). Nonetheless, such data are needed to fully understand the amount of life history variation within populations (McPhee et al. 2014) and to improve predictive models (Sloat et al. 2014). Combining data on environment and life histories at the population scale with individual genetic and conditional influences is therefore an important next step in teasing out how different factors select for anadromy and residency in *O. mykiss*.

Overall, we found tremendous variability in the patterns of anadromy and residency in *O. mykiss* and that population-level patterns reflect a suite of genetic and environmental effects operating at different scales. These patterns appear to reflect fitness trade-offs specific to the wide range of environments inhabited by *O. mykiss*. We also emphasize the importance of recognizing fundamental differences in male and female life histories because the fitness trade-offs for anadromy and residency differ between the sexes. While life history patterns certainly reflect a strong influence of the environment, they also have considerable capacity to evolve in response to changing selective pressures (e.g., Thériault et al. 2008). Consequently, recovery strategies should consider both the ecological and evolutionary processes that facilitate life history diversity within this iconic species.

Acknowledgements

We gratefully acknowledge the National Research Council for postdoctoral research funding (for N. Kendall) and NOAA (for J. McMillan) for supporting this research. Discussions with Haley Ohms were insightful. Alexander Stefankiv created Fig. 6. Jim Myers, Barry Berejikian, and two anonymous reviewers provided very helpful comments on this manuscript.

References

Álvarez, D., Cano, J.M., and Nicieza, A.G. 2006. Microgeographic variation in metabolic rate and energy storage of brown trout: countergradient selection or thermal sensitivity? Evol. Ecol. **20**: 345–363. doi:10.1007/s10682-006-0004-1.

Ardren, W.R., and Kapuscinski, A.R. 2003. Demographic and genetic estimates of effective population size (N_e) reveals genetic compensation in steelhead trout. Mol. Ecol. **12**: 35–49. doi:10.1046/j.1365-294X.2003.01705.x. PMID:12492876.

Armstrong, J.B., Schindler, D.E., Omori, K.L., Ruff, C.P., and Quinn, T.P. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology, **91**: 1445–1454. doi:10.1890/09-0790.1. PMID:20503876.

Atcheson, M.E., Myers, K.W., Beauchamp, D.A., and Mantua, N.J. 2012. Bioenergetic response by steelhead to variation in diet, thermal habitat, and climate in the North Pacific Ocean. Trans. Am. Fish. Soc. **141**(4): 1081–1096. doi:10.1080/00028487.2012.675914.

Aubin-Horth, N., Landry, C.R., Letcher, B.H., and Hofmann, H.A. 2005. Alternative life histories shape brain gene expression profiles in males of the same population. Proc. R. Soc. B Biol. Sci. **272**: 1655–1662. doi:10.1098/rspb.2005.3125.

Aubin-Horth, N., Bourque, J.-F., Daigle, G., Hedger, R., and Dodson, J.J. 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**(9): 2067–2075. doi:10.1139/f06-103.

Augerot, X., and Foley, D.N. 2005. Atlas of Pacific salmon. University of California Press, Berkeley and Los Angeles, Calif.

Bacon, P.J., Gurney, W.S.C., Jones, W., McLaren, I.S., and Youngson, A.F. 2005. Seasonal growth patterns of wild juvenile fish: partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (*Salmo salar*) parr. J. Anim. Ecol. **74**: 1–11. doi:10.1111/j.1365-2656.2004.00875.x.

Baum, D., Laughton, R., Armstrong, J.D., and Metcalfe, N.B. 2004. Altitudinal variation in the relationship between growth and maturation rate in salmon parr. J. Anim. Ecol. **73**: 253–260. doi:10.1111/j.0021-8790.2004.00803.x.

Beakes, M.P., Satterthwaite, W.H., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Trans. Am. Fish. Soc. **139**(5): 1263–1275. doi:10.1577/T09-146.1.

Beere, M.C. 2004. Movements of Babine River summer run steelhead tagged with surgically and gastrically implanted radio transmitters Skeena Fisheries Report SK139. British Columbia Ministry of Environment, Lands and Parks. Fisheries Branch.

Behnke, R.J. 2002. Trout and salmon of North America. The Free Press, New York.

Bell, E., Albers, S.M., Krug, J.M., and Dagit, R. 2011. Juvenile growth in a population of southern California steelhead (*Oncorhynchus mykiss*). Calif. Fish Game, **97**(1): 25–35.

Benjamin, J.R., Connolly, P.J., Romine, J.G., and Perry, R.W. 2013. Potential effects of changes in temperature and food resources on life history trajectories of juvenile *Oncorhynchus mykiss*. Trans. Am. Fish. Soc. **142**(1): 208–220. doi:10.1080/00028487.2012.728162.

Bentley, K.T., Schindler, D.E., Armstrong, J.B., Zhang, R., Ruff, C.P., and Lisi, P.J. 2012. Foraging and growth responses of stream-dwelling fishes to interannual variation in a pulsed resource subsidy. Ecosphere, **3**(12): Article 113.

Berejikian, B.A., Johnson, T., Endicott, R.S., and Lee-Waltermire, J. 2008. Increases in steelhead (*Oncorhynchus mykiss*) redd abundance resulting from two conservation hatchery strategies in the Hamma Hamma River, Washington. Can. J. Fish. Aquat. Sci. **65**(4): 754–764. doi:10.1139/f08-014.

Berejikian, B.A., Campbell, L.A., and Moore, M.E. 2013. Large-scale freshwater habitat features influence the degree of anadromy in eight Hood Canal *Oncorhynchus mykiss* populations. Can. J. Fish. Aquat. Sci. **70**(5): 756–765. doi:10.1139/cjfas-2012-0491.

Berejikian, B.A., Bush, R.A., and Campbell, L.A. 2014. Maternal control over offspring life history in a partially anadromous species, *Oncorhynchus mykiss*. Trans. Am. Fish. Soc. **143**(2): 369–379. doi:10.1080/00028487.2013.862181.

Bjornn, T.C. 1978. Survival, production, and yield of trout and chinook salmon in the Lemhi River, Idaho A Final Report for Federal Aid to Fish Restoration, Project F-49-R, Salmon and Steelhead Investigations. Idaho Cooperative Fishery Research Unit, College of Forestry, Wildlife and Range Sciences, University of Idaho.

Boughton, D.A., Fish, H., Pope, J., and Holt, G. 2009. Spatial patterning of habitat for *Oncorhynchus mykiss* in a system of intermittent and perennial streams. Ecol. Freshw. Fish. **18**: 92–105. doi:10.1111/j.1600-0633.2008.00328.x.

Brannon, E.L., Powell, M.S., Quinn, T.P., and Talbot, A. 2004. Population structure of Columbia River Basin chinook salmon and steelhead trout. Rev. Fish. Sci. **12**(2–3): 99–232. doi:10.1080/10641260490280313.

Brett, J.R. 1952. Temperature tolerance in young Pacific Salmon, genus *Oncorhynchus* sp. J. Fish. Res. Board Can. **9**(6): 265–323. doi:10.1139/f52-016.

Brett, J.R. 1979. Energetic factors and growth. *In* Fish Physiol. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 599–675.

Busby, P.J., Wainwright, T.C., Bryant, E.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W., and Lagomarsino, I.V. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Northwest Fisheries Science Center, Seattle, Wash.

Carlson, S.M., and Seamons, T.R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evol. Appl. **1**(2): 222–238. doi:10.1111/j.1752-4571.2008.00025.x.

Christie, M.R., Marine, M.L., and Blouin, M.S. 2011. Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Mol. Ecol. **20**: 1263–1276. doi:10.1111/j.1365-294X.2010.04994.x.

Collis, K., Roby, D.D., Craig, D.P., Ryan, B.A., and Ledgerwood, R.D. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia river estuary: vulnerability of different salmonid species, stocks, and rearing types. Trans. Am. Fish. Soc. **130**(3): 385–396. doi:10.1577/1548-8659(2001)130<0385:CWPOJS>2.0.CO;2.

Courter, I., Justice, C., and Cramer, S. 2009. Flow and temperature effects on life history diversity of *Oncorhynchus mykiss* in the Yakima River basin. Cramer Fish Sciences, Gresham, Ore.

Courter, I.I., Child, D.B., Hobbs, J.A., Garrison, T.M., Glessner, J.J.G., and Duery, S. 2013. Resident rainbow trout produce anadromous offspring in a large interior watershed. Can. J. Fish. Aquat. Sci. **70**(5): 701–710. doi:10.1139/cjfas-2012-0457.

Cramer, S.P., Lister, D.B., Monk, P.A., and Witty, K.L. 2003. A review of abundance trends, hatchery and wild fish interactions, and habitat features for the Middle Columbia steelhead ESU. S.P. Cramer and Associates, Sandy, Ore.

Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Verein. Theor. Angew. Limnol. **18**: 1–158.

Currens, K.P., Schreck, C.B., and Li, H.W. 1990. Allozyme and morphological divergence of rainbow trout (*O. mykiss*) above and below waterfalls in the Deschutes River, Oregon. Copeia, **1990**: 730–746.

Debes, P.V., Fraser, D.J., Yates, M.C., and Hutchings, J.A. 2014. The between-population genetic architecture of growth, maturation, and plasticity in Atlantic salmon. Genetics, **196**(4): 1277–1291. doi:10.1534/genetics.114.161729. PMID:24473933.

Docker, M.F., and Heath, D.D. 2003. Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia. Conserv. Genet. **4**: 227–231. doi:10.1023/A:1023355114612.

Doctor, K., Berejikian, B., Hard, J.J., and Van Doornik, D. 2014. Growth-mediated life history traits of steelhead reveal phenotypic divergence and plastic response to temperature. Trans. Am. Fish. Soc. **143**: 317–333. doi:10.1080/00028487.2013.849617.

Dodson, J.J., Aubin-Horth, N., Thériault, V., and Páez, D.J. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biol. Rev. **88**(3): 602–625. doi:10.1111/brv.12019. PMID:23347290.

Einum, S., and Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proc. R. Soc. B Biol. Sci. **266**: 1995–2000. doi:10.1098/rspb.1999.0893.

Farmer, G.J., Ritter, J.A., and Ashfield, D. 1978. Seawater adaptation and parr–smolt transformation of juvenile Atlantic salmon, *Salmo salar*. J. Fish. Res. Board Can. **35**(1): 93–100. doi:10.1139/f78-013.

Feldhaus, J.W. 2006. The physiological ecology of redband rainbow trout (*Oncorhynchus mykiss gairdneri*) in the South Fork John Day River, Oregon. Masters of Science thesis, Oregon State University, Corvallis, Ore.

Finstad, A.G., and Hein, C.L. 2012. Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char. Global Change Biol. **18**: 2487–2497. doi:10.1111/j.1365-2486.2012.02717.x.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Rev. Fish Biol. Fish. **6**: 379–416. doi:10.1007/BF00164323.

Fleming, I.A., and Reynolds, J.D. 2004. Salmonid breeding systems. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford. pp. 264–294.

Forseth, T., Naesje, T.F., Jonsson, B., and Harsåker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. J. Anim. Ecol. **68**: 783–793. doi:10.1046/j.1365-2656.1999.00329.x.

Garrett, I.D.F. 2013. Gene expression life history markers in a hatchery and a wild population of young-of-the-year *Oncorhynchus mykiss*. Masters of Science thesis, Portland State University, Portland, Ore.

Gibson, R.J. 1978. Recent changes in the population of juvenile Atlantic salmon in the Matamek River, Quebec, Canada. ICES J. Mar. Sci. **38**(2): 201–207. doi:10.1093/icesjms/38.2.201.

Grant, J.W.A., and Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. J. Fish Biol. **67**(Suppl. B): 100–110. doi:10.1111/j.0022-1112.2005.00916.x.

Grant, J.W.A., Steingrímsson, S.Ó., Keeley, E.R., and Cunjak, R.A. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. Can. J. Fish. Aquat. Sci. **55**(S1): 181–190. doi:10.1139/d98-018.

Groot, C., and Margolis, L. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, B.C.

Gross, M.R. 1987. Evolution of diadromy in fishes. Am. Fish. Soc. Symp. **1**: 14–25.

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology, **72**(4): 1180–1186. doi:10.2307/1941091.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol. Evol. **11**: 92–98. doi:10.1016/0169-5347(96)81050-0. PMID:21237769.

Gross, M.R., and Repka, J. 1998. Stability with inheritance in the conditional strategy. J. Theor. Biol. **192**: 445–453. doi:10.1006/jtbi.1998.0665. PMID:9782102.

Gross, M.R., Coleman, R.M., and McDowall, R.M. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science, **239**(4845): 1291–1293. doi:10.1126/science.239.4845.1291. PMID:17833216.

Haidle, L., Janssen, J.E., Gharbi, K., Moghadam, H.K., Ferguson, M.M., and Danzmann, R.G. 2008. Determination of quantitative trait loci (QTL) for early maturation in rainbow trout (*Oncorhynchus mykiss*). Mar. Biotechnol. **10**: 579–592. doi:10.1007/s10126-008-9098-5. PMID:18491191.

Hale, M.C., Thrower, F.P., Berntson, E.A., Miller, M.R., and Nichols, K. 2013. Evaluating adaptive divergence between migratory and nonmigratory ecotypes of a salmonid fish, *Oncorhynchus mykiss*. G3: Genes Genomes Genetics, **3**: 1273–1285. doi:10.1534/g3.113.006817.

Hanson, K.C., Gale, W.L., Simpson, W.G., Kennedy, B.M., and Ostrand, K.G. 2011. Physiological characterization of hatchery-origin juvenile steelhead *Oncorhynchus mykiss* adopting divergent life-history strategies. J. Fish Wildl. Manage. **2**(1): 61–71. doi:10.3996/092010-JFWM-032.

Hard, J.J., Myers, J.M., Ford, M.J., Kope, R.G., Pess, G.R., Waples, R.S., Winans, G.A., Berejikian, B.A., Waknitz, F.W., Adams, P.B., Bisson, P.A., Campton, D.E., and Reisenbichler, R.R. 2007. Status review of Puget Sound steelhead (*Oncorhynchus mykiss*) NOAA Technical Memorandum NMFS-NWFSC-81. NOAA National Marine Fisheries Service.

Harvey, B.C., Nakamoto, R.J., and White, J.L. 2006. Reduced streamflow lowers dry-season growth of rainbow trout in a small stream. Trans. Am. Fish. Soc. **135**: 998–1005. doi:10.1577/T05-233.1.

Hayes, S.A., Hanson, C.V., Pearse, D.E., Bond, M.H., Garza, J.C., and MacFarlane, R.B. 2012. Should I stay or should I go? The influence of genetic origin on emigration behavior and physiology of resident and anadromous juvenile *Oncorhynchus mykiss*. N. Am. J. Fish. Manage. **32**(4): 772–780.

Hazel, W.N., Smock, R., and Johnson, M.D. 1990. A polygenic model for the evolution and maintenance of conditional strategies. Proc. R. Soc. B Biol. Sci. **242**: 181–187. doi:10.1098/rspb.1990.0122.

Hecht, B.C., Campbell, N.R., Holecek, D.E., and Narum, S.R. 2013. Genome-wide association reveals genetic basis for the propensity to migrate in wild populations of rainbow and steelhead trout. Mol. Ecol. **22**: 3061–3076. doi:10.1111/mec.12082. PMID:23106605.

Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford. pp. 92–125.

High, B., Peery, C.A., and Bennett, D.H. 2006. Temporary staging of Columbia River summer steelhead in coolwater areas and its effect on migration rates. Trans. Am. Fish. Soc. **135**(2): 519–528. doi:10.1577/T04-224.1.

Hodge, B. 2010. Life history variation in *Oncorhynchus mykiss* from the Lower Klamath River basin. Masters of Science thesis, Humboldt State University, Arcata, Calif.

Holm, J.C., Refstie, T., and Bo, S. 1990. The effect of fish density and feeding regimes on individual growth rate and mortality in rainbow trout (*Oncorhynchus mykiss*). Aquaculture, **89**: 225–232.

Howell, P., Jones, K., Scarnecchia, D., LaVoy, L., Kendra, W., Ortmann, D., Neff, C., Petrosky, C., and Thurow, R. 1985. Stock assessment of Columbia River anadromous salmonids. Vol. II: steelhead stock summaries stock transfer guidelines - information needs. Prepared for the US Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, Contract No. DE-AI79-84BP12737, Project No. 83-335.

Hutchings, J.A. 2011. Old wine in new bottles: reaction norms in salmonid fishes. Heredity, **106**: 421–437. doi:10.1038/hdy.2010.166. PMID:21224878.

Hutchings, J.A., and Myers, R.A. 1994. The evolution of alternative mating strategies in variable environments. Evol. Ecol. **8**(3): 256–268. doi:10.1007/BF01238277.

Imre, I., Grant, J.W.A., and Keeley, E.R. 2004. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). Oecologia, **138**: 371–378.

Jepsen, S., Aarestrup, K., Økland, F., and Rasmussen, G. 1998. Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. Dev. Hydrobiol. **130**: 347–353. doi:10.1007/978-94-011-5090-3_39.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Trans. Am. Fish. Soc. **114**(2): 182–194. doi:10.1577/1548-8659(1985)114<182:LHPOFR>2.0.CO;2.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes Rev. Fish Biol. Fish. **3**: 348–365. doi:10.1007/BF00043384.

Kammerer, B.D., and Heppell, S.A. 2013. Individual condition indicators of thermal habitat quality in field populations of redband trout (*Oncorhynchus mykiss gairdneri*). Environ. Biol. Fishes, **96**(7): 823–835. doi:10.1007/s10641-012-0078-2.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology, **82**(5): 1247–1259. doi:10.1890/0012-9658(2001)082[1247:DRTFAS]2.0.CO;2.

Kesner, W.D., and Barnhart, R.A. 1972. Characteristics of the fall-run steelhead trout (*Salmo gairdneri gairdneri*) of the Klamath River system with emphasis on the half-pounder. Calif. Fish Game, **58**: 204–220.

Koellner, T., and Schmitz, O.J. 2006. Biodiversity, ecosystem function, and investment risk. Bioscience, **56**(12): 977–985. doi:10.1641/0006-3568(2006)56[977:BEFAIR]2.0.CO;2.

Kostow, K. 2003. Factors that influence evolutionarily significant unit boundaries and status assessment in a highly polymorphic species, *Oncorhynchus mykiss*, in the Columbia Basin Information Report #2003-04. Oregon Department of Fish and Game and NOAA Fisheries.

Krogius, F.V. 1981. The role of resident fish in the reproduction of anadromous sockeye salmon, *Oncorhynchus nerka*. J. Ichthyol. **21**: 14–21.

Kuzishchin, K.V., Mal'tsev, A.Y., Gruzdeva, M.A., Savvaitova, K.A., Pavlov, D.S., and Stanford, D.A. 2007. On joint spawning of anadromous and resident mykiss *Parasalmo mykiss* in rivers of western Kamchatka. J. Ichthyol. **47**(5): 348–352. doi:10.1134/S0032945207050037.

Lapointe, M., Eaton, B., Driscoll, S., and Latulippe, C. 2000. Modelling the probability of salmonid egg pocket scour due to floods. Can. J. Fish. Aquat. Sci. **57**(6): 1120–1130. doi:10.1139/f00-033.

Larsen, D., Beckman, B.R., Strom, C.R., Parkins, P.J., Cooper, K.A., Fast, D.E., and Dickhoff, W.W. 2006. Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook salmon: a comparison with wild fish. Trans. Am. Fish. Soc. **135**: 1017–1032. doi:10.1577/T05-200.1.

Le Bras, Y., Dechamp, N., Krieg, F., Filangi, O., Guyomard, R., Boussaha, M., Bovenhuis, H., Pottinger, T.G., Prunet, P., Le Roy, P., and Quillet, E. 2011. Detection of QTL with effects on osmoregulation capacities in the rainbow trout (*Oncorhynchus mykiss*). BMC Genet. **12**: 46. doi:10.1186/1471-2156-12-46. PMID:21569550.

Lehman, C.L., and Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. Am. Nat. **156**: 534–552. doi:10.1086/303402.

Liberoff, A.L., Miller, J.A., Riva-Rossi, C.M., Hidalgo, F.J., Fogel, M.L., and Pascual, M.A. 2014*a*. Transgenerational effects of anadromy on juvenile growth traits in an introduced population of rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **71**(3): 398–407. doi:10.1139/cjfas-2013-0466.

Liberoff, A.L., Quiroga, A.P., Riva-Rossi, C.M., Miller, J.A., and Pascual, M.A. 2014*b*. Influence of maternal habitat choice, environment and spatial distribution of juveniles on their propensity for anadromy in a partially anadromous population of rainbow trout (*Oncorhynchus mykiss*). Ecol. Freshw. Fish. doi:10.1111/eff.12157.

Lough, M.J. 1980. Radio telemetry studies of summer run steelhead trout in the Skeena River drainage, 1979, with particular reference to Morice, Suskwa, Kispiox, and Zymoetz River stocks Skeena Fisheries Report SK29. British Columbia Ministry of Environment, Lands and Parks, Fisheries Branch.

Martínez, A., Garza, J.C., and Pearse, D.E. 2011. A microsatellite genome screen identifies chromosomal regions under differential selection in steelhead and rainbow trout. Trans. Am. Fish. Soc. **140**: 829–842. doi:10.1080/00028487.2011.588094.

Martinez, J.L., Moran, P., Perez, J., De Gaudemar, B., Beall, E., and 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. PMID:10736027.

McHenry, E.T., Russell, R.B., and Chlupach, R.S. 1975. Rainbow trout life history studies in Lower Talarik Creek – Kvichak drainage Study G-II, Job No. G-II-E, Vol. 16. Alaska Department of Fish and Game, Division of Sport Fish, Juneau, Alaska.

McMillan, J.R. 2009. Early maturing males in a partially migratory population of anadromous and resident rainbow trout *Oncorhynchus mykiss*: influences of individual condition and stream temperature. M.Sc. thesis, Oregon State University, Corvallis, Ore.

McMillan, J.R., Katz, S.L., and Pess, G.R. 2007. Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow trout mating system on the Olympic Peninsula, Washington State. Trans. Am. Fish. Soc. **136**(3): 736–748. doi:10.1577/T06-016.1.

McMillan, J.R., Dunham, J., Reeves, G.H., Mills, J.S., and Jordan, C.E. 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.

McMillan, J.R., Liermann, M.C., Starr, J., Pess, G.R., and Augerot, X. 2013. Using a stream network census of fish and habitat to assess models of juvenile salmonid distribution. Trans. Am. Fish. Soc. **142**: 942–956. doi:10.1080/00028487.2013.790846.

McPhee, M.V., Utter, F., Stanford, J.A., Kuzishchin, K.V., Savvaitova, K.A., Pavlov, D.S., and Allendorf, F.W. 2007. Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. Ecol. Freshw. Fish, **16**: 539–547. doi:10.1111/j.1600-0633.2007.00248.x.

McPhee, M.V., Whited, D.C., Kuzishchin, K.V., and Stanford, J.A. 2014. The effects of riverine physical complexity on anadromy and genetic diversity in steelhead or rainbow trout *Oncorhynchus mykiss* around the Pacific Rim. J. Fish Biol. **85**(1): 132–150. doi:10.1111/jfb.12286. PMID:24766581.

Mills, J.S., Dunham, J.B., Reeves, G.H., McMillan, J.R., Zimmerman, C.E., and Jordan, C.E. 2012. Variability in expression of anadromy by female *Oncorhynchus mykiss* within a river network. Environ. Biol. Fishes, **93**: 505–517.

Montgomery, D.R., Beamer, E.M., Pess, G.R., and Quinn, T.P. 1999. Channel type and salmonid spawning distribution and abundance. Can. J. Fish. Aquat. Sci. **56**(3): 377–387. doi:10.1139/f98-181.

Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. J. Anim. Ecol. **83**(5): 1035–1046. doi:10.1111/1365-2656.12212.

Moore, M.E., Berejikian, B.A., and Tezak, E.P. 2010. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. Trans. Am. Fish. Soc. **139**(1): 49–61.

Morán, P., Pendás, A.M., Beall, E., and García-Vazquez, E. 1996. Genetic assessment of the reproductive success of Atlantic salmon precocious parr by means of VNTR loci. Heredity, **77**: 655–660. doi:10.1038/hdy.1996.193.

Morinville, G.R., and Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **60**(4): 401–410. doi:10.1139/f03-036.

Morita, K., and Nagasawa, T. 2010. Latitudinal variation in the growth and maturation of masu salmon (*Oncorhynchus masou*) parr. Can. J. Fish. Aquat. Sci. **67**(6): 955–965. doi:10.1139/F10-028.

Morita, K., Yamamoto, S., and Hoshino, N. 2000. Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. Can. J. Fish. Aquat. Sci. **57**(6): 1300–1306. doi:10.1139/f00-050.

Narum, S.R., Powell, M.S., Evenson, R., Sharp, B., and Talbot, A.J. 2006. Microsatellites reveal population substructure of Klickitat River native steelhead and genetic divergence from an introduced stock. N. Am. J. Fish. Manage. **26**: 147–155. doi:10.1577/M05-055.1.

Narum, S.R., Zendt, J.S., Graves, D., and Sharp, W.R. 2008. Influence of landscape on resident and anadromous life history types of *Oncorhynchus mykiss*. Can. J. Fish. Aquat. Sci. **65**(6): 1013–1023. doi:10.1139/F08-025.

Narver, D.W. 1969. Age and size of steelhead trout in the Babine River, British Columbia. J. Fish. Res. Board Can. **26**(10): 2754–2760. doi:10.1139/f69-269.

Neave, F. 1944. Racial characteristics and migratory habits in *Salmo gairdneri*. J. Fish. Res. Board Can. **6c**(3): 245–251. doi:10.1139/f42-030.

Neff, B.D., and Pitcher, T.E. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. Mol. Ecol. **14**(1): 19–39. PMID:15643948.

Nichols, K.M., Edo, A.F., Wheeler, P.A., and Thorgaard, G.H. 2008. The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. Genetics, **179**: 1559–1575. doi:10.1534/genetics.107.084251. PMID:18562654.

Nordeng, H. 1983. Solution to the “char problem” based on Arctic char (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. **40**(9): 1372–1387. doi:10.1139/f83-159.

Null, R.E., Niemela, K.S., and Hamelberg, S.F. 2013. Post-spawn migrations of hatchery-origin *Oncorhynchus mykiss* kelts in the Central Valley of California. Environ. Biol. Fishes, **96**: 341–353. doi:10.1007/s10641-012-0075-5.

Ohms, H.A., Sloat, M.R., Reeves, G.H., Jordan, C.E., and Dunham, J.B. 2014. Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **71**(1): 70–80. doi:10.1139/cjfas-2013-0274.

Okuzawa, K. 2002. Puberty in teleosts. Fish Physiol. Biochem. **26**: 31–41. doi:10.1023/A:1023395025374.

Olsen, J.B., Wuttig, K., Fleming, D., Kretschmer, E.J., and Wenburg, J.K. 2006. Evidence of partial anadromy and resident-form dispersal bias on a fine scale in populations of *Oncorhynchus mykiss*. Conserv. Genet. **7**: 613–619. doi:10.1007/s10592-005-9099-0.

Olsson, I.C., and Greenberg, L.A. 2004. Partial migration in a landlocked brown trout population. J. Fish Biol. **65**: 106–121. doi:10.1111/j.0022-1112.2004.00430.x.

Olsson, I.C., Greenberg, L.A., Bergman, E., and Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecol. Lett. **9**: 645–651. doi:10.1111/j.1461-0248.2006.00909.x. PMID:16706909.

O'Neal, S.L., and Stanford, J.A. 2011. Partial migration in a robust brown trout population of a Patagonian river. Trans. Am. Fish. Soc. **140**(3): 623–635. doi:10.1080/00028487.2011.585577.

Pascual, M.A., Bentzen, P., Riva Rossi, C., Mackey, G., Kinnison, M.T., and Walker, R. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. Trans. Am. Fish. Soc. **130**: 53–67. doi:10.1577/1548-8659(2001)130<0053:FDCOAI>2.0.CO;2.

Pavlov, D.S., and Savvaitova, K.A. 2008. On the problem of ratio of anadromy and residence in salmonids (Salmonidae). J. Ichthyol. **48**(9): 778–791. doi:10.1134/S0032945208090099.

Pavlov, D.S., Savvaitova, K.A., and Kuzishchin, K.V. 2001*a*. Theoretical aspects of the problem of the distribution pattern and formation of life-history strategy of mikizha (*Parasalmo mykiss* (Walbaum), Salmonidae, Salmoniformes) on the Kamchatka peninsula. J. Ichthyol. **379**: 344–346.

Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., Gruzdeva, M.A., Pavlov, S.D., Mednikov, B.M., and Maksimov, S.V. 2001*b*. The Pacific noble salmons and trouts of Asia. Scientific World, Moscow, Russia.

Pavlov, D.S., Nemova, N.N., Kirillov, P.I., Kirillova, E.A., Nefedova, Z.A., and Vasil'eva, O.B. 2007. Lipid status and feeding habits of salmonid juveniles in the year preceding seaward migration as factors controlling their future smoltification. J. Ichthyol. **47**(3): 241–245. doi:10.1134/S003294520703006X.

Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., Gruzdeva, M.A., Mal'tsev, A.Y., and Stanford, J.A. 2008. Diversity of life strategies and population structure of Kamchatka mykiss *Parasalmo mykiss* in the ecosystems of small salmon rivers of various types. J. Ichthyol. **48**(1): 37–44. doi:10.1134/S0032945208010049.

Pavlov, D.S., Nemova, N.N., Kirillov, P.I., Kirillova, E.A., Nefedova, Z.A., and Vasil'eva, O.B. 2010*a*. The lipid status and feeding habits of yearlings of mykiss *Parasalmo mykiss* and coho salmon *Oncorhynchus kisutch* in autumn. J. Ichthyol. **50**(7): 543–551. doi:10.1134/S0032945210070064.

Pavlov, D.S., Nemova, N.N., Nefedova, Z.A., Ruokolainen, T.R., Vasil'eva, O.B., Kirillov, P.I., and Kirillova, E.A. 2010*b*. The lipid status of young of the year mykiss *Parasalmo mykiss* and coho salmon *Oncorhynchus kisutch*. J. Ichthyol. **50**(1): 116–126. doi:10.1134/S0032945210010145.

Pearsons, T.N., McMichael, G.A., Bartrand, E.L., Fisher, M., Monahan, J.T., Leider, S.A., Strom, G.R., and Murdoch, A.R. 1993. Yakima species interactions study, 1992 annual report. Washington Department of Fish and Wildlife.

Pearsons, T.N., Temple, G.M., Fritts, A.L., Johnson, C.L., and Webster, T.D. 2008. Ecological interactions between non-target taxa of concern and hatchery supplemented salmon, 2007 Annual Report Project number 1995-063-25. Washington Deparment of Fish and Wildlife.

Piché, J., Hutchings, J.A., and Blanchard, W. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proc. R. Soc. B Biol. Sci. **275**: 1571–1575. doi:10.1098/rspb.2008.0251.

Prevost, E., Chadwick, E.M.P., and Claytor, R.R. 1992. Influence of size, winter duration and density on sexual maturation of Atlantic salmon (*Salmo salar*) juveniles in Little Codroy River (southwest Newfoundland). J. Fish Biol. **41**: 1013–1019. doi:10.1111/j.1095-8649.1992.tb02728.x.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash.

Quinn, T.P., and Myers, K.W. 2004. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Rev. Fish Biol. Fish. **14**(4): 421–442. doi:10.1007/s11160-005-0802-5.

Quinn, T.P., Seamons, T.R., Vøllestad, L.A., and Duffy, E. 2011. Effects of growth and reproductive history on the egg size–fecundity tradeoff in steelhead. Trans. Am. Fish. Soc. **140**: 45–51.

Railsback, S.F., and Rose, K.A. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Trans. Am. Fish. Soc. **128**(2): 241–256. doi:10.1577/1548-8659(1999)128<0241:BMOSTG>2.0.CO;2.

Reiser, D.W., Huang, C.-M., Beck, S., Gagner, M., and Jeanes, E. 2006. Defining flow windows for upstream passage of adult anadromous salmonids at cascades and falls. Trans. Am. Fish. Soc. **135**: 668–679. doi:10.1577/T05-169.1.

Richter, A., and Kolmes, S.A. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Rev. Fish Sci. **13**(1): 23–49. doi:10.1080/10641260590885861.

Rieman, B.E., Beamesderfer, R.C., Vigg, S., and Poe, T.P. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Trans. Am. Fish. Soc. **120**(4): 448–458. doi:10.1577/1548-8659(1991)120<0448:ELOJST>2.3.CO;2.

Rieman, B.E., Isaak, D., Adams, S., Horan, D., Nagel, D., Luce, C., and Myers, D. 2007. Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. Trans. Am. Fish. Soc. **136**: 1552–1565. doi:10.1577/T07-028.1.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. J. Fish Biol. **56**: 328–346. doi:10.1111/j.1095-8649.2000.tb02110.x.

Rikardsen, A.H., Thorpe, J.E., and Dempson, J.B. 2004. Modelling the life-history variation of Arctic charr. Ecol. Freshw. Fish, **13**: 305–311. doi:10.1111/j.1600-0633.2004.00070.x.

Riva-Rossi, C., Pascual, M.A., Babaluk, J.A., García-Asorey, M., and Halsen, N.M. 2007. Intra-population variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. J. Fish Biol. **70**: 1780–1797. doi:10.1111/j.1095-8649.2007.01449.x.

Robards, M.D., and Quinn, T.P. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. Trans. Am. Fish. Soc. **131**(3): 523–536. doi:10.1577/1548-8659(2002)131<0523:TMTOAS>2.0.CO;2.

Roff, D.A. 1997. Evolutionary quantitative genetics. Chapman and Hall, New York.

Rogers, L.A., and Schindler, D.E. 2008. Asynchrony in population dynamics of sockeye salmon in southwest Alaska. Oikos, **117**(10): 1578–1586. doi:10.1111/j.0030-1299.2008.16758.x.

Romer, J.D., Leblanc, C.A., Clements, S., Ferguson, J.A., Kent, M.L., Noakes, D., and Schreck, C.B. 2013. Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, U.S.A. Environ. Biol. Fishes, **96**: 849–863.

Roni, P., and Quinn, T.P. 1995. Geographic variation in size and age of North American chinook salmon. N. Am. J. Fish. Manage. **15**: 325–345. doi:10.1577/1548-8675(1995)015<0325:GVISAA>2.3.CO;2.

Rosengrave, P., Gemmell, N.J., Metcalfe, V., McBride, K., and Montgomerie, R. 2008. A mechanism for cryptic female choice in chinook salmon. Behav. Ecol. **19**(6): 1179–1185. doi:10.1093/beheco/arn089.

Rounsefell, G.A. 1958. Anadromy in North American Salmonidae. Fish. Bull. **131**: 171–185.

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

Rowe, D.K., Thorpe, J.E., and Shanks, A.M. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. **48**(3): 405–413. doi:10.1139/f91-052.

Rundio, D.E., Williams, T.H., Pearse, D.E., and Lindley, S.T. 2012. Male-biased sex ratio of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in California. Ecol. Freshw. Fish, **21**(2): 293–299. doi:10.1111/j.1600-0633.2011.00547.x.

Russell, R. 1974. Rainbow trout life history studies in Lower Talarik Creek - Kvichak drainage Study G-II, Job No. G-II-E, Vol. 15. Alaska Department of Fish and Game, Division of Sport Fish, Juneau, Alaska.

Russell, R. 1977. Completion report for rainbow trout life history studies in Lower Talarik Creek - Kvichak drainage Study G-II, Job No. G-II-E, Vol. 18. Alaska Department of Fish and Game, Division of Sport Fish, Juneau, Alaska.

Ruzycki, J.R., Clarke, L.M., Flesher, M.W., Carmichael, R.W., and Eddy, D.L. 2009. Performance of progeny from steelhead and rainbow trout crosses. Oregon Department of Fish and Wildlife, Fish Research and Development, NE Region.

Sahashi, G., and Morita, K. 2013. Migration costs drive convergence of threshold traits for migratory tactics. Proc. R. Soc. B Biol. Sci. **280**(1773): 20132539. doi:10.1098/rspb.2013.2539.

Sandford, B.P., Zabel, R.W., Gilbreath, L.G., and Smith, S.G. 2012. Exploring latent mortality of juvenile salmonids related to migration through the Columbia River hydropower system. Trans. Am. Fish. Soc. **141**(2): 343–352. doi:10.1080/00028487.2012.664601.

Sargent, J., Henderson, R.J., and Tocher, D.R. 1989. Lipids. *In* Fish nutrition. *Edited by* J.E. Halver. Academic Press, London. pp. 153–218.

Satterthwaite, T.D. 1988. Influence of maturity on straying rates of summer steelhead into the Rogue River, Oregon. Calif. Fish Game, **74**(4): 203–207.

Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. 2009. Steelhead life history on California's Central Coast: insights from a state-dependent model. Trans. Am. Fish. Soc. **138**: 532–548. doi:10.1577/T08-164.1.

Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. Evol. Appl. **3**: 221–243. doi:10.1111/j.1752-4571.2009.00103.x.

Satterthwaite, W.H., Hayes, S.A., Merz, J.E., Sogard, S.M., Frechette, D.M., and Mangel, M. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Trans. Am. Fish. Soc. **141**(3): 781–794. doi:10.1080/00028487.2012.675912.

Savvaitova, K.A. 1975. The population structure of *Salmo mykiss* in Kamchatka. J. Ichthyol. **15**(6): 876–888.

Savvaitova, K.A., Kuzishchin, K.V., Maksimov, S.V., and Pavlov, D.S. 1997. Population structure of mikizha, *S. mykiss* in the Utkholok River (western Kamchatka). J. Ichthyol. **37**: 216–225.

Savvaitova, K.A., Tutukov, M.A., Kuzishchin, K.V., and Pavlov, D.S. 2002. Changes in the population structure of mikizha *Parasalmo mykiss* from the Utkholok River, Kamchatka, during the fluctuation in its abundance. J. Ichthyol. **42**(3): 238–242.

Savvaitova, K.A., Kuzishchin, K.V., Gruzdeva, M.A., Pavlov, D.S., Stanford, J.A., and Ellis, B.K. 2003. Long-term and short-term variation in the population structure of Kamchatka steelhead *Parasalmo mykiss* from rivers of western Kamchatka. J. Ichthyol. **43**(9): 757–768.

Savvaitova, K.A., Pavlov, D.S., Kuzishchin, K.V., Gruzdeva, M.A., and Kucheryavyi, A.V. 2007. Ecological analogies in the Pacific lamprey *Lethenteron camtschaticum* and the mykiss *Parasalmo mykiss* in Kamchatka. J. Ichthyol. **47**: 341–347. doi:10.1134/S0032945207050025.

Schill, D.J., LaBar, G.W., Mamer, E.R.J.M., and Meyer, K.A. 2010. Sex ratio, fecundity, and models predicting length at sexual maturity of redband trout in Idaho desert streams. N. Am. J. Fish. Manage. **30**: 1352–1363. doi:10.1577/M10-021.1.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, **465**(7298): 609–612. doi:10.1038/nature09060. PMID: 20520713.

Schonher, T., and Nicholson, S.E. 1989. The relationship between California rainfall and ENSO events. J. Clim. **2**(11): 1258–1269. doi:10.1175/1520-0442(1989)002<1258:TRBCRA>2.0.CO;2.

Schroeder, R.K., and Smith, L.H. 1989. Life history of rainbow trout and effects of angling regulations in the Deschutes River, Oregon Information report (fish) 89-6. Oregon Department of Fish and Wildlife, Portland, Ore.

Schwanke, C.J., and Hubert, W.A. 2003. Structure, abundance, and movements of an allacustrine population of rainbow trout in the Naknek River, southwest Alaska. Northwest Sci. **77**(4): 340–348.

Schwartz, K.M., and Orme, A.R. 2005. Opening and closure of a seasonal river mouth: the Malibu estuary–barrier–lagoon system, California. Z. Geomorphol. Suppl. **141**: 91–109.

Seamons, T.R., Bentzen, P., and Quinn, T.P. 2004. The mating system of steelhead, *Oncorhynchus mykiss*, inferred by molecular analysis of parents and progeny. Environ. Biol. Fishes, **69**(1–4): 333–344. doi:10.1023/B:EBFI.0000022893.88086.8f.

Shapovalov, L., and Taft, A.C. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Fish Bulletin 98.

Sharpe, C.S., Beckman, B.R., Cooper, K.A., and Hulett, P.L. 2007. Growth modulation during juvenile rearing can reduce rates of residualism in the progeny of wild steelhead broodstock. N. Am. J. Fish. Manage. **27**: 1355–1368. doi:10.1577/M05-220.1.

Silverstein, J.T., Shearer, K.D., Dickhoff, W.W., and Plisetskaya, E.M. 1998. Effects of growth and fatness on sexual development of chinook salmon (*Oncorhynchus tshawytscha*) parr. Can. J. Fish. Aquat. Sci. **55**(11): 2376–2382. doi:10.1139/f98-111.

Simpson, A.L. 1992. Differences in body size and lipid reserves between maturing and nonmaturing Atlantic salmon parr, *Salmo salar* L. Can. J. Zool. **70**(9): 1737–1742. doi:10.1139/z92-241.

Sloat, M.R. 2013. Born to run? Integrating individual behavior, physiology, and life histories in poartially migratory steelhead and rainbow trout (*Oncorhynchus mykiss*). Ph.D. dissertation, Oregon State University, Corvallis, Ore.

Sloat, M.R., and Osterback, A.-M.K. 2013. Maximum stream temperature and the occurrence, abundance, and behavior of steelhead trout in a southern California stream. Can. J. Fish. Aquat. Sci. **70**(1): 64–73. doi:10.1139/cjfas-2012-0228.

Sloat, M.R., and Reeves, G.H. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. Can. J. Fish. Aquat. Sci. **71**(4): 491–501. doi:10.1139/cjfas-2013-0366.

Sloat, M.R., Fraser, D.J., Dunham, J.B., Falke, J.A., Jordan, C.E., McMillan, J.R., and Ohms, H.A. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. Rev. Fish Biol. Fish. **24**(3): 689–707. doi:10.1007/s11160-014-9344-z, 10.1007/s11160-014-9344-z.

Sogard, S.M., Merz, J.E., Satterthwaite, W.H., Beakes, M.P., Swank, D.R., Collins, E.M., Titus, R.G., and Mangel, M. 2012. Contrasts in habitat characteristics and life history patterns of *Oncorhynchus mykiss* in California's central coast and central valley. Trans. Am. Fish. Soc. **141**(3): 747–760. doi:10.1080/00028487.2012.675902.

Steen, R.P., and Quinn, T.P. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. Can. J. Zool. **77**(5): 836–841. doi:10.1139/z99-020.

Stewart, T.J., and Bowlby, J.N. 2009. Chinook salmon and rainbow trout catch and temperature distributions in Lake Ontario. J. Gt. Lakes Res. **35**(2): 232–238. doi:10.1016/j.jglr.2008.11.012.

Sutton, S.G., Bult, T.P., and Haedrich, R.L. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. Trans. Am. Fish. Soc. **129**: 527–538. doi:10.1577/1548-8659(2000)129<0527:RAFWBW>2.0.CO;2.

Taranger, G.L., Carrillo, M., Schulz, R.W., Fontaine, P., Zanuy, S., Felip, A., Weltzien, F.-A., Dufour, S., Karlsen, Ø., Norberg, B., Andersson, E., and Hansen, T. 2010. Control of puberty in farmed fish. Gen. Comp. Endocrinol. **165**(3): 483–515. doi:10.1016/j.ygcen.2009.05.004. PMID:19442666.

Thériault, V., and Dodson, J.J. 2003. Body size and the adoption of a migratory tactic in brook charr. J. Fish Biol. **63**: 1144–1159. doi:10.1046/j.1095-8649.2003.00233.x.

Thériault, V., Garant, D., Bernatchez, L., and Dodson, J.J. 2007. Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). J. Evol. Biol. **20**: 2266–2277. doi:10.1111/j.1420-9101.2007.01417.x. PMID:17956389.

Thériault, V., Dunlop, E.S., Dieckmann, U., Bernatchez, L., and Dodson, J.J. 2008. The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evol. Appl. **1**: 409–423. doi:10.1111/j.1752-4571.2008.00022.x.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evol. Ecol. **12**: 581–599. doi:10.1023/A:1022351814644.

Thrower, F.P., and Joyce, J.E. 2004. Effects of 70 years of freshwater residency on survival, growth, early maturation, and smolting in a stock of anadromous rainbow trout from southeast Alaska. Am. Fish. Soc. Symp. **44**: 485–496.

Thrower, F.P., Hard, J.J., and Joyce, J.E. 2004. Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead. J. Fish Biol. **65**(s1): 286–307. doi:10.1111/j.0022-1112.2004.00551.x.

Tipping, J.M., and Byrne, J.B. 1996. Reducing feed levels during the last month of rearing enhances emigration rates of hatchery-reared steelhead smolts. Prog. Fish-Cult. **58**(2): 128–130. doi:10.1577/1548-8640(1996)058<0128:RFLDTL>2.3.CO;2.

Tocher, D.R. 2003. Metabolism and functions of lipids and fatty acids in teleost fish. Rev. Fish. Sci. **11**(2): 107–184. doi:10.1080/713610925.

Todd, A.S., Coleman, M.A., Konowal, A.M., May, M.K., Johnson, S., Veiria, N.K.M., and Saunders, J.F. 2008. Development of new water temperature criteria to protect Colorado's fisheries. Fisheries, **33**: 433–443. doi:10.1577/1548-8446-33.9.433.

Waples, R.S., Zabel, R.W., Scheuerell, M.D., and Sanderson, B.L. 2008. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. Mol. Ecol. **17**: 84–96. doi:10.1111/j.1365-294X.2007.03510.x. PMID:18268786.

Ward, B.R., and Slaney, P.A. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. **45**(7): 1110–1122. doi:10.1139/f88-135.

Welch, D.W., Ishida, Y., Nagasawa, K., and Eveson, J.P. 1998. Thermal limits on the ocean distribution of steelhead trout (*Oncorhynchus mykiss*). North Pac. Anadromous Fish Comm. Bull. **1**: 396–404.

Wood, C.C. 1995. Life history variation and population structure in sockeye salmon. Am. Fish. Soc. Symp. **17**: 195–216.

Zabel, R.W., Faulkner, J., Smith, S.G., Anderson, J.J., Van Holmes, C., Beer, N., Iltis, S., Krinke, J., Fredricks, G., Bellerud, B., Sweet, J., and Giorgi, A. 2008. Comprehensive passage (COMPASS) model: a model of downstream migration and survival of juvenile salmonids through a hydropower system. Hydrobiologia, **609**: 289–300. doi:10.1007/s10750-008-9407-z.

Zimmerman, C.E., and Ratliff, D.E. 2003. Controls on the distribution and life history of fish populations in the Deschutes River: geology, hydrology, and dams. *In* A peculiar river: geology, geomorphology, and hydrology of the Deschutes River, Oregon. *Edited by* J.E. O'Connor and G.E. Grant. American Geophysical Union, Washington, D.C. pp. 51–70.

Zimmerman, C.E., and Reeves, G.H. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Can. J. Fish. Aquat. Sci. **57**(10): 2152–2162. doi:10.1139/f00-192.

Zimmerman, C.E., and Reeves, G.H. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Trans. Am. Fish. Soc. **131**(5): 986–993. doi:10.1577/1548-8659(2002)131<0986:IOSARR>2.0.CO;2.

Zimmerman, C.E., Kuzishchin, K.V., Gruzdeva, M.A., Pavlov, D.S., Stanford, J.A., and Savvaitova, K.A. 2003. Experimental determination of the life history strategy of the Kamchatka *Mykizha Parassalmo mykiss* (Walb) (Salmonidae, Salmoniformes) on the basis of analysis of the Sr/Ca Ratio in otoliths. Doklady Biol. Sci. **389**(1–6): 138–143. [Translated from Doklady Akademii Nauk.] doi:10.1023/A:1023474926447.

Zimmerman, C.E., Edwards, G.W., and Perry, K. 2009. Maternal origin and migratory history of steelhead and rainbow trout captured in rivers of the Central Valley, California. Trans. Am. Fish. Soc. **138**: 280–291. doi:10.1577/T08-044.1.