Contrasts in habitat characteristics and life history patterns of steelhead trout in California's central coast and Central Valley

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Suggested running head: Life history patterns in California steelhead

Abstract

Steelhead trout *Oncorhynchus mykiss* exhibit high plasticity in life history patterns, with fish emigrating to the ocean at a broad range of ages or remaining in freshwater as residents and maturing at varying ages. Individual life history decisions are hypothesized to result from the interaction of genetic thresholds shaped by local adaptation with variation in environmental factors influencing growth and condition trajectories. We compared growth rates and life history patterns in two coastal creeks (Scott and Soquel) and two Central Valley rivers (American and Mokelumne) in California. The two regions differed markedly in habitat and physical factors. Growth rates of age-0 fish averaged approximately 0.1 mm/d in the summer/fall and 0.2 mm/d in the winter/spring. In the Central Valley, growth rates were up to 10 times faster than on the coast and differed in seasonality, with faster growth in the summer/fall than in the winter/spring. Growth also differed between rivers, with means on the American River of 1.0 mm/d in the summer/fall and 0.7 mm/d in the winter/spring and means on the Mokelumne River of 0.7 mm/d in the summer/fall and 0.5 mm/d in the winter/spring. Life history expression and age structures in the coastal creeks were similar, with populations dominated by age-0 fish, but also including residents up to age 6. The two Central Valley populations were strikingly different in life history expression. On the American River, a single cohort was present, with nearly all fish emigrating in the spring following their birth year. On the Mokelumne River, a broad diversity of ages was present, with a large proportion of presumed residents. The observed variation in life histories aligned with predictions based on state dependent life history models developed for the four streams, providing further demonstration of the adaptability of *O. mykiss* to contrasting rearing environments.

Introduction

Steelhead rainbow trout *Oncorhynchus mykiss* exhibit a remarkable diversity of life histories. At the end of their first year, they follow three possible trajectories: smolt transformation and emigration to the ocean, remaining in freshwater as immature parr, or maturation. Each year following the first year, multiple pathways are again possible, such as emigration or continued freshwater residence (Behnke 2002). Some individuals never emigrate and are identified as rainbow trout, the non-anadromous form of *O. mykiss*, whereas the anadromous form is identified as steelhead. Hereafter we refer to all forms as steelhead for brevity. In contrast to other Pacific salmonids, steelhead are iteroparous and may spawn over several years, returning to the ocean between spawnings. This plasticity in life history is presumed to confer resilience to the population in the face of a variable environment (Via et al. 1995; Greene et al. 2010; Schindler et al. 2010). Understanding the conditions that lead to adoption of different life history strategies and how they vary in subsequent contribution to the adult population is essential for reversing ongoing declines in steelhead abundance. In addition, an improved understanding of how individuals arrive at a particular life history pathway will improve our ability to monitor and predict effects of changing or restored environments on steelhead populations.

Extensive studies on life history plasticity in salmonids have contributed to a general theory to explain underlying mechanisms (Mangel 1994; Thorpe et al. 1998; Rikardsen et al. 2004; Mangel and Satterthwaite 2008; Piche et al. 2008; Satterthwaite et al. 2009; 2010). Individual state (e.g., size, growth rate, lipid content) at various developmental time steps plays a key role in shaping life history decisions such as smolt transformation and emigration. These decision windows occur well in advance of the transition itself (Mangel 1994; Thorpe et al. 1998). The pathway exhibited by an individual is presumed to be the consequence of an interaction between genetic thresholds and the environmental context; i.e., the genetic program is cued by the environment. Within this framework, the threshold state determining a decision is predicted to vary as a consequence of local adaptation. Steelhead have a particularly broad geographic range, occurring from southern California, USA, throughout the North Pacific to Kamchatka, Russia, and thus are exposed to a broad suite of environmental conditions. Local adaptation of steelhead appears to be extensive; within California high levels of genetic differentiation among stream systems have been observed along the coast (Garza et al. 2004) as well as in the Central Valley (Nielsen et al. 2005).

For purposes of conservation, steelhead in California have been assigned to six Distinct Population Segments (DPSs), with boundary delineations based primarily upon biogeographic and genetic considerations (Busby et al. 1996); all but one DPS are currently listed as either threatened or endangered under the Endangered Species Act. Ecological differences among the DPSs are not well described. Ideally, a recovery plan should be tailored to population-level criteria within each DPS, taking into account specific biological characteristics and differences in the inherent productive capacities of the habitats that may underlie these biological differences (Spence et al. 2008). In most cases, however, such population-specific information is not currently available. Providing tools to more clearly describe the relationships of life history patterns with environmental conditions within contrasting DPSs will help managers make informed decisions on the identification and protection of key factors that influence the persistence of steelhead populations.

In this study, we examined steelhead ecology in four stream systems, two creeks in the California Central Coast DPS (Scott and Soquel) and two rivers in the Central Valley DPS (American and Mokelumne). We focused on estimation of growth rates, which are hypothesized to play a major role in determining life history pathways, and the patterns of life history expression within each stream, potentially a function of local adaptation to large differences in the rearing environment. Although prior studies have documented basic ecology of the two coastal systems (Hayes et al. 2008; Sogard et al. 2009), limited published information is available for Central Valley steelhead populations. McEwan (2001) provides a thorough review of distribution and abundance, potential factors involved in population declines, and management concerns for steelhead in the Central Valley. However, explicit comparisons among geographic locations have not been made, nor have explicit comparisons been made between seasons within the Central Valley. These field results complemented a larger effort to evaluate the roles of water management and future climate change in altering life history patterns of California steelhead, incorporating field studies, lab experiments, and modeling (Beakes et al. 2010; Satterthwaite et al. 2009; 2010; Collins et al. in prep). Our overall focus was to understand the mechanisms underlying variability in growth rates and whether or not the rearing environment predicts consequent life history pathways.

In laboratory experiments, we examined life history decisions in two steelhead populations, one from the Central Coast DPS and one from the Central Valley DPS (Beakes et al. 2010). We reared age-0 fish with different treatments of food availability and determined their selected life history at age 1 (smolt versus non-smolt) based on seawater challenges in the spring. We observed a clear effect of body size on the smolting decision, with larger fish in both populations more likely to survive in saltwater. We also observed a significant effect of population, with Central Valley fish exhibiting a larger size threshold for adopting the emigration pathway than Central Coast fish. Behavior and growth capacity also differed, with Central Valley fish appearing to display risk-prone behavior and full exploitation of enhanced growth opportunities, whereas Central Coast fish displayed risk-averse behavior and more moderate growth under the same conditions (Beakes et al. 2010). These results suggested local adaptation induced a divergence in ecological responses between the two populations.

In modeling studies using preliminary estimates of growth rates and size at age in these systems, we developed predictions of life history patterns of female steelhead in Central Coast (Satterthwaite et al. 2009) and Central Valley (Satterthwaite et al. 2010) populations, based on estimated thresholds for optimal decisions during a particular time window as a function of tradeoffs between future growth and survival. These tradeoffs result from the fecundity advantage accrued by females that emigrate to the ocean and grow to large sizes versus the potential survival advantage accrued by females that remain in freshwater for additional years, either smolting at larger sizes, thereby increasing the probability of ocean survival, or adopting a resident life history. For the Central Coast, the results suggested that, given the likely range of variation in individual sizes and growth rates, the range of optimal decisions for a suite of individuals includes a mix of life histories dominated by fish smolting at a range of ages. For the highly regulated rivers of the Central Valley, we predicted a different composition of life history pathways for the American River versus the Mokelumne River, consistent with their different environments. For the American River, we predicted a dominance of one life history strategy, emigration at age 1, even under a broad range of survival probabilities at different stages, although very poor ocean survival combined with high river survival led to predicted residency. In contrast, for the Mokelumne River, we predicted a mixed strategy, with the composition of different phenotypes highly dependent on the survival scenarios used.

In the models, the early emergence and rapid growth rate of American River fish put them far above the predicted threshold (given baseline survival assumptions) for smolting at their first opportunity as opposed to waiting to mature or smolt at an older age. Because they were far from this threshold, small to moderate movements of the threshold due to variation in survival were unlikely to change the proportion of fish above versus below the threshold and thus were unlikely to change the predicted distribution of life histories. By contrast, the later emergence and slower growth rate of Mokelumne River fish, along with a higher variability in growth rates, meant that there were fish on both sides of the threshold for smolting (given baseline survival) and thus the proportions of different life histories were easily changed by even small changes in survival. Larger changes (such as combining poor ocean survival with high river survival) were sufficient to shift the thresholds enough that distributions became entirely on one side of the threshold or the other, causing the predicted loss of a life history type. These results suggested that the optimal life history pathway is a complex function of environmental conditions within the rearing location as well as along the migratory corridor to the ocean and back to the natal stream.

Methods

Study systems

On the coast, we sampled in Scott and Soquel creeks. Both are undammed, free flowing streams arising in the Santa Cruz Mountains and entering the Pacific Ocean over beaches that are regularly closed by sand bars in the summer and fall, creating small lagoonal estuaries. They have similar watershed areas, gradients, riparian vegetation, streambed geology, and hydrography (Table 1), with flows dependent on local rainfall patterns. The low diversity of the fish communities is typical of small coastal creeks, limited to steelhead, sculpin *Cottus* spp., Pacific lamprey *Lampetra tridentata*, three-spined sticklebacks *Gasterosteus aculeatus* and Sacramento suckers *Catostomus occidentalis*. Coho salmon *Oncorhynchus kisutch* occurred regularly in Scott Creek until recent years and historically occurred in Soquel Creek. A small conservation hatchery on Scott Creek produces steelhead that are released as age-0 smolts and largely migrate directly to the ocean, resulting in minimal interaction with naturally produced juveniles (Hayes et al. 2004).

Genetic analysis of steelhead along the California coast indicates a high concordance with geographic proximity (Garza et al. 2004; Aguilar and Garza 2006). Although Soquel Creek was not included in these studies, it is in the same genetic group as Scott Creek, which indicates that the two populations are likely to be genetically very similar

In the Central Valley, we sampled steelhead populations on the American and Mokelumne rivers. Both are highly regulated, snow-fed streams beginning high on the west slope of the Sierra Nevada at elevations over 3,000 m. Impassable dams block anadromous fish access to most of the historic, higher gradient spawning areas of both rivers, and steelhead are now constrained to very limited sections that differ radically from the natural rearing habitat (McEwan 2001). Although the two Central Valley rivers drain much larger watersheds, reach length of available rearing habitat is now comparable to that of the central coast creeks (Table 1). Stream sections available to steelhead in both systems are now highly urbanized and sediment starved, with degraded channels that are oversimplified (James 1997; Pasternack et al. 2004). Camanche Dam on the Mokelumne River and Folsom Dam on the American River block gravel delivery from upstream, and historic mining operations have resulted in depleted instream gravel storage, altering downstream riverbed complexity (James 1997; Merz and Moyle 2006).

Regulation of water releases from upstream reservoirs has dramatically altered the ecology of both rivers, dampening the range of both flow and temperature and altering the timing of seasonal patterns in physical factors such as flow and biological factors such as prey delivery. Fish communities in Central Valley rivers are far more diverse than those of the coast and include a large number of non-native species (Table 1).

Genetic analysis suggests that steelhead throughout the Central Valley are relatively closely related and that southern populations within the DPS are similar to northern populations, potentially a consequence of extensive incorporation of Eel River fish in the broodstock of Nimbus Hatchery on the American River (Garza and Pearse 2008). Based on the geographic proximity of the American and Mokelumne rivers and the sharing of broodstock between the two systems, we presumed a high degree of genetic similarity between these populations. However, the introduction of fish from the Eel River and consequent introgression of hatchery fish into natural populations may have resulted in divergence of current genotypes from those historically present in the two rivers.

Physical habitat data

We monitored water temperatures in each system with TidBit recorders (Onset Corp.) placed in several locations and recording every 30 min. We obtained additional temperature data for years prior to our study from the California Department of Fish and Game (CDFG) for the American River and from the East Bay Municipal Utility District (EBMUD) for the Mokelumne River. For the coastal streams, temperature differences between upstream and downstream sites were minor. We used temperature data from upstream sites because they included a longer time span than our downstream sites. For both of the Central Valley rivers, summer water temperatures increased downstream of the dams that delimit the boundary of rearing areas for steelhead. We used temperatures recorded at a mid-point (Watt Avenue on the American River and Mackville Road on the Mokelumne River) within the available rearing section to illustrate general seasonal patterns.

We obtained flow data from the USGS National Water Information System web site for California streams (http://waterdata.usgs.gov/ca/nwis/nwis). We used long term data for Soquel Creek at the town of Soquel (located near the mouth), the American River at Fair Oaks, and the Mokelumne River below Camanche Dam to calculate the mean proportion of annual water flow occurring in each month. USGS data were not available for Scott Creek, so we assumed that the monthly flow patterns were similar to those occurring on nearby Soquel Creek.

Biological data

Shallow depths and generally low flows in the small coastal systems allowed us to derive quantitative estimates of fish density. We conducted multiple pass depletion electrofishing in June, October, and December of 2006 and 2007, and June of 2008 at each of four 100m long sites in each watershed (Figure 1). We placed block nets at the upper and lower ends of a site prior to sampling to prevent entry and exit of fish during sampling. We estimated the total abundance of steelhead from the number of fish captured on each of three passes using the formula of Pollock and Otto (1983).

We could not conduct such quantitative sampling in the larger rivers of the Central Valley. We used a variety of methods, including seining, boat electrofishing, and hook and line sampling to capture steelhead at three sites in the American River and two sites in the Mokelumne River (Figure 1). Sampling was conducted on an opportunistic basis throughout 2006, 2007, and 2008. We supplemented these collections with prior data from seining and electrofishing conducted on the American River (CDFG) and on the Mokelumne River (EBMUD). We excluded all hatchery-origin fish (denoted by adipose fin clips) from analyses; thus, all reported results refer to juveniles derived from in-river spawning. We compiled size data across years to examine annual patterns in length frequencies.

We tagged all fish > 65 mm FL with a Passive Integrated Transponder (PIT, Allflex Corp.) tag, allowing recognition of individuals at subsequent recapture. Recaptures at the eight coastal sites were common and provided a wealth of information on growth patterns. For the Central Valley systems, we supplemented our recaptures with additional tag and recapture data from CDFG and EBMUD for the American River and Mokelumne River, respectively. We computed growth rates as increase in fork length (mm) per day. We divided growth estimates into two seasons, summer/fall, with measurements taken between May and December, and winter/spring, with measurements between December and May. We excluded growth data for fish tagged in one season and only recaptured in subsequent seasons. We compared growth data separately for presumed age-0 and age-1+ fish, with age categories based on visual inspection of length-frequency modes at each site and scale analyses. Mean growth rates among streams were compared using analysis of variance (ANOVA), with post-hoc Tukey tests ($\alpha = 0.05$) for individual comparisons.

In addition to direct estimates of growth from recaptured tagged fish, we evaluated growth rates based on the progression of length frequencies over time. This method is indirect and is influenced by selective mortality and variation in age composition if cohorts overlap in size. Therefore, we applied length-frequency analysis only to age-0 fish, which generally comprised a discrete mode compared to older fish and could be readily tracked over time. Because cohorts older than age-0 overlapped in size distributions, we were not able to estimate growth rates of age-1+ fish from change in mean size over time. As before, we estimated growth within two seasons, summer/fall and winter/spring. For the coastal streams, we sampled three times per year, in June, September/October, and December. We regressed the mean lengths of age-0 fish on time for the three times each year to estimate summer/fall growth, and from December to the following June to estimate winter/spring growth. Data were available for 2006 and 2007 in both creeks. For both Central Valley rivers, additional length data were available for years prior to our study. For the summer/fall season, we had sufficient data for analysis for 5 years (2001, 2002, 2004, 2006, 2007) on the American River and for 14 years (1995-2008) on the Mokelumne River. For the winter/spring season, we had sufficient data for only 1 year on the American River (2007) but for 11 years on the Mokelumne River (1995-2007, except 1999 and 2003). To estimate growth, we regressed fish length on time during the respective seasons, using the mean lengths of fish during 10-day intervals; i.e. each interval was represented by a single point consisting of the mean of all fish caught during that interval. This approach reduced any bias associated with variable sampling effort over time. We used the slope of the regression as an estimate of daily growth in length.

We aged random samples of fish from each system from scale annuli following the methods of Davis and Light (1985). In addition, we were able to determine age of some PIT-tagged fish based on recaptures in subsequent years. These individuals were first tagged at a size believed to correspond to the age 0 cohort. We assigned fish to age 1 in March following their birth year.

Results

Physical habitat patterns

Seasonal patterns in water temperature differed among the four streams (Figure 2). Although the annual cycle in the two coastal systems was similar, Scott Creek tended to have temperatures about 1.4^{o}C cooler in the summer and about 1.3^{o}C warmer in the winter compared to Soquel Creek. The highest temperatures occurred in August, with a daily mean of 15.3^{o}C in Scott Creek and 16.5^{o}C in Soquel Creek, and the coolest temperatures were in January, with means of 7.3 and 5.6^{o}C, respectively. In the Central Valley, temperature patterns differed markedly between the two rivers. In the American River, the warmest temperatures were in August, with a daily mean of 19.2^{o}C, whereas in the Mokelumne River the warmest temperatures were in September, with a mean of 15.2^{o}C. The coolest temperatures were in January on the American River, with a mean of 9.1^{o}C, and in February on the Mokelumne River, with a mean of 10.2^{o}C. Daily maximum temperatures in the summer regularly exceeded 20^{o}C on the American River but did so only rarely on the Mokelumne River or the coastal streams.

The annual pattern of water delivery differed dramatically between the free flowing creeks of the central coast and the regulated rivers of the Central Valley (Figure 2). Flow rates on Soquel Creek, which we presumed to provide an appropriate proxy for Scott Creek, demonstrated the expected pattern for central coast streams, with flashy flows associated with rainstorms in the winter and gradually decreasing flows with the onset of the dry season. Soquel Creek received on average 65% of its annual flow during the winter months of January, February, and March, and only 2.3% during the summer from July through September. In contrast, flows on the Central Valley rivers were more evenly distributed throughout the year, matching regulated releases from reservoirs above the dams. The American River received on average 34% of its annual flow during the 3 winter months and 18% during the 3 summer months. Similarly, the Mokelumne River received on average 31% of its flow during the winter months and 20% during the summer.

Size distributions

We observed striking differences in the size-frequency distribution of steelhead between the Central Coast and Central Valley, as well as between the two rivers within the Central Valley

(Figure 3). In spring, all four streams had a large mode of age-0 fish. In the coastal streams there was also a small mode of older fish in a size range of about 100 to 200 mm FL. Steelhead in the American River largely comprised a single year class, with minimal evidence of fish older than age 0. Excluding mature fish returning from the ocean, our dataset included 4,257 fish measured in the American River from 2001 to 2008. Of these, only two fish, caught in July at sizes of 318 and 360 mm FL, were presumed to be older than age 0. They were likely age-1 fish that did not migrate in the spring with the rest of the age-0 cohort. In contrast, older fish were common on the Mokelumne River, with a wide range of sizes present, suggesting multiple age classes and a large proportion of fish with a resident life history. In the fall, growth differences among the four streams were evident in the size distribution of the age-0 cohort. Slow growth of age-0 coastal fish resulted in only a minor progression of sizes. In the American River, the single mode comprised of age-0 fish was retained but shifted to much larger sizes due to extremely rapid growth rates. All cohorts showed moderate growth in the Mokelumne River. Patterns observed in the fall were largely maintained in the subsequent winter size-frequency distributions.

Growth estimates

Indirect growth estimates based on regressions of age-0 sizes over time suggested major differences between the coastal and Central Valley streams in both absolute growth and patterns by season (Figure 4). The two coastal streams had similar rates, with an average of 0.11 mm/d and 0.14 mm/d in summer/fall on Scott Creek and Soquel Creek, respectively. Growth estimates for the Central Valley populations far exceeded those of the coastal populations. On the American River, summer/fall growth rates were about 10 times faster than on the coast, with an estimated mean of 1.12 mm/d. On the Mokelumne River, growth rates in summer/fall were about 5 times faster than on the coast, with a mean among 14 years of 0.60 mm/d. Seasonal patterns also differed between the coast and Central Valley. Age-0 growth rates approximately doubled during the winter/spring season on the coast, with estimated means of 0.24 mm/d and 0.21 mm/d on Scott Creek and Soquel Creek, respectively. In contrast, growth in the Central Valley was slower in winter/spring than in summer/fall, with an estimate of 0.61 mm/d for the one year of data for the American River and a mean of 0.46 mm/d for the 11 years of data on the Mokelumne River.

Direct growth estimates of age-0 fish based on recaptures of PIT-tagged individuals were generally similar to those estimated from size progressions over time (Figure 4). On the coast, summer/fall growth averaged 0.05 mm/d on Scott Creek and 0.07 mm/d on Soquel Creek. In the winter/spring season these rates increased to 0.20 and 0.18 mm/d, respectively. For the American River we did not have recaptures in winter/spring, but summer/fall growth rates of age-0 tagged fish averaged 0.98 mm/d. On the Mokelumne River, growth rates of age-0 PIT-tagged fish averaged 0.81 mm/d in summer/fall and 0.44 mm/d in winter/spring. ANOVAs comparing age-0 growth in summer/fall indicated significant differences among streams ($F_{3,400}$ = 754.45, $P < 0.001$), with the American River growth faster than that of the Mokelumne River, which in turn was faster than for the two coastal sites, which did not differ from each other (post-hoc Tukey tests). Likewise, growth during the winter/spring differed among streams ($F_{2,116}$ = 29.5, $P < 0.001$), with Mokelumne River growth faster than the two coastal sites, which did not differ from each other (post-hoc Tukey tests).

Growth rates of age-1+ fish calculated from recaptured PIT-tagged fish were generally low in all of the streams where older fish occurred (older fish occurred at only very low frequency on the American River). On the coast, growth rates of age-1+ fish were similar to those of age-0 fish, with means of 0.05 mm/d and 0.03 mm/d on Scott Creek and Soquel Creek, respectively, in summer/fall and 0.26 mm/d and 0.08 mm/d on Scott Creek and Soquel Creek in winter/spring (Figure 4). On the Mokelumne River, older fish displayed a marked decrease in growth compared to the age-0 cohort, with means of 0.20 mm/d in summer/fall and 0.14 mm/d in winter/spring. ANOVAs comparing age-1+ growth in summer/fall indicated significant differences among streams ($F_{2,521}$ = 53.5, $P < 0.001$), with the Mokelumne River growth faster than for the two coastal sites, which did not differ from each other (post-hoc Tukey tests). Growth during the winter/spring again differed among streams ($F_{2,62}$ = 11.5, $P < 0.001$), but in this season Scott Creek fish grew faster than Mokelumne River and Soquel Creek fish, which did not differ from each other (post-hoc Tukey tests).

Age estimates

Age estimates generally concurred with growth estimates (Figure 5). Ages of fish from the two coastal creeks spanned a range from 0 to 6 years. For the American River, all scales examined, which included some of the largest fish captured, were assigned to age 0. After

March 1, our arbitrary cutoff designating when fish advanced to age 1, no large fish were captured on the American River with the exception of two individuals (scales not available), suggesting nearly all of an annual cohort emigrated during the spring following their birth year. For the Mokelumne River, age estimates ranged from 0 to 4. Some of the large fish captured in the winter (Figure 3) may have been adults returning from the ocean. However, the broad range of sizes and ages for fish captured from spring through fall on the Mokelumne River indicated a large proportion of fish that adopted the resident life history and were able to attain a large size entirely in freshwater. Of 43 fish estimated to be at least 2 years old, 28 appeared to have spawned, based on checks present on scales, confirming their status as residents. The larger sizes of older fish on the Mokelumne River compared to the coast reflected their much faster growth rates.

Discussion

Juvenile steelhead rearing in Central Coast creeks and Central Valley rivers experience radically different environmental conditions. Physical factors of flow and temperature on the Central Coast largely exhibit high seasonal variation driven by solar input and rain patterns. Water temperatures on the coast are primarily controlled by air temperature and can range from lows of < 5°C in the winter to near 20°C in the summer, although summer temperatures are largely moderate due to the coastal climate. In the Central Valley, historical water temperatures prior to dam construction would have likely exceeded those of Central Coast streams in the summer and dropped to comparable lows in the winter, also following air temperatures, although snowmelt presumably moderated rising temperatures in late spring (Williams 2006). Additionally, steelhead would have had access to cooler water in stream sections now blocked by reservoirs. At present, however, temperatures are controlled by dam releases of reservoir water, with a greatly moderated range. Temperatures in the winter rarely fall below 8°C. In the summer, temperatures depend on the amount of water released and the thermal structure of the reservoir. For the American River, temperatures can reach daily maxima of 23°C in a dry year with minimal water released, but only 18°C in a wet year with higher releases (U.S. Dept. Int. 2008). For the Mokelumne River, water released from below the reservoir thermocline results in more moderate summer temperatures than on the American River. Within both Central Valley rivers, summer temperatures increase rapidly downstream of the reservoir due to high air temperatures.

Flow rates on the coast are flashy in the winter and slowly decrease after the rainy season to minimal levels in the fall. On the Central Valley rivers, flow rates depend on dam releases and variability is greater among than within years. In a dry year, flow rates may be relatively constant throughout the year, but in a wet year releases will be increased to lower reservoirs as needed to create storage space for runoff for future flood protection downstream of the dams. Historical flow patterns would have been influenced by winter storms and rainfall, similar to the coast, but also by melting snowpack in the upper watersheds during spring and early summer, not a factor on the coast. Snowmelt is still a factor in the Central Valley, but greatly dampened by flow regulation.

Additional habitat differences between the Central Coast and Central Valley include substrate composition, geomorphology of the streams, riparian structure and canopy, and aquatic community composition. Central Coast fish communities are depauperate, particularly in the upper sections of the watershed. In contrast, in the Central Valley steelhead encounter a diverse community of potential competitors and predators, including introduced species (e.g., striped bass *Morone saxatilis*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieui*) with a high capacity for consumption (Johnson et al. 1992; Tabor et al. 2007). In addition to the major contrasts in habitat, Central Coast steelhead can emigrate directly into the ocean, whereas anadromous Central Valley steelhead have a much longer migration corridor upon emigration from rearing habitats (Table 1). Once anadromous fish have entered the ocean, whether there is any spatial segregation among populations is virtually unknown. Large scale bottom-up processes driving interannual variability in productivity are likely to be similar for Central Coast and Central Valley populations, although differences in timing of ocean entry and fish size may confer differences in initial mortality risk.

The combined suite of natural and anthropogenic environmental differences presumably plays a major role in the marked biological contrasts of the two steelhead DPSs compared in this study. Growth rate differences are particularly striking. In the summer/fall, growth on the Central Coast is slow, negatively density-dependent and decreases with body size (Hayes et al. 2008; Sogard et al. 2009; this study). Other coastal creeks in California also have relatively poor growth of juvenile steelhead during the summer (Harvey et al. 2005; Boughton et al. 2007; McCarthy et al. 2009), presumably a consequence of low food availability during the low flows of the dry season. Harvey et al. (2005) manipulated stream flow in a northern California creek and found that fish in control stream sections grew 8.5 times faster than those in sections with reduced flows. In a southern California creek, specific growth in weight was near 0 in control groups (0.038 d^{-1}) but rose to 2.28 d^{-1} for groups supplemented with additional food (Boughton et al. 2007). Summer growth rates that were 10 (American River) to 5 (Mokelumne River) times faster than on the coast suggest few constraints on growth, particularly for the American River population. Both Central Valley rivers had substantially higher abundances of invertebrate prey than the coastal creeks (Collins et al. unpublished data), in part attributable to the delivery of pelagic prey from reservoirs behind the dams. For example, juvenile steelhead in the Mokelumne River consume large numbers of cladocerans, a prey item never observed in diets of coastal fish (Merz 2002; Collins et al. unpublished data). Although total invertebrate densities in the drift are generally higher on the Mokelumne River than on the American River, the small size of cladocerans may make them of lower quality than the insect taxa that dominant drift communities and steelhead diets on the American River (Merz and Vanicek 1996; Collins et al. unpublished data). In addition, the warmer temperatures on the American River presumably also enhance growth rates. For the American River's hatchery strain (Nimbus), growth rates at 19^{o}C were 1.3 to 1.7 times faster than growth at 15 or 11^{o}C (Myrick and Cech 2005). We were not able to quantify densities on the two rivers, but lower densities of steelhead in the American River may also contribute to their rapid growth by reducing competition.

The two DPSs also differed in the seasonality of growth, with faster growth in the winter/spring than in the summer/fall in the coastal creeks and the opposite pattern in the Central Valley rivers, although winter growth rates in the Central Valley still greatly exceeded those on the coast. On the coast the seasonal difference likely reflects the increased delivery of prey as flows increase with winter storms. In the Central Valley, reduced winter growth rates are likely a function of lower temperatures, as abundances of drift invertebrates remain high (Collins et al. unpublished data).

In addition to the environmental factors underlying foraging opportunity in the different systems, there are likely to be local adaptation effects influencing inherent growth capacity in the two DPSs. In common-garden laboratory experiments, growth rates of a Central Coast population (Scott Creek, Monterey Bay Salmon and Trout Project [MBSTP] hatchery) were significantly slower than those of a northern Central Valley population (Battle Creek, Coleman National Fish Hatchery), particularly under enhanced opportunities of warmer temperatures (Beakes et al. 2010). Behavioral differences between the two populations were evident, with the Central Coast fish appearing to be risk-averse and the Central Valley fish appearing to be risk-prone, aggressive feeders that rarely used available shelters (Beakes et al. 2010). Because the Coleman spawner population comprises a mix of hatchery produced and natural adults (although the grand-parentage of natural adults is unknown), the risk-prone behavior of the juveniles may reflect selection for success in a hatchery environment, whereas the use of only wild adults in spawning for the MBSTP hatchery (although again grand-parentage of natural adults is unknown) suggests less of a hatchery influence on behavior. The high similarity of growth in the wild for Scott Creek (possible hatchery influence) and Soquel Creek (hatchery influence limited to occasional strays) in this study suggests that the inherent growth capacity of the Scott Creek fish reflects that of the DPS. The muddled ancestry of the American River and Mokelumne River populations, in contrast, makes it difficult to determine if their faster growth rates compared to Central Coast populations are solely due to environmental feeding opportunities or if they reflect selection for rapid growth in a hatchery environment, or if wild Central Valley populations have experienced natural selection for faster growing genotypes even in the absence of hatchery influences.

The two DPSs also differ in size at emigration. Steelhead in the Central Coast creeks emigrate primarily at a size of < 190 mm (Shapovalov and Taft 1954; Bond et al. 2008), although some smaller downstream migrants may oversummer in coastal estuaries, where rapid growth allows them to attain sizes of over 200 mm prior to final emigration to the ocean (Bond et al. 2008). In contrast, Central Valley fish emigrating to the ocean appear overall to leave at a size of around 200-250 mm, with minimal variability among years or populations (U.S. Dept. Int. 2008; Williams 2006). Likewise, emigrating steelhead smolts captured at salvage facilities generally range from 226-250 mm (U.S. Dept. Int. 2008). American River smolts even range over 300 mm, as evidenced by the size of age-0 fish in December (Figure 3).

In addition to major differences in growth rates, there are large differences in life history expression among the four streams. Coastal streams are largely represented by immature fish that are likely the progeny of anadromous parents. Age-1 fish are present but in much lower numbers than age-0 fish, suggesting either high overwinter mortality or high rates of emigration at age 1. The latter is unlikely due to the small size and thus poor survival probability of age-1 emigrants (Ward et al. 1989; Bond et al. 2008), although growth in the lagoon may boost the effective size of young migrants (Hayes et al. in press), and Shapovalov and Taft (1954) reported nontrivial returns of fish that emigrated at age 1 despite their presumably low ocean survival. Fish aged 2 and older are also present, but may be represented largely by early maturing males, which then remain in the stream. At one site on Soquel Creek (Ashbury) there is a downstream waterfall that was a full barrier to migrating anadromous adults prior to 1989, when it was dynamited, and is now an intermittent barrier. Here the steelhead population is comprised of a wide range of sizes, and multiple recaptures over several years suggests a large proportion of resident fish. At the other Soquel Creek sites and all of the Scott Creek sites, which have no apparent migration barriers, presumed residents are few in number. On the American River, the steelhead population consists of very nearly a single cohort, with almost all members emigrating after their first winter, at age 1. Extremely rapid growth rates result in a large size at the time of emigration, with a presumably much greater likelihood of survival in the marine environment compared to age-1 emigrants from the coastal populations. On the Mokelumne River, there is a large contingent of older fish presumed to be residents based on their body size. We captured large numbers of fish on the Mokelumne River that exceeded 300 mm and thus were larger than most Central Valley emigrants. These fish displayed the darker coloration typical of the resident life history, and many had spawning checks on their scales.

The life history pathways exhibited by steelhead in the four systems were accurately predicted for females by our state-dependent models (Satterthwaite et al. 2009, 2010) and tracked the large variation in growth rates among systems in the expected way. As discussed above, we infer that the coastal creeks were dominated by anadromous fish smolting at age 2, along with some younger and some older emigrants. Examining the winter size-frequencies in Figure 3 along with the size at age in Figure 5, we see that the vast majority of age-0 coastal fish are below the putative 100-110 mm smolting threshold in December (Satterthwaite et al. 2009; their Figure 3), whereas most but not all age-1 fish are above it. Thus, the model predicts a predominance of age-2 smolts on the coast, but with a mix of smolt ages since some age-2 fish are too small to initiate smolting and predicted to do so at age 3, and the largest observed age-1 fish would also be predicted to smolt. By contrast, every American River fish sampled in the winter was over 200 mm (Figure 3), suggesting that all or nearly all age-0 fish in winter are larger than the predicted 130-140 mm threshold size (Satterthwaite et al. 2010; their Figure 5) and leading to the prediction of a population consisting entirely of anadromous fish smolting in the spring just after they become age 1. Finally, from Figure 4 we see that the mean growth rate of Mokelumne River age-0 steelhead was around 0.4-0.5 mm/day in winter/spring and 0.6-0.8 mm/day in summer/fall. At these growth rates, the latest emerging fish would be predicted to adopt a resident life history (Satterthwaite et al. 2010; their Figure 6) with the remainder smolting. In addition, individual fish on the Mokelumne River displayed a wide range of growth rates (0.034 - 1.17 mm/day for age-0 fish in winter/spring), and residency would be predicted for the slower growing fish within this range.

The Mokelumne River population presents the largest discrepancy from model predictions, since the model predicts a mixture of anadromous and resident fish but with anadromous fish dominating, given baseline survival assumptions. This may be inconsistent with the large number of residents inferred above. In addition, Del Real et. al (in press) demonstrated with acoustically tagged fish that downstream migration was rare; 74% of natural origin fish were presumed to be residents based on their fine scale movements within the study reach. However, as mentioned in the introduction, the model's predicted balance between residents and anadromous fish is sensitive to highly uncertain survival estimates, and it is entirely possible that the baseline survival assumptions do not adequately describe real conditions on the Mokelumne River. Future field work estimating survival in the Mokelumne River would be helpful in determining the extent to which the model can successfully predict the balance between residency and anadromy.

The large variability in growth rates and life history expression found in this study provides additional testament to the remarkable plasticity of *O. mykiss* and the species' ability to adapt to different freshwater environments while inhabiting a common marine environment (for the anadromous individuals). Management decisions affecting the growth environment, including habitat availability, food delivery via drift, and physical conditions such as temperature, can potentially alter the natural distribution of life history patterns exhibited in steelhead populations. Likewise, shifts in the probability of mortality along the migration corridor can change the likelihood of expression of different life histories. Our results confirm the contrast between two DPSs of steelhead in California but also demonstrate major differences in patterns within a single DPS.

Acknowledgments

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Table 1. Habitat characteristics of the four study systems. Data sources include *Recovery Plan for Evolutionarily Significant Unit of Central California Coast Coho Salmon* Public Draft Version: March 2010 (http://swr.nmfs.noaa.gov/recovery/Coho_Recovery_Plan_031810.htm) and the *Central Valley public draft recovery plan* (http://swr.nmfs.noaa.gov/recovery/centralvalleyplan.htm).

Variable	American River	Mokelumne River	Scott Creek	Soquel Creek
Drainage area (km^2)	5120	1624	78	110
Mouth distance to ocean (km)	182	137	0	0
Mean annual total discharge (m^3)	3.4×10^9	6.4×10^8	3.4×10^7	3.8×10^7
Length of potential rearing habitat (km)	37	41	26	51
Maximum gradient in rearing habitat (%)	0.1	0.1	4.5	5.0
Riparian vegetation - primary	Valley foothill riparian/urban	Agriculture	Conifer forest	Conifer forest
Riparian vegetation - secondary	Valley oak woodland	Valley oak woodland	Shrub	Shrub
Mean proportion of flow from snowmelt (%)	40	10	<1	<1
Fish diversity – native species	10	12	6	6
Fish diversity – exotic species	20	26	0	0

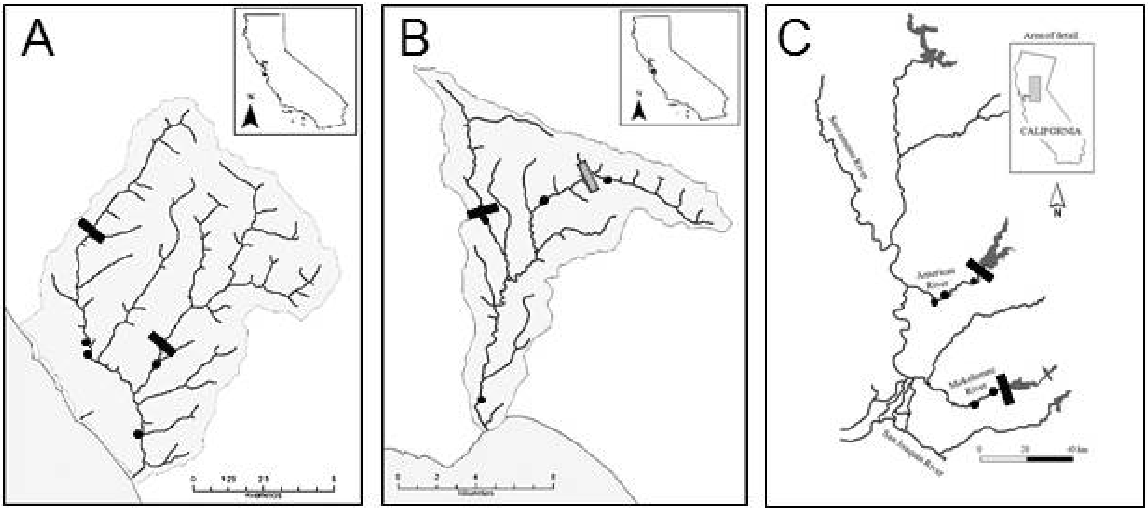

Figure 1. Location of sampling sites on two coastal creeks (A, Scott; B, Soquel) and two Central Valley rivers (C, American and Mokelumne). Black rectangles are impassable falls or dams, gray rectangle (Soquel Creek) is an intermittent barrier, and black circles are sampling sites.

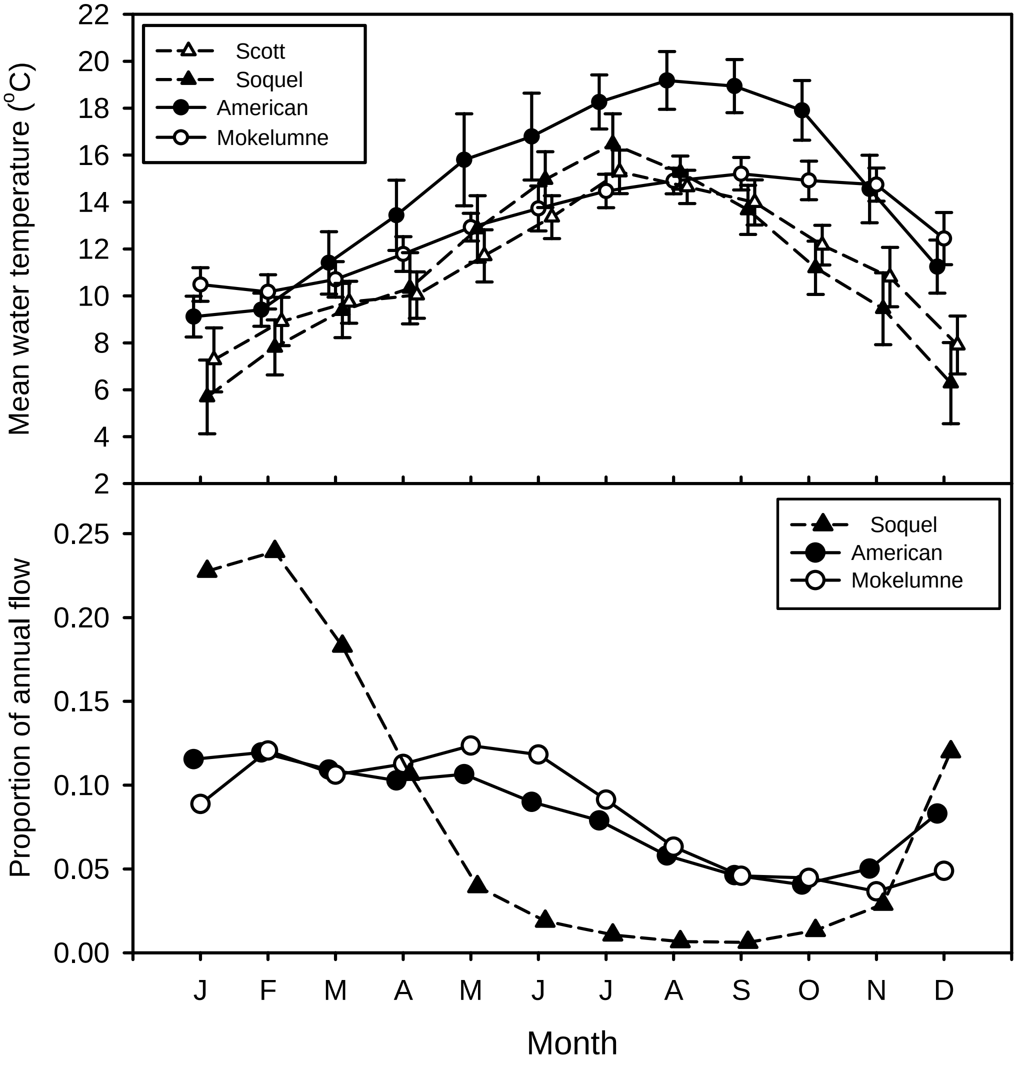

Figure 2. Annual cycle of water temperature and flow on the study streams. Temperatures are the monthly means (± S.D.) over multiple years (Scott Creek and Soquel Creek 2006-2009; American River 2001-2008; Mokelumne River 1997-2004). Flow data are the proportions of annual flow occurring each month, based on multiple years (Soquel Creek and American River 1951-2010; Mokelumne River 1993-2010). Flow data were not available for Scott Creek.

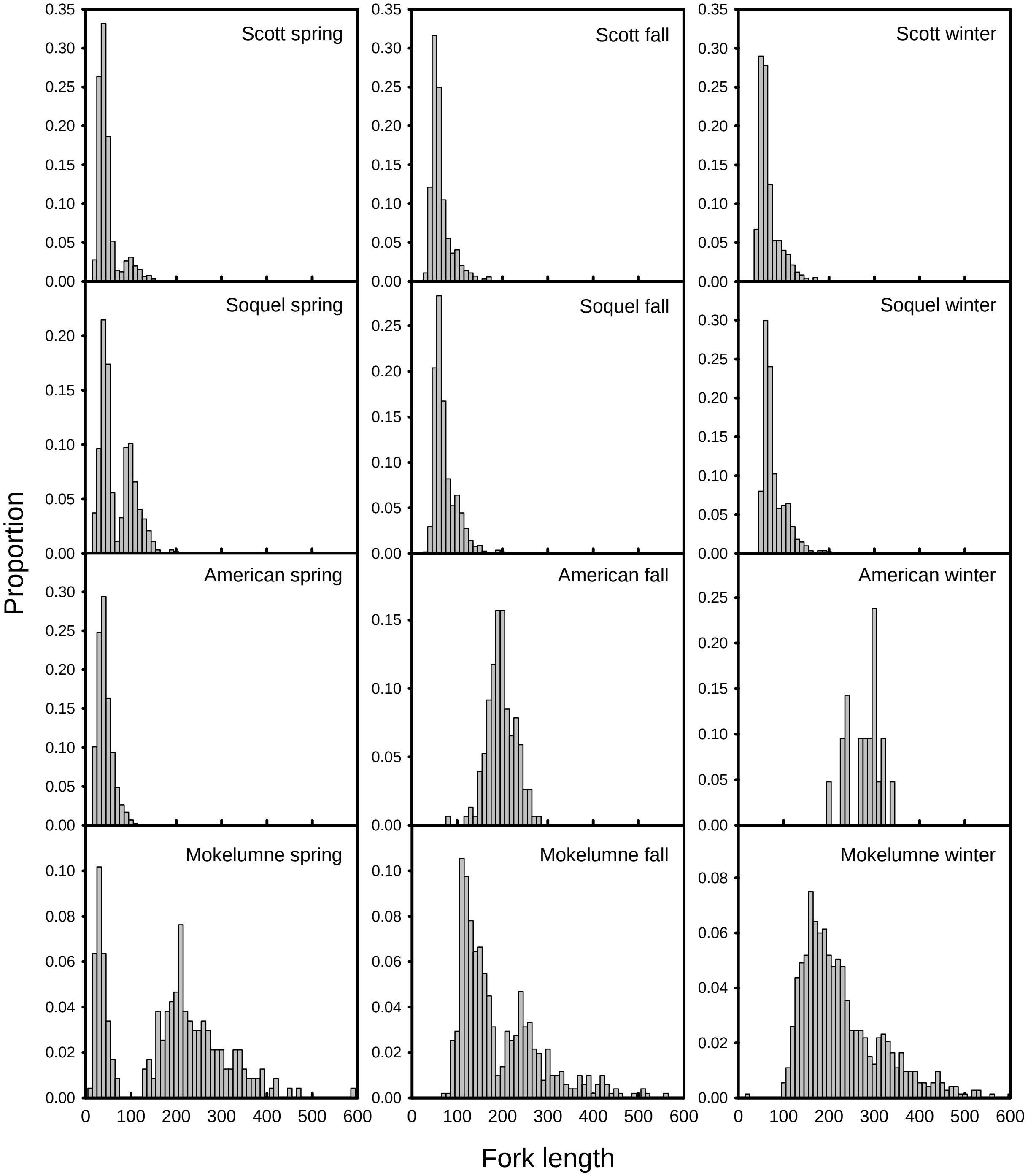

Figure 3. Length-frequency patterns of *Oncorhynchus mykiss* in four California streams during seasons of spring (sampling in May-June), fall (sampling in September-October), and winter (sampling in December-January). Bars indicate proportion of fish in each 10 mm size class.

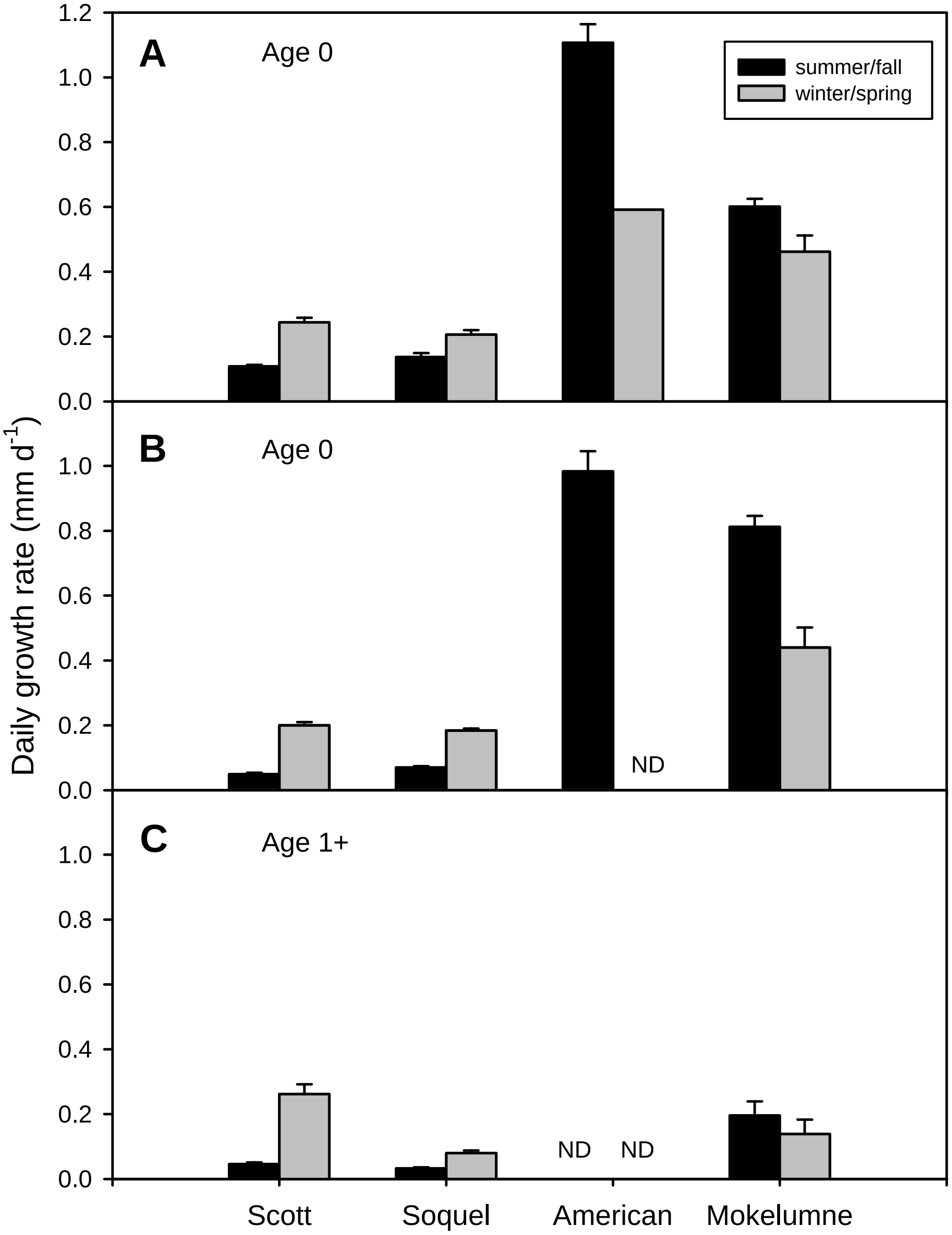

Figure 4. Estimated growth rates (mean + S.E.) of *Oncorhynchus mykiss* for age-0 fish (A and B) and age-1+ fish (C) in four California streams. A) estimates derived indirectly from length-frequency progressions over time. B, C) estimates derived directly from recaptures of PIT-tagged fish. Results were divided into two seasons, summer/fall (May-December) and winter/spring (December-May). ND = no data available.

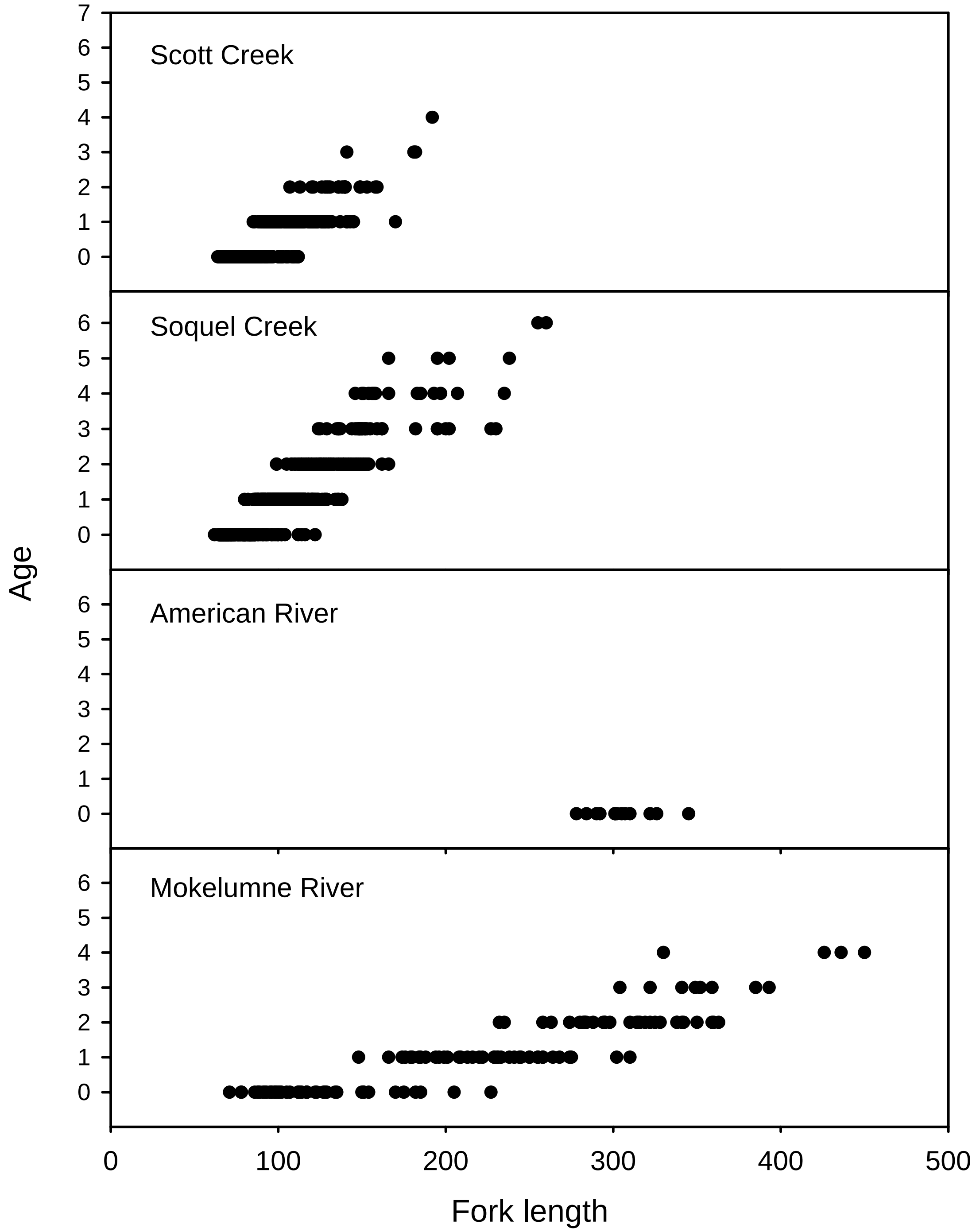

Figure 5. Ages of *Oncorhynchus mykiss* in four California streams based on scale analyses or recaptures of fish initially PIT-tagged at age 0. Fish were assigned to age 1 in March following their birth year.