

# Monitoring Steelhead Populations in the San Joaquin Basin - Life-History Variation in *Oncorhynchus mykiss*

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## Introduction

*Oncorhynchus mykiss* exhibits the most diverse life-history patterns among California's native salmonids (Williams 2006). Unlike Chinook salmon (*Oncorhynchus tshawytscha*), *O. mykiss* can complete their life cycle in freshwater creating two distinct life-history variants including an anadromous form (i.e., steelhead) and freshwater residents (i.e., Rainbow trout). Between the anadromous and resident life-history variants there exists a considerable array of diverse pathways through which *O. mykiss* can complete their life cycle. Past research has documented over 35 unique steelhead life-history variants in watersheds across the west coast of North America (Thorpe 2007, Moore et al. 2014, Hodge et al. 2016). In most cases, discrete life-history variants are characterized by differences in the years spent rearing in freshwater and saltwater and age of maturation and spawning (Figure 1). As such, the number of possible life-history pathway permutations tends to increase with the average lifespan of fish in the population, where additional permutations can emerge from protracted freshwater or ocean residence (Moore et al. 2014), repeat spawning incidence (Hodge et al. 2016), and habitat specific rearing phases (e.g., estuarine; Hayes et al. 2011).

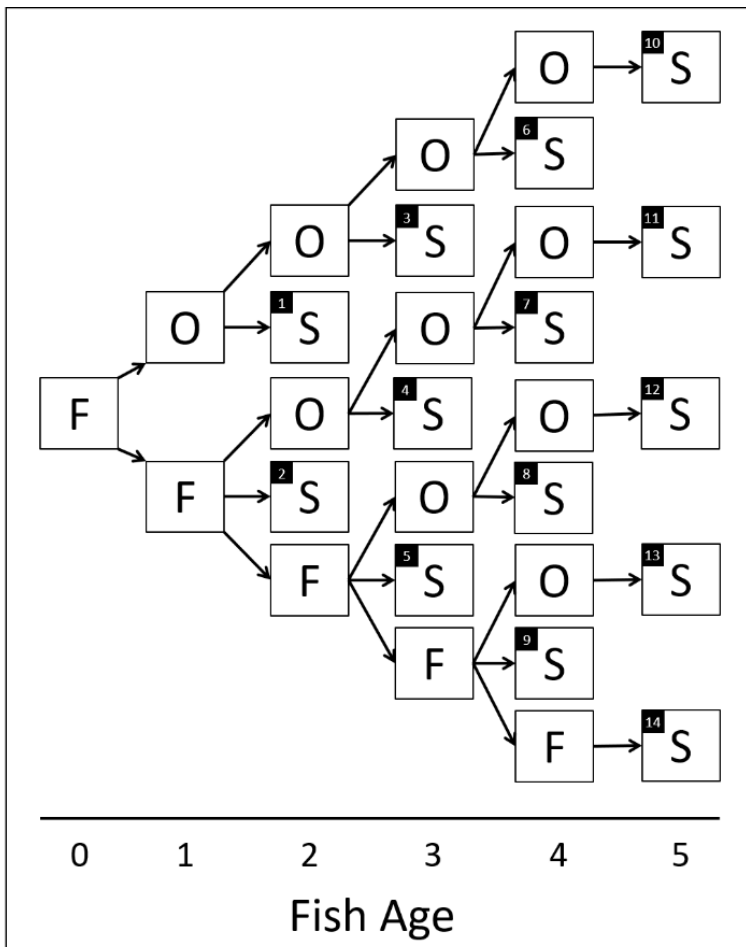


Figure 1. Conceptual illustration of 14 alternative *O. mykiss* life-history pathways that differ by years spent rearing in freshwater (F) or the ocean (O) prior to maturation and spawning (S). Note this illustration does not include life-history permutations resulting from repeat spawning, discrete habitat rearing phases, and/or fish that live beyond five years.

Figure 1 illustrates how *O. mykiss* can complete its life-cycle through diverse combinations of years spent rearing in freshwater or the ocean, migrating early in life or later, or spawning early in life or later. Each unique combination is considered a life-history pathway. In this example, we show 14 unique life-history pathway but note that additional combinations can be generated from repeat spawning, discrete habitat rearing phases, and fish that live beyond five years.

A considerable body of research on *O. mykiss* life history variation has been completed since Shapovalov and Taft's seminal work in 1954. Kendall et al. (2015) published one of the more recent and comprehensive reviews of research on the topic of anadromy and residency in steelhead and rainbow trout. Reproducing a review comparable to Kendall et al. (2015) is beyond the scope of this document, thus here we sought to provide a summary of key concepts and conclusions discussed in Kendall et al. (2015) relevant to the California Central Valley. We encourage readers to see Kendall et al. (2015) for a more thorough and in-depth discussion of *O. mykiss* life-history expression.

## Patterns and processes of *O. mykiss* life-history expression

The creation and maintenance of a distinct life-history pathway comes from complex interactions between the genetic makeup and internal condition of individual fish, and the external environment (Kendall et al. 2015). These interactions create variability in a fish's state during key developmental phases (Thorpe et al. 1998, Satterthwaite et al. 2009, 2010, Beakes et al. 2010) that impact its life-history trajectory (i.e., anadromy or residency, Figure 2). As a result, genetically dissimilar fish in the same environment, or genetically similar fish in different environments, may all end up on different life-history trajectories.

Disparate life-history pathways have tradeoffs in potential costs and benefits for individual fish and their expected life-time fitness (e.g., Satterthwaite et al. 2009, 2010). In general, the costs of freshwater residency for females include smaller size at maturation leading to lower fecundity, smaller egg size, smaller suitable spawning gravel sizes and shallower redds that may be more susceptible to scour. In males these costs are associated with decreased competitive advantage and female choice compared to their anadromous counterparts (Kendall et al. 2015), which can lead to fewer mating opportunities and spawning with smaller females in a given year. The benefits conferred through the resident life-history pathway include reduced mortality risks during migration and at sea and increased chance of iteroparity for both sexes. The costs of anadromy include increased mortality risks during migration and at sea, older age at maturation and decreased chance of iteroparity for both sexes. Whereas the benefits of anadromy include accelerated growth and large body size attained at sea, which leads to increased fecundity and egg size, wider range of suitable spawning gravels for females, and enhanced competitive advantage for mate selection relative to their resident counterparts for males.

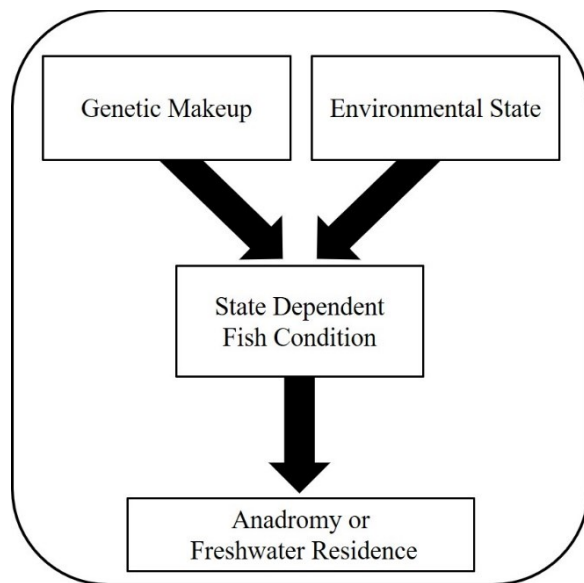


Figure 2. Pathway diagram illustrating how genetic makeup and the environment interact to alter fish condition and subsequent life-stage transitions such as maturation in freshwater or migration to sea.

Figure 2 emphasizes how *O. mykiss* genetics and the environment interactively control the state-dependent condition of individual fish. The state-dependent condition of individual fish controls which

life-history pathway it takes. In other words, life-history variability in this species is not only controlled by genetics or the environment but rather the combination of both factors.

The patterns of aquatic productivity and the physical challenges associated with migration (e.g., environmental gradient, flow, temperature, predation risk) form an adaptive landscape on which anadromy evolves and environmental conditions provide proximate cues for whether it is expressed. In partially anadromous species, like *O. mykiss*, the expression of anadromy is in part influenced by the cost of migration. Specifically, when migration distance, elevation gained, or risk of mortality is high during migration, the anadromous contingents within a species is expected to become less common (Hendry et al., 2004, McMillan et al., 2007). Even where latitude or migratory difficulty are approximately equal, differences in habitat characteristics and growing conditions of adjacent watersheds can generate divergent rates of anadromy (Pavlov et al. 2011, Finstad and Hein 2012, Berejikian et al. 2013, Kendall et al. 2015). This adaptive landscape has driven the local adaptation of many different anadromous life-history strategies (e.g., Quinn 2005). Heritable differences in traits associated with migration (e.g. size-at-migration, age-at-migration, timing of migration, morphology of migrants) have been documented for many populations (Carlson and Seamons 2008), including heritability of migration (e.g. steelhead populations in Alaska,  $h^2 = 0.73$  (Thrower et al. 2004) and California,  $h^2 = 0.91$  (Phillis et al. 2016).

Environmental conditions also influence the expression of anadromy in partially anadromous populations. Food availability, water temperature, and stream flow have been associated with patterns of anadromy in *O. mykiss*. For example, low and variable summer stream flows produce warmer temperatures and greater competition for food as suitable habitat contracts. As the conditions become growth-limiting due to density-dependent competition or increasing metabolic demands of the individual anadromy becomes more common (Pearsons et al., 2008, Courter et al., 2009, Berejikian et al., 2013). Body size or growth rate is often considered a proxy for growth conditions, but whether anadromy is expressed will depend on the context. Faster growth has been associated with anadromy in field and lab experiments, however, cooler temperatures and lower individual metabolic rates produce higher rates of freshwater maturation for equivalent somatic growth, particularly in females (McMillan et al., 2012, Sloat and Reeves 2014).

In reality, the propensity of individuals to adopt the steelhead phenotype is the product of interactions between genetic and environmental controls (Figure 3). Further, recent research has shown some gene complexes associated with anadromy (e.g., *Omy5*) indirectly impact life-history expression through mediation of early somatic growth rates (Kelson et al. 2020). The indirect genetic control on migration in *O. mykiss* can be described as a reaction norm wherein expression of the migratory tactic is dependent on an individual's status (the integration of the environment experienced) relative to a genetically-controlled threshold state (Tomkins and Hazel 2007, Hutchings 2011, Pulido 2011, Dodson et al. 2013). Growth rate and body-size thresholds above which emigration takes place have been described theoretically (Thorpe et al. 1998, Rikardsen et al. 2004, Mangel and Satterthwaite 2008) and documented empirically for several salmonid species, including steelhead (Thrower et al. 2004, Satterthwaite et al. 2010, Beakes et al. 2010, Phillis et al. 2016). The outcome of these genotype-environment interactions will vary within populations (e.g. males vs. females) and between populations

according to the costs and benefits of seaward migration versus freshwater residency for any given system.

## Knowledge gaps and next steps

Although we have learned much about the patterns and processes that drive life-history variation in *O. mykiss* there is still a lot we don't fully understand. This is especially true in the California Central Valley where research and monitoring of *O. mykiss* has been spatiotemporally inconsistent in past decades and often ancillary to other species on which monitoring programs are focused (Eilers 2010). Thus, resolving uncertainty will be critical for developing a juvenile production estimate and other useful management metrics for the anadromous contingent of Central Valley *O. mykiss* populations. Uncertainties and knowledge gaps include but are not limited to three broad categories: 1) importance of non-natal habitats in supporting divergent life-history types (e.g., intermittent streams and the Bay-Delta), 2) *O. mykiss* genetics (e.g., Omy5) as a tool for management and predicting anadromy (e.g., Kelson et al. 2019), and 3) the effects of water management, salmon management, and climate change on the environmental and genetic controls of steelhead life-history diversity. By coordinating and focusing future research and monitoring on management-relevant questions within the categories listed above we will accelerate our learning and improve management of California Central Valley *O. mykiss*.

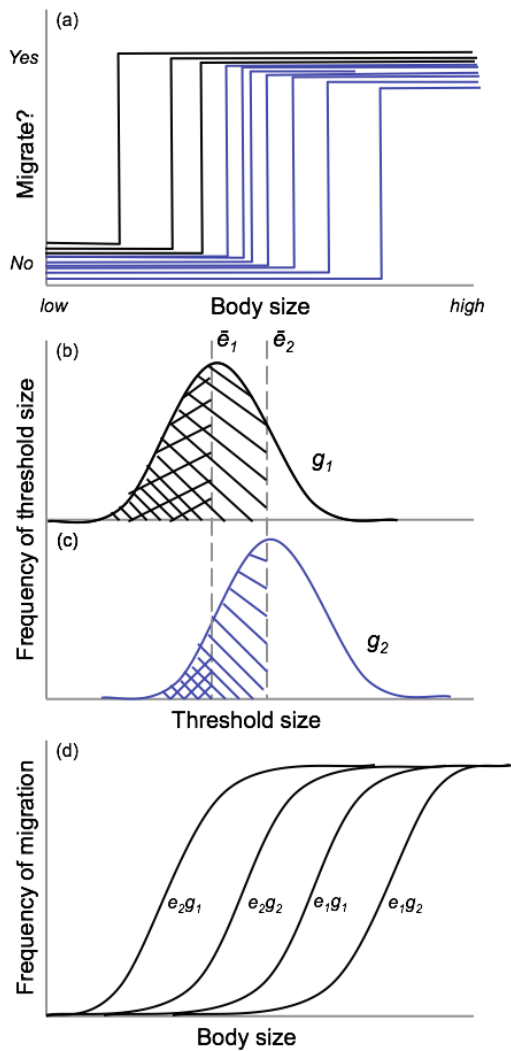


Figure 3. The environmental threshold model of partial anadromy. Partial anadromy as a threshold trait (adapted from Hazel et al. 1990). (a) The decision to migrate is determined by an individual's state (here inferred from body size) relative to a threshold switch point (vertical lines). (b) Genotypes for the threshold vary continuously within a population following some distribution ( $g_1$ ; here depicted as a normal distribution). Individuals will migrate if their threshold size is less than their body size. Body size varies with the environment (dashed vertical lines); therefore, the number of individuals that migrate in environment 1 ( $e_1$ ) is a subset of those individuals that migrate in environment 2 ( $e_2$ ). (c) A second population with a more costly seaward migration or more favorable freshwater conditions selects for individuals with larger threshold sizes ( $g_2$ ; blue lines in (a)) resulting in fewer migrants in each environment. (d) The number of migrants in a population takes on a cumulative frequency distribution.

A conceptual depiction of the environmental threshold model of partial anadromy. Individuals' threshold size for expressing anadromy are presented along a continuum of body size. The threshold sizes within a population are represented as being normally distributed and the migratory phenotypes are all those

individuals whose body size exceeds their threshold size for migration. In a lower growth environment the frequency of migration is lower than in a higher growth environment. Under similar growth environments, a population with a larger mean thresholds size for migration has a lower frequency of migration than a population with a smaller mean threshold for migration.

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