

This article was downloaded by: [University of California Santa Cruz]

On: 25 May 2012, At: 08:38

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Contrasts in Habitat Characteristics and Life History Patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley

Susan M. Sogard^a, Joseph E. Merz^{b,c}, William H. Satterthwaite^{a,d}, Michael P. Beakes^e, David R. Swank^f, Erin M. Collins^g, Robert G. Titus^g & Marc Mangel^{d,h}

^a National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, California, 95060, USA

^b Cramer Fish Sciences, 13300 New Airport Road, Suite 102, Auburn, California, 95602, USA

^c Institute of Marine Sciences, University of California-Santa Cruz, 1156 High Street, Santa Cruz, California, 95064, USA

^d Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California-Santa Cruz, Santa Cruz, California, 95060, USA

^e Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada

^f National Marine Fisheries Service, 650 Capitol Mall, Suite 8-300, Sacramento, California, 95814, USA

^g California Department of Fish and Game, 8175 Alpine Avenue, Suite F, Sacramento, California, 95826, USA

^h Department of Biology, University of Bergen, Postboks 7803, Bergen, 5020, Norway

Available online: 25 May 2012

To cite this article: Susan M. Sogard, Joseph E. Merz, William H. Satterthwaite, Michael P. Beakes, David R. Swank, Erin M. Collins, Robert G. Titus & Marc Mangel (2012): Contrasts in Habitat Characteristics and Life History Patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley, *Transactions of the American Fisheries Society*, 141:3, 747-760

To link to this article: <http://dx.doi.org/10.1080/00028487.2012.675902>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

ARTICLE

Contrasts in Habitat Characteristics and Life History Patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley

Susan M. Sogard*

National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, California 95060, USA

Joseph E. Merz

Cramer Fish Sciences, 13300 New Airport Road, Suite 102, Auburn, California 95602, USA; and
Institute of Marine Sciences, University of California–Santa Cruz, 1156 High Street, Santa Cruz,
California 95064, USA

William H. Satterthwaite

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of
California–Santa Cruz, Santa Cruz, California 95064, USA; and National Marine Fisheries Service,
110 Shaffer Road, Santa Cruz, California 95060, USA

Michael P. Beakes

Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

David R. Swank

National Marine Fisheries Service, 650 Capitol Mall, Suite 8-300, Sacramento, California 95814, USA

Erin M. Collins and Robert G. Titus

California Department of Fish and Game, 8175 Alpine Avenue, Suite F, Sacramento,
California 95826, USA

Marc Mangel

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics,
University of California–Santa Cruz, Santa Cruz, California 95064, USA; and Department of Biology,
University of Bergen, Postboks 7803, Bergen 5020, Norway

Abstract

Oncorhynchus mykiss exhibit high plasticity in their life history patterns. Individual life history decisions are hypothesized to result from genetic thresholds shaped by local adaptation, with variation in environmental factors influencing the trajectories of growth and condition (e.g., Fulton's K , lipid content). We compared growth rates and life history patterns in two coastal creeks (Scott and Soquel) and two Central Valley (CV) rivers (American and Mokelumne) in California. The two regions differed markedly in habitat and physical factors, including hydrograph timing and amplitude, temperature regime, and food availability (measured as drift). Growth rates of coastal age-0 fish averaged 0.1 mm/d in summer–fall and 0.2 mm/d in winter–spring. Growth rates of CV fish were up to 10 times faster than those of fish on the coast and had the opposite seasonal pattern, in which growth in summer–fall was faster than that in winter–spring. Fish growth also differed between CV rivers; the mean growth rates were 1.0 mm/d in summer–fall and 0.7 mm/d in winter–spring among American River fish and 0.7 mm/d in summer–fall and 0.5 mm/d

*Corresponding author: susan.sogard@noaa.gov
Received May 10, 2011; accepted December 6, 2011

in winter–spring among Mokelumne River fish. The life history expression and age structures of *O. mykiss* in the coastal creeks were similar, with populations being dominated by age-0 fish but including mature residents up to age 6. The two CV populations were strikingly different in life history expression. In the American River, a single cohort was present and nearly all fish emigrated in the spring following their birth year. In the Mokelumne River, a broad diversity of ages (up to 4 years) 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, further demonstrating the adaptability of *O. mykiss* to contrasting rearing environments.

Coastal rainbow trout *Oncorhynchus mykiss irideus*, which includes steelhead, 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 after 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 nonanadromous form, whereas the anadromous form is identified as steelhead. Hereafter, we refer to all forms as *O. mykiss* for brevity. In contrast to other Pacific salmonids, anadromous *O. mykiss* 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 abundance of anadromous *O. mykiss*. 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 *O. mykiss* 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. *Oncorhynchus mykiss* have a particularly broad geographic range, occurring from Baja California, Mexico, throughout the North Pacific Ocean to Kamchatka, Russia, and thus are exposed to a broad suite of environmental conditions. Within California high levels of genetic differentiation in *O. mykiss* among stream systems have been observed along

the coast (Garza et al. 2004) as well as in the Central Valley (Nielsen et al. 2005), suggesting there is an opportunity for local adaptation to occur.

In modeling studies using preliminary estimates of growth rates and size at age, we developed predictions of female *O. mykiss* life history patterns in central coast (Satterthwaite et al. 2009) and Central Valley (Satterthwaite et al. 2010) populations. Models were 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 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 anadromous individuals emigrating at a range of ages. For the Central Valley, we predicted a different composition of life history pathways for the American River versus the Mokelumne River populations, consistent with their different environments. For the American River, we predicted a dominant life history strategy, with emigration at age 1. This strategy prevailed even under a broad range of survival probabilities at different stages, except when very poor ocean survival combined with high river survival led to predicted residency (Satterthwaite et al. 2010). In contrast, for the Mokelumne River, we predicted a mixed strategy, in which the composition of different phenotypes is highly dependent on the survival scenarios used.

We examined *O. mykiss* ecology in four stream systems: two creeks (Scott and Soquel) in the California Central Coast Distinct Population Segment (DPS) and two rivers (American and Mokelumne) in the Central Valley DPS (Figure 1). We focused on the 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, which is 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 *O. mykiss* populations (but see Merz and Vanicek 1996; Merz 2002). McEwan (2001) provides a thorough

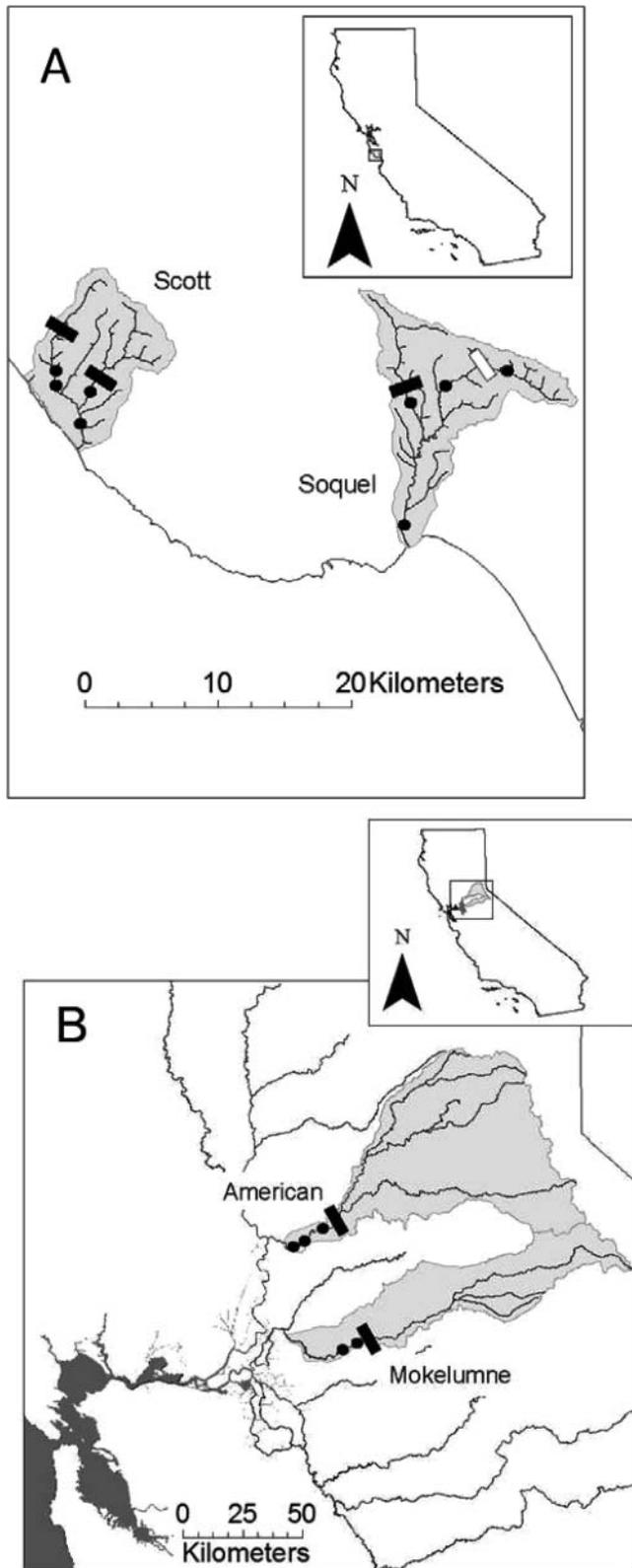


FIGURE 1. Location of sampling watersheds on (A) two coastal creeks (Scott and Soquel) and (B) two Central Valley rivers (American and Mokelumne). Black rectangles are impassable falls on the coastal creeks and impassable dams on the Central Valley rivers, the white rectangle on Soquel Creek is an intermittent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

review of distribution and abundance, potential factors involved in population declines, and management concerns for *O. mykiss* 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. Our overall focus was to understand the mechanisms underlying variability in growth rates and whether the rearing environment predicts consequent life history pathways.

METHODS

Study systems.—Scott and Soquel creeks are undammed, free-flowing streams that arise in the Santa Cruz Mountains and enter the Pacific Ocean over beaches 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 that are dependent on local rainfall patterns. The low diversity of the fish communities is typical of small coastal creeks and is limited to *O. mykiss*, sculpins *Cottus* spp., Pacific lampreys *Lamprologus tridentata*, threespine sticklebacks *Gasterosteus aculeatus*, and Sacramento suckers *Catostomus occidentalis*. Coho salmon *O. kisutch* occurred regularly in Scott Creek until recent years and historically occurred in Soquel Creek. A small conservation hatchery on Scott Creek produces *O. mykiss* 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).

The American and Mokelumne rivers are snow-fed streams that begin high on the west slope of the Sierra Nevada mountain range at elevations over 3,000 m. Impassable dams block anadromous fish access to most of the historic, higher-gradient spawning areas of both rivers. Based on habitat models developed by Lindley et al. (2006), *O. mykiss* are now constrained to approximately 3% and 12% of the historically available habitat on the American and Mokelumne rivers, respectively. Consequently, although the two Central Valley rivers drain much larger watersheds, reach length of available rearing habitat is now comparable with that of the central coast creeks (Table 1). Camanche Dam on the Mokelumne River and Folsom Dam on the American River block coarse sediment delivery from upstream, and historic mining operations have resulted in depleted instream gravel storage, altering downstream riverbed complexity (James 1997; Merz et al. 2006). Stream sections available to *O. mykiss* in both systems are now highly urbanized and sediment starved, and have degraded channels that are oversimplified (James 1997; Pasternack et al. 2004). Regulation of water releases from upstream reservoirs has dramatically altered the ecology of both rivers by dampening the range of both flow and temperature and altering the timing of seasonal patterns in these physical factors as well as 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 nonnative species (Table 1).

Genetic analysis suggests that *O. mykiss* throughout the Central Valley are relatively closely related and that southern

TABLE 1. Habitat characteristics of the four study systems. Data sources include the Recovery Plan for an Evolutionarily Significant Unit of Central California Coast Coho Salmon (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)	5,120	1,624	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

populations within the DPS are similar to northern populations, potentially as 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) 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 varied by less than 1°C. We used temperature data from upstream sites because they included a longer time span than did our downstream sites. For both of the Central Valley rivers, summer water temperatures increased downstream from the dams that delimit the boundary of rearing areas for *O. mykiss*. We used temperatures recorded at a midpoint (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 U.S. Geological Survey (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. We also obtained daily mean flows for these three streams for 2007 and 2008 to illustrate daily variability in flow. Data from

USGS were not available for Scott Creek; thus, we assumed that the monthly flow patterns were similar to those occurring on nearby Soquel Creek.

Biological data.—The contrasting habitats in the two regions (narrow, shallow, low-flow streams on the coast versus broad, deep, high-flow rivers in the Central Valley) required different sampling methods. For the coastal creeks, we conducted multiple-pass depletion electrofishing, matching methods reported in Sogard et al. (2009), in June, October, and December of 2006 and 2007, and June of 2008 at each of four 100-m-long sites in each watershed. For the Central Valley rivers, we used a variety of methods, including seining, boat electrofishing, and hook-and-line sampling, to capture fish at three sites in the American River and two sites in the Mokelumne River, with sampling 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, unpublished data) and on the Mokelumne River (EBMUD, unpublished data). Because these methods were not quantitative, we were not able to estimate population densities for the Central Valley rivers. There was also a potential bias of size-selectivity associated with the different methods. For our estimates of growth we compared size-frequencies of age-0 fish over time, using fish primarily captured by seine, which may have biased our samples toward smaller fish, resulting in underestimates of growth. We also measured growth of marked and recaptured individuals, which should not have been biased by capture method. All hatchery-reared *O. mykiss* in California have their adipose fins clipped before release. We excluded all hatchery fish from analyses; thus, all reported results refer to juveniles derived from in-river spawning (although their parents could have been produced in hatcheries).

We compiled size data across years to examine annual patterns in length frequencies. All size, age, and growth data reported here were based on wild fish captured in freshwater habitats of the four streams, thus including juvenile stages of

individuals that will eventually emigrate to the ocean as well as both juvenile and adult stages of resident individuals. We did not examine emigrating smolts or returning adults.

We tagged all fish >65 mm fork length (FL) with a passive integrated transponder (PIT) tag (Allflex) to allow us to recognize individuals at subsequent recapture. Recaptures at the eight coastal sites were common and provided considerable 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 and Mokelumne rivers, respectively. We computed growth rates as daily increase in FL (mm/d). 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 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 by using ANOVA followed by post hoc Tukey's 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 with 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, and 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 by using the mean lengths of fish during 10-d intervals; i.e., each interval was represented by a single point consisting of the mean length 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 the age of some PIT-tagged

fish based on recaptures in subsequent years. These individuals were first tagged at a size presumed to correspond to the age-0 cohort. We assigned fish to age 1 in March following their birth year.

To provide an index of drifting invertebrates available as prey for juvenile fish, we conducted monthly sampling at each site in each of the four stream systems. Two 1.0-m drift nets, with mouth opening of 0.1 m² and mesh size of 500 μ m, were placed side by side directly into the current and fished for 10–60 min. The nets were positioned at the interface between the tailout of a pool or run and the head of a riffle, corresponding to the preferred feeding locations of stream salmonids described by Fausch (1984). Captured organisms were identified to the nearest order or the lowest practical taxonomic level, measured for length (nearest millimeter), and assigned to a life stage (larva, pupa, or adult) and size-class (Merz and Chan 2005). Dry biomass was determined for each taxon by using the methods of Merz (2002) and summed for each sample. We used these totals to estimate drift rate and drift density. Drift rate was the total biomass (in grams) passing through a 1-m² area per hour, which provided a comparison of feeding opportunities among the four streams without adjustment for flow rates. Drift density was the total biomass (in milligrams) present in a 1-m³ volume of water, which thus allowed for the comparison of the abundance of potential prey after adjusting for differences in flow rate among streams.

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°C cooler in the summer and about 1.3°C warmer in the winter compared with Soquel Creek. The highest temperatures occurred in August, with a daily mean of 15.3°C in Scott Creek and 16.5°C in Soquel Creek, and the coolest temperatures were in January, with means of 7.3°C and 5.6°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°C, whereas in the Mokelumne River, the warmest temperatures were in September, with a mean of 15.2°C. The coolest temperatures were in January on the American River, with a mean of 9.1°C, and in February on the Mokelumne River, with a mean of 10.2°C. Daily maximum temperatures in the summer regularly exceeded 20°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 free-flowing Soquel Creek on the central coast and the regulated rivers of the Central Valley (Figure 2). Soquel Creek received on average 65% of its annual flow during the rainy winter months of January through March, and only 2.3% during the summer from July through September. In contrast, flows in the

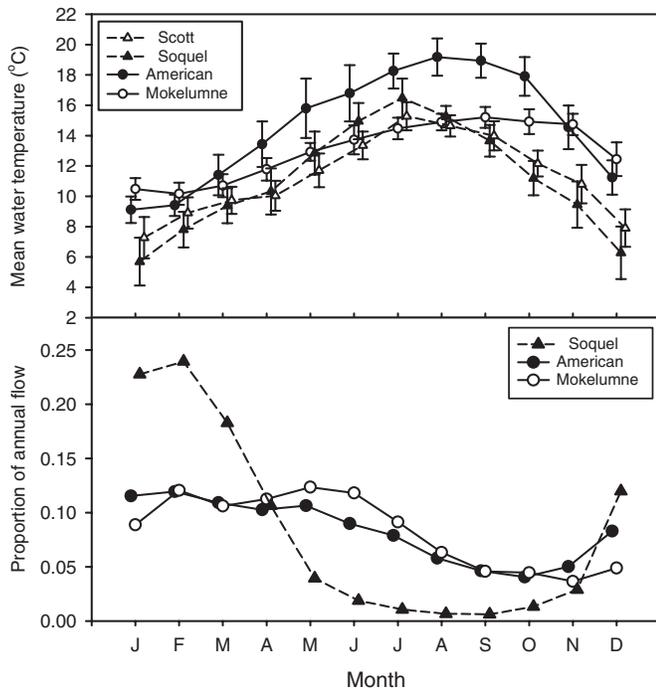


FIGURE 2. Annual cycle of water temperature and flow on the study streams. Temperatures are the monthly means \pm SD over multiple years (Scott Creek and Soquel Creek 2006–2009; American River 2001–2008; Mokelumne River 1997–2004). Flow data are the proportions of annual flow occurring each month, based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

Central Valley rivers were more evenly distributed throughout the year and matched regulated releases from reservoirs above the dams. The American River received on average 34% of its annual flow during the three winter months and 18% during the three summer months. Similarly, the Mokelumne River received on average 31% of its flow during the winter months and 20% during the summer. Daily flow patterns likewise varied between the central coast and Central Valley (Figure 3). Flows on the American and Mokelumne rivers reflected interannual differences in scheduled dam releases. Flows on Soquel Creek, in contrast, demonstrated the expected pattern for central coast streams, in which flashy flows were associated with rainstorms in the winter and minimal flows during the dry season.

Drift Invertebrates

Whether estimated as drift rate (biomass passing through over time, unadjusted for flow rate) or drift density (biomass per volume of water), the availability of invertebrate prey was highly variable within a stream but overall much higher in the Central Valley rivers than in the central coast creeks (Figure 4). Differences among the streams were large in spring and summer months and less apparent in winter months. Within a stream, drift biomass was higher in the winter than in the summer for the coastal creeks and higher in the summer than in the winter for the Central Valley rivers.

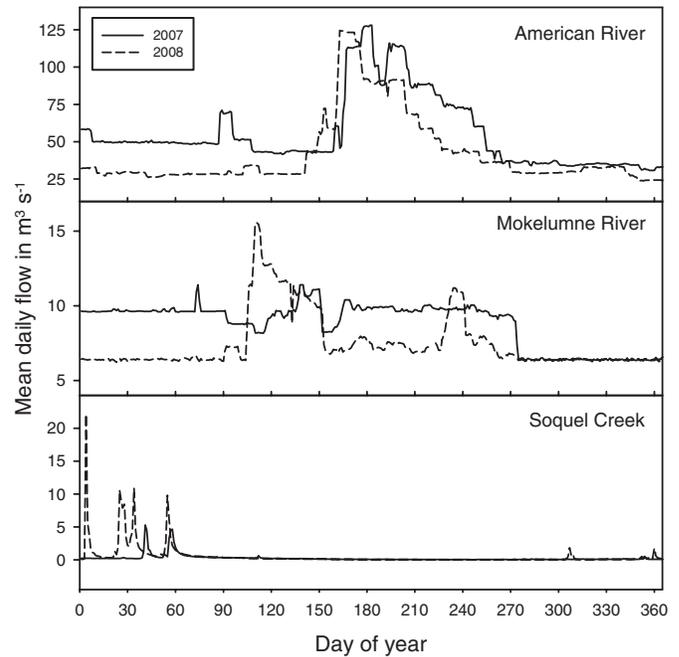


FIGURE 3. Mean daily flows in the American River, Mokelumne River, and Soquel Creek during 2007 and 2008. Note different ranges of values on y-axes.

Size Distributions

We observed striking differences in the size-frequency distribution of *O. mykiss* between the central coast and Central Valley,

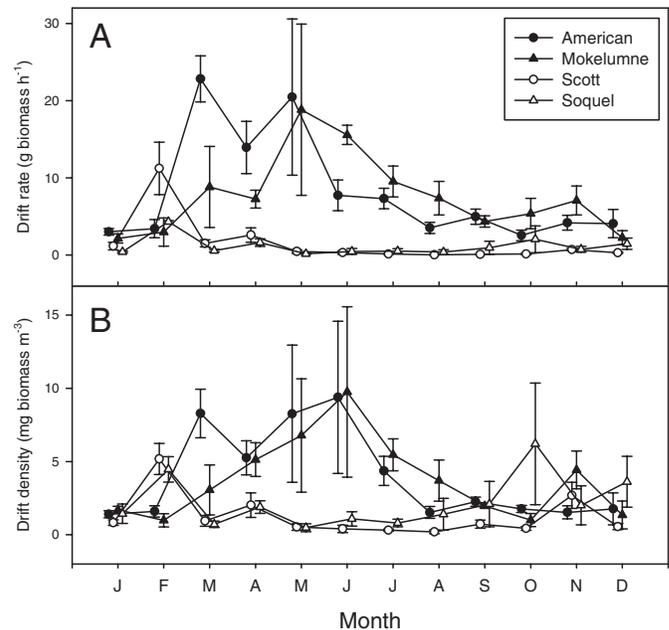


FIGURE 4. Mean \pm SE total biomass of invertebrates (dry weight) captured in drift nets in each stream in each month. Samples from different sites and different years are combined. (A) Drift rate indicates the biomass (in grams) passing through a 1-m² area in 1 h, with no adjustment for differences in flow rates. (B) Drift density indicates the biomass (in milligrams) contained in 1 m³ of water, thus adjusting for differences in flow among streams and months.

as well as between the two rivers within the Central Valley (Figure 5). 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 100–200 mm FL. *Oncorhynchus mykiss* in the American River largely comprised a single year-class, and there was minimal evidence of fish older than age-0. Excluding mature fish returning from the ocean, our data set 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 probably age-1 fish that did not migrate in the spring with the rest of the age-0 cohort. In contrast, older fish were common in the Mokelumne River and a wide range of sizes were present, suggesting there were 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 composed 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 6). Fish in the two coastal streams had similar growth rates, with an average of 0.11 and 0.14 mm/d in summer–fall in Scott Creek and Soquel Creek, respectively. Growth estimates for the Central Valley populations far exceeded those of the coastal populations. In the American River, summer–fall growth rates of *O. mykiss* 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 five times faster than on the coast, with a mean for the 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 and 0.21 mm/d on Scott Creek and Soquel Creek, respectively. In contrast, fish growth in the Central Valley was slower in winter–spring than in summer–fall, with an estimate of 0.61 mm/d for the single year of data for the American River and a mean of 0.46 mm/d for the 11 years of data for 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 6), suggesting that any gear bias associated with our indirect estimates was minimal. On the coast, summer–fall growth of recaptured fish averaged 0.05 mm/d in Scott Creek and 0.07 mm/d in 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 re-

captures in winter–spring, but summer–fall growth rates of age-0 tagged fish averaged 0.98 mm/d. In 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. Analyses of variance comparing age-0 growth in summer–fall indicated significant differences among streams ($F_{3,400} = 754.45$, $P < 0.001$), and the growth of fish in the American River was faster than that in the Mokelumne River, which in turn was faster than for the two coastal sites, which did not differ from each other (post hoc Tukey's tests). Likewise, growth during the winter–spring differed among streams ($F_{2,116} = 29.5$, $P < 0.001$), and growth of Mokelumne River fish was faster than in the two coastal sites, which did not differ from each other (post hoc Tukey's 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 in the American River). On the coast, growth rates of age-1+ fish were similar to those of age-0 fish, and mean rates were 0.05 and 0.03 mm/d on Scott Creek and Soquel Creek, respectively, in summer–fall and 0.26 and 0.08 mm/d on Scott Creek and Soquel Creek, respectively, in winter–spring (Figure 6). In the Mokelumne River, older fish displayed a marked decrease in growth compared with the age-0 cohort, and means were 0.20 mm/d in summer–fall and 0.14 mm/d in winter–spring. Analyses of variance comparing age-1+ growth in summer–fall indicated significant differences among streams ($F_{2,521} = 53.5$, $P < 0.001$), and the growth of Mokelumne River fish was faster than for the two coastal sites, which did not differ from each other (post hoc Tukey's tests). Fish 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's tests).

Age Estimates

Age estimates generally concurred with growth estimates (Figure 7). Ages of *O. mykiss* 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 in 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 of fish ranged from 0 to 4. Some of the large fish captured in the winter (Figure 5) may have been adults returning from the ocean. However, the broad range of sizes and ages for fish captured from spring through fall in 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 in the Mokelumne River compared

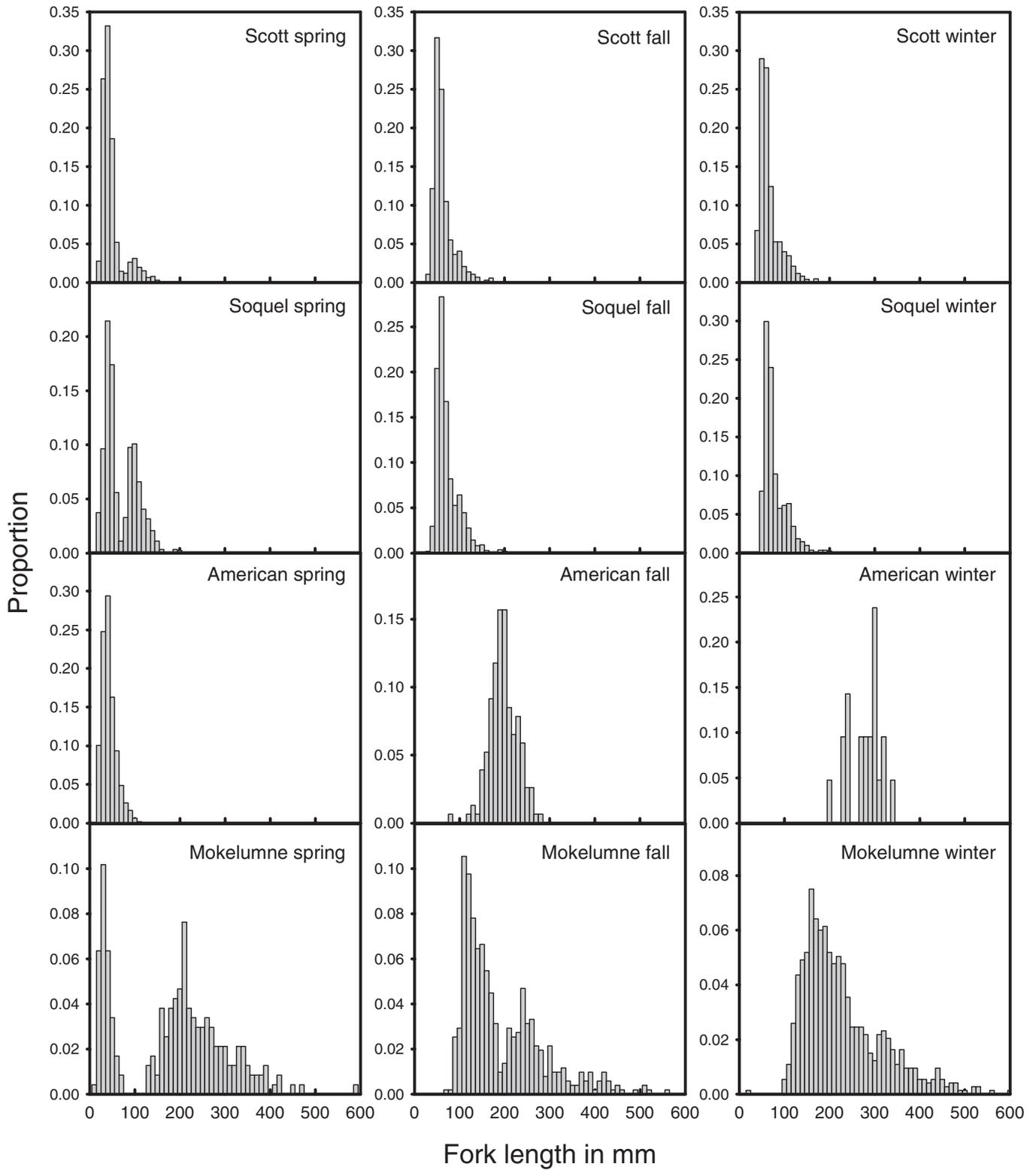


FIGURE 5. Length-frequency patterns of *Oncorhynchus mykiss* in four California streams during seasons of spring (sampling in May–June), fall (sampling in September–October), and winter (sampling in December–January). Bars indicate the proportion of fish in each 10-mm size-class.

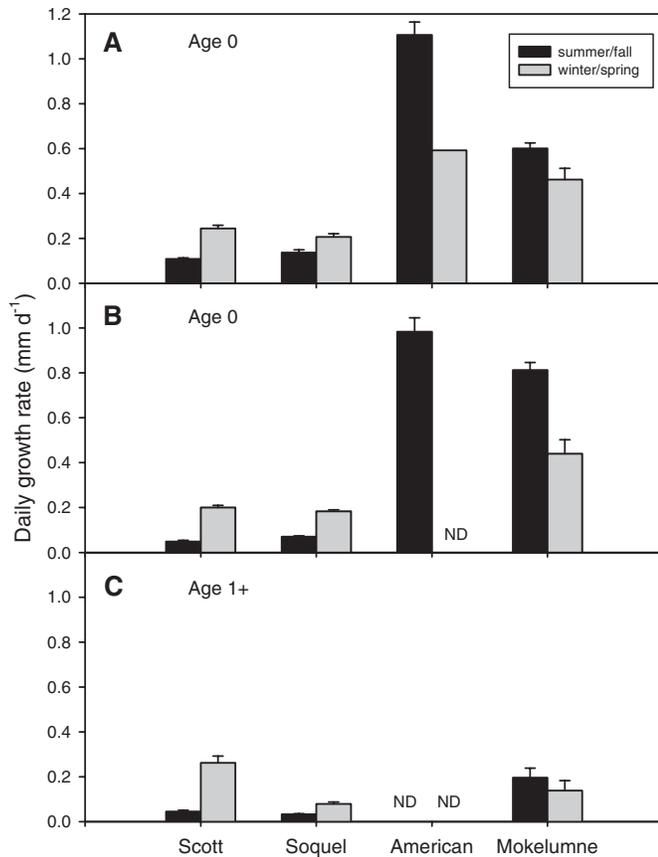


FIGURE 6. Estimated growth rates (mean + SE) of *Oncorhynchus mykiss* for (A, B) age-0 fish and (C) age-1+ fish in four California streams. (A) Estimates are derived indirectly from length-frequency progressions over time, and (B, C) estimates are derived directly from recaptures of PIT-tagged fish. Results were divided into two seasons, summer-fall (May–December) and winter-spring (December–May). ND = no data available.

with those on the coast reflected their much faster growth rates.

DISCUSSION

Juvenile *O. mykiss* 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 owing to the coastal climate. In the Central Valley, 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 when minimal water is released, but only 18°C in a wet year when re-

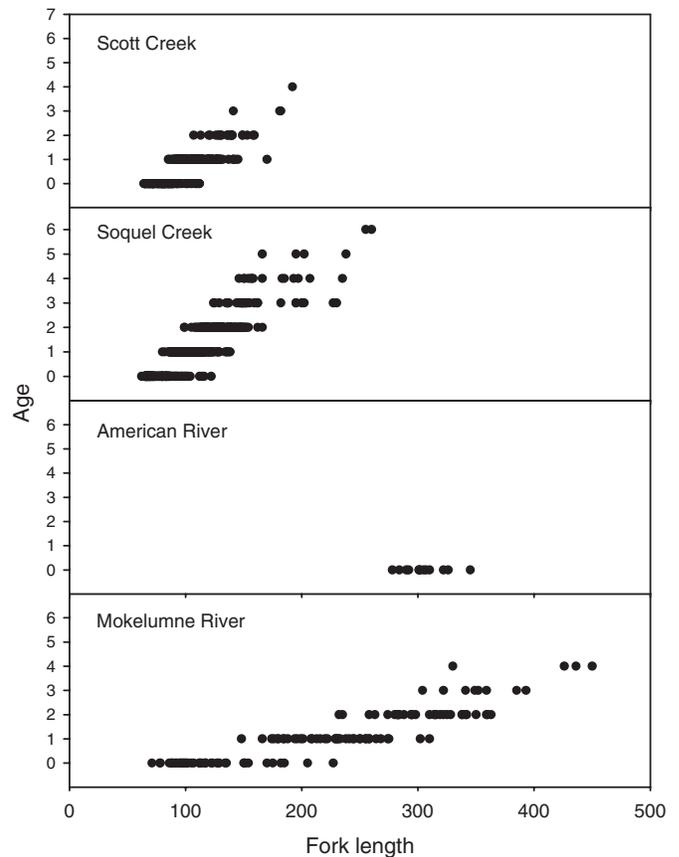


FIGURE 7. Ages of *Oncorhynchus mykiss* in four California streams based on scale analyses or recaptures of fish initially PIT-tagged at age 0. Fish were assigned to age 1 in March following their birth year.

leases are higher (U.S. Department of the Interior 2008). For the Mokelumne River, water released from below the reservoir thermocline results in more moderate summer temperatures than for the American River. Within both Central Valley rivers, summer temperatures increase rapidly downstream from the reservoir owing 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. In 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 reservoir levels as needed for future flood protection. Another potentially important physical difference is the distance from rearing habitats to the ocean. Central coast *O. mykiss* can emigrate directly into the ocean, whereas anadromous *O. mykiss* of the Central Valley have a much longer migration corridor (Table 1).

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 *O. mykiss* 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. dolomieu*) with a high capacity for consumption (Johnson et al. 1992; Tabor et al. 2007). Our estimates of invertebrate prey available in the drift suggest there are much higher biomasses in the Central Valley than on the central coast and that seasonality is opposite in the two regions. Some of these differences reflect the delivery of pelagic prey (e.g., cladocerans) from reservoirs behind the dams. Such prey can comprise a large contribution of the diet of juvenile *O. mykiss* in Central Valley rivers (Merz 2002), but are unavailable in coastal streams.

The combined suite of natural and anthropogenic environmental differences presumably plays a major role in the marked biological contrasts of the populations compared in this study. Growth rate differences are particularly prominent. In the summer–fall, growth of fish on the central coast is slow and 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 *O. mykiss* during the summer (Harvey et al. 2005; Boughton et al. 2007; McCarthy et al. 2009), presumably as 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) but rose to 2.28/d for groups supplemented with additional food (Boughton et al. 2007). Summer growth rates of *O. mykiss* in the Central Valley that were 5 (Mokelumne River) to 10 (American River) times faster than on the coast suggest few constraints on growth, particularly for the American River population.

Growth rates of juvenile *O. mykiss* in Pacific Northwest systems more closely match those of the California central coast creeks, although they have the opposite seasonal pattern of higher growth in summer than in winter. For an Oregon creek, Reisenbichler and McIntyre (1977) observed summer growth rates of 0.04–0.25 mm/d and winter growth rates of 0.01–0.08 mm/d. For another Oregon system, Tattam (2006) found the highest growth rates were in spring, intermediate growth occurred in summer, and lowest growth was in fall and winter. When converted to specific growth in weight, summer rates in the coastal streams in our study averaged 0.3%/d, whereas the Mokelumne River fish averaged 1.5%/d and the American River fish averaged 2.4%/d. Specific growth rates calculated in summer for age-0 fish in British Columbia and Washington streams were generally <0.8%/d (Hume and Parkinson 1988; Tatara et al. 2009). In fall, at the end of the summer growth season in Pacific Northwest streams, age-0 *O. mykiss* attain sizes of 50–90 mm FL and 2–7 g (Reisenbichler and McIntyre 1977; Johnson and Kucera 1985; Hume and Parkinson 1987; Johnston et al. 1990), which are comparable with the sizes we observed for the

coastal streams. Summer growth rates in midwestern and eastern U.S. streams are intermediate to our results for California. In Michigan creeks, Godby et al. (2007) found specific growth rates of 1.0–2.2%/d in summer and 0.2–0.3%/d in winter for landlocked steelhead. Sizes of age-0 fish in fall ranged from 70 to 100 mm FL and 6–12 g (Johnson 1980; Wentworth and LaBar 1984; Seelbach 1993; Godby et al. 2007). In contrast, mean fall sizes of age-0 fish in the Mokelumne and American rivers were 140 mm and 42 g and 210 mm and 115 g, respectively.

Growth of juvenile fish is highly dependent on the interaction between food availability and temperature; higher temperatures can support faster growth if sufficient food is available to fuel increased metabolic rates (Brett et al. 1969; Sogard and Olla 2001). Growth versus temperature relationships typically follow a parabolic pattern that shifts with food availability, although some species exhibit a sharp decline in growth at upper thermal limits (Sogard and Olla 2001). Although reduced summer growth of *O. mykiss* in the coastal streams suggests there is a correlation with warmer temperatures, growth rates in Soquel Creek are even lower in the fall despite more moderate temperatures (Sogard et al. 2009), again pointing to food availability as the limiting factor. The extremely rapid growth rates observed in fish in the American River suggest that warm summer temperatures enhance rather than inhibit growth and food is not limiting. In laboratory experiments with the American River's hatchery strain (Nimbus), growth rates at 19°C were 1.3–1.7 times faster than those at 15°C or 11°C (Myrick and Cech 2005). More moderate summer temperatures on the Mokelumne River may limit growth compared to the American River. We were not able to quantify densities on the two rivers, but lower densities of *O. mykiss* in the American River may also contribute to their rapid growth by reducing competition.

The two regions also differed in the seasonality of growth, and faster fish growth occurred in the winter–spring than in the summer–fall in the coastal creeks and the opposite pattern occurs in the Central Valley rivers, although winter growth rates of age-0 fish in the Central Valley still greatly exceeded those on the coast. On the coast the seasonal difference probably reflects the increased delivery of drift prey as flows increase with winter storms (Figure 4). Benthic prey in the interstices of gravel and attached to rocks were more abundant in summer–fall than in winter–spring for a stream in the south-central California coast DPS (Rundio and Lindley 2008), but growth rates of juvenile *O. mykiss* were higher in winter–spring than in summer–fall (D. E. Rundio, National Marine Fisheries Service, unpublished data), potentially a consequence of increased drift delivery. In the Central Valley, reduced winter growth rates are potentially a function of lower temperatures as well as reduced abundances of drift invertebrates. In undammed Pacific Northwest systems, higher flows occur in the winter rainy season, potentially increasing drift prey abundances, but low temperatures probably inhibit growth.

In addition to the environmental factors underlying foraging opportunity in the different systems, there are potentially

local adaptation effects influencing inherent growth capacity. In common-garden laboratory experiments, growth rates of a central coast *O. mykiss* population (Scott Creek, Monterey Bay Salmon and Trout Project hatchery) were significantly lower 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, and the central coast fish appeared to be risk-averse and the Central Valley fish appeared to be risk-prone, aggressive feeders that rarely used available shelters (Beakes et al. 2010). The unresolved ancestry of the American and Mokelumne river populations makes it difficult to determine whether their faster growth rates compared with central coast populations are solely due to environmental feeding opportunities. It is possible that they reflect selection for rapid growth in a hatchery environment; Johnsson et al. (1993) found that progeny of wild anadromous *O. mykiss* crossed with nonanadromous hatchery fish and held on unlimited rations had growth rates intermediate to the two parental types. It is also possible that wild Central Valley populations have experienced natural selection for faster growing genotypes even in the absence of hatchery influences.

The two regions also differ in size at emigration. *Oncorhynchus mykiss* 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 spend the summer in coastal estuaries, where rapid growth allows them to attain sizes of >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 (Williams 2006; U.S. Department of the Interior 2008). Likewise, emigrating *O. mykiss* smolts captured at salvage facilities generally range from 226 to 250 mm (U.S. Department of the Interior 2008). American River smolts even exceed 300 mm, as evidenced by the size of age-0 fish still present in the river in December.

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 probably 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 owing 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. 2011), and Shapovalov and Taft (1954) report nontrivial returns of fish that emigrated at age 1 despite their presumably low ocean survival. However, Shapovalov and Taft (1954) report a predominance of age-2 and older emigrants for Waddell Creek, California, and Hayes et al. (2011) report fish “smolting” twice in Scott Creek, migrating to the ocean after rearing in the lagoon the previous year. Fish of age 2 and older are also present in

coastal systems, 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 before 1989, when it was dynamited, and is now an intermittent barrier depending on winter flow levels. Here the *O. mykiss* population is composed of a wide range of sizes, and multiple recaptures over several years suggest there is 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 *O. mykiss* population consists of very nearly a single cohort, of which almost all members emigrate 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 with 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 *O. mykiss* in the four systems were largely 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, and slow growth rates largely inhibited emigration before age 2. Fish in this system advance in age-class on March 1 and emigrants leave during the spring. Thus, a fish last seen in the winter at age 1 would be age 2 at the time it emigrates, but we would not see any age-2 fish in the coastal streams until our June sampling event and thus would miss fish that had emigrated at age 2. Examining the winter size-frequencies in Figure 5 along with the size at age in Figure 7, 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, we predict few age-0 fish will initiate smolting in time to emigrate the following spring at age 1, but many age-1 fish will initiate smolting in time to emigrate at age 2. 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. Further exploration of the frequency of age-1 fish emigrating directly to the ocean (as opposed to rearing in the lagoon) would aid in evaluating model performance in predicting smolt ages, and the model might be modified to account explicitly for lagoon rearing. The presence of residents above the intermittent (previously permanent) barrier in Soquel Creek is also consistent with model predictions. From the perspective of the above-falls population, any decrease

in the probability of adult fish returning is effective mortality of anadromous fish, and as Satterthwaite et al. (2009, 2010) note, decreasing emigrant survival is predicted to lead to increased residency.

By contrast, every American River fish sampled in the winter was over 200 mm (Figure 5), 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 that emigrate in the spring just after they become age 1. Finally, from Figure 6 we see that the mean growth rate of Mokelumne River age-0 fish was around 0.4–0.5 mm/d in winter–spring and 0.6–0.8 mm/d 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 adopting an anadromous life history. In addition, individual fish on the Mokelumne River displayed a wide range of growth rates (0.034–1.17 mm/d 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. (2012) demonstrated with acoustically tagged wild 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 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.

An alternative explanation for the near-complete absence of older juveniles in the American River relates to the higher water temperatures in this system. Despite the apparent growth benefits of warmer temperatures for age-0 juveniles (Myrick and Cech 2005; this study), there may be negative aspects that were not addressed in our study, such as disease or reduced thermal tolerance of older juveniles. Myrick and Cech's (2005) study did not include older juveniles, which may have a lower thermal preference. Thus, the emigration of annual cohorts in the spring following their birth year could also be a function of the American River's thermal regime. Spina (2007), however, found that *O. mykiss* residing in southern California streams exhibited behavioral activity suggesting adaptation to temperatures that regularly exceed 20°C. Although fish ages in Spina's (2007) study were not noted, behavioral data recorded for fish from 100 to 280 mm in size suggested fish were mostly older than age-0.

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). Our results suggest major differences both between the Central Valley and Central Coast DPSs and within the Central Valley DPS. The marked contrast in growth and life history attributes of the two Central Valley rivers underscores the difficulty of developing common management goals even at the level of the DPS. The importance of habitat in determining life history expression is further complicated by the genetic ancestry of the local populations and the extent to which they reflect adaptations to the original habitats for transplanted stocks. 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 *O. mykiss* populations. Sensitivity analyses conducted by Satterthwaite et al. (2010), however, suggest that patterns of life history expression of *O. mykiss* in the American and Mokelumne rivers are relatively robust to changes in their respective habitats, and shifts in the probability of mortality along the migration corridor may have the greatest potential for changing these patterns. Our results document striking differences in habitat and growth rates in the freshwater environment of different stream systems. Further information on survival rates of *O. mykiss* throughout the potential geographic range traveled by anadromous individuals is needed to better understand the life history pathways selected by both future smolts and future mature residents.

ACKNOWLEDGMENTS

This material is based upon work supported by the CALFED Science Program under Science Program Project SCI-05–140 to Marc Mangel, Susan Sogard, and Rob Titus under grant agreement U-05-SC-40. National Oceanic and Atmospheric Administration's Center for Stock Assessment Research and Southwest Fisheries Science Center and California Department of Fish and Game provided additional support. Leora Nanus created the maps used in Figure 1. We thank East Bay Municipal Utility District for providing unpublished data from the Mokelumne River. We thank Noah Parker for technical and logistic support, as well as numerous volunteers who assisted with field collections. Sean Hayes provided a review of an early draft of the paper.

REFERENCES

- Beakes, M. P., W. H. Satterthwaite, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. *Transactions of the American Fisheries Society* 139:1263–1275.
- Behnke, R. J. 2002. *Trout and salmon of North America*. Free Press, New York.

- Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2242–2252.
- Boughton, D. A., M. Gibson, R. Yedor, and E. Kelly. 2007. Stream temperature and the potential growth and survival of juvenile *Oncorhynchus mykiss* in a southern California creek. *Freshwater Biology* 52:1353–1364.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2363–2394.
- Davis, N. D., and J. T. Light. 1985. Steelhead age determination techniques. Fisheries Research Institute, Document FRI-UW 8506, University of Washington, Seattle.
- Del Real, C. S., M. Workman, and J. Merz. 2012. Migration characteristics of hatchery and natural-origin *Oncorhynchus mykiss* from the lower Mokelumne River, California. *Environmental Biology of Fishes* 94:363–375.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62:441–451.
- Garza, J. C., L. Gilbert-Horvath, J. Anderson, T. Williams, B. Spence, and H. Fish. 2004. Population structure and history of steelhead trout in California. North Pacific Anadromous Fish Commission, Technical Report 5, Vancouver.
- Garza, J. C., and D. E. Pearse. 2008. Population genetic structure of *Oncorhynchus mykiss* in the California Central Valley. California Department of Fish and Game, Final Report for Contract PO485303, Santa Cruz.
- Godby, N. A., Jr., E. S. Rutherford, and D. M. Mason. 2007. Diet, feeding rate, growth, mortality, and production of juvenile steelhead in a Lake Michigan tributary. *North American Journal of Fisheries Management* 27: 578–592.
- Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2010. Improved viability of populations with diverse life-history portfolios. *Biology Letters* 6:382–386.
- Harvey, B. C., J. L. White, and R. J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* 62:650–658.
- Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. *Transactions of the American Fisheries Society* 137:114–128.
- Hayes, S. A., M. H. Bond, C. V. Hanson, A. W. Jones, A. J. Ammann, J. A. Harding, A. L. Collins, J. Perez, and R. B. MacFarlane. 2011. Down, up, down and “smolting” twice? seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1341–1350.
- Hayes, S. A., M. H. Bond, C. V. Hanson, and R. B. MacFarlane. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? *Journal of Fish Biology* 65:101–121.
- Hume, J. M. B., and E. A. Parkinson. 1987. Effect of stocking density on the survival, growth, and dispersal of steelhead trout fry (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences* 44:271–281.
- Hume, J. M. B., and E. A. Parkinson. 1988. Effects of size at and time of release on the survival and growth of steelhead fry stocked in streams. *North American Journal of Fisheries Management* 8:50–57.
- James, L. A. 1997. Channel incision on the lower American River, California, from streamflow gage records. *Water Resources Research* 33:485–490.
- Johnson, J. H. 1980. Production and growth of subyearling coho salmon, *Oncorhynchus kisutch*, Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York. U.S. National Marine Fisheries Service Fishery Bulletin 78: 549–554.
- Johnson, J. H., and P. A. Kucera. 1985. Summer-autumn habitat utilization of subyearling steelhead trout in tributaries of the Clearwater River, Idaho. *Canadian Journal of Zoology* 63:2283–2290.
- Johnson, J. H., A. A. Nigro, and R. Temple. 1992. Evaluating enhancement of striped bass in the context of potential predation on anadromous salmonids in Coos Bay, Oregon. *North American Journal of Fisheries Management* 12:103–108.
- Johnsson, J. I., W. C. Clarke, and R. E. Withler. 1993. Hybridization with domesticated rainbow trout (*Oncorhynchus mykiss*) reduces seasonal variation in growth of steelhead trout (*O. mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:480–487.
- Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. *Canadian Journal of Fisheries and Aquatic Sciences* 47:862–872.
- Lindley, S. T., R. Schick, A. Agrawal, M. Goslin, T. Pearson, E. Mora, J. Anderson, B. May, S. Greene, C. Hanson, A. Low, D. McEwan, R. MacFarlane, C. Swanson, and J. Williams. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. *San Francisco Estuary and Watershed Science* [online serial] 4(1):article 3.
- Mangel, M. 1994. Life history variation and salmonid conservation. *Conservation Biology* 8:879–880.
- Mangel, M., and W. H. Satterthwaite. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Bulletin of Marine Science* 83:107–130.
- McCarthy, S. G., J. J. Duda, J. M. Emlen, G. R. Hodgson, and D. A. Beauchamp. 2009. Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River watershed, California. *Transactions of the American Fisheries Society* 138:506–521.
- McEwan, D. R. 2001. Central Valley steelhead. California Department of Fish and Game Fish Bulletin 179:1–43.
- Merz, J. E. 2002. Seasonal feeding habits, growth, and movement of steelhead trout in the lower Mokelumne River, California. California Fish and Game 88:95–111.
- Merz, J. E., and L. K. O. Chan. 2005. Effects of gravel augmentation on macroinvertebrate assemblages in a regulated California river. *River Research and Applications* 21:61–74.
- Merz, J. E., G. B. Pasternack, and J. M. Wheaton. 2006. Sediment budget for salmonid spawning habitat rehabilitation in a regulated river. *Geomorphology* 77:207–228.
- Merz, J. E., and C. D. Vanicek. 1996. Comparative feeding habits of juvenile Chinook salmon, steelhead, and Sacramento squawfish in the lower American River, California. California Fish and Game 82:149–159.
- Myrick, C. A., and J. J. Cech Jr. 2005. Effects of temperature on the growth, food consumption, and thermal tolerance of age-0 Nimbus-strain steelhead. *North American Journal of Aquaculture* 67:324–330.
- Nielsen, J. L., S. A. Pavey, T. Wiacek, and I. Williams. 2005. Genetics of Central Valley *O. mykiss* populations: drainage and watershed scale analyses. *San Francisco Estuary and Watershed Science* [online serial] 3(2): article 3.
- Pasternack, G. B., C. L. Wang, and J. E. Merz. 2004. Application of a 2D hydrodynamic model to design of reach-scale spawning gravel replenishment on the Mokelumne River, California. *River Research and Applications* 20:205–225.
- Piche, J., J. A. Hutchings, and W. Blanchard. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. *Proceedings of the Royal Society of London B* 275: 1571–1575.
- Reisenbichler, R. R., and J. D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 34:123–128.
- Rikardsen, A. H., J. E. Thorpe, and J. B. Dempson. 2004. Modelling the life-history variation of Arctic charr. *Ecology of Freshwater Fish* 13:305–311.
- Rundio, D. E., and S. T. Lindley. 2008. Seasonal patterns of terrestrial and aquatic prey abundance and use by *Oncorhynchus mykiss* in a California coastal basin with a Mediterranean climate. *Transactions of the American Fisheries Society* 137:467–480.
- Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2009. Steelhead life history on

- California's central coast: insights from a state-dependent model. *Transactions of the American Fisheries Society* 138:532–548.
- Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. *Evolutionary Applications* 3:221–243.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature (London)* 465:609–613.
- Seelbach, P. W. 1993. Population biology of steelhead in a stable-flow, low-gradient tributary of Lake Michigan. *Transactions of the American Fisheries Society* 122:179–198.
- Shapovalov, L., and A. Taft. 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. *California Department of Fish and Game Fish Bulletin* 98:1–373.
- Sogard, S. M., and B. L. Olla. 2001. Growth and behavioral responses to elevated temperatures by juvenile sablefish *Anoplopoma fimbria* and the interactive role of food availability. *Marine Ecology Progress Series* 217: 121–134.
- Sogard, S. M., T. H. Williams, and H. Fish. 2009. Seasonal patterns of abundance, growth, and site fidelity of juvenile steelhead in a small coastal California stream. *Transactions of the American Fisheries Society* 138: 549–563.
- Spina, A. P. 2007. Thermal ecology of juvenile steelhead in a warm-water environment. *Environmental Biology of Fishes* 80:23–34.
- Tabor, R. A., B. A. Footen, K. L. Fresh, M. T. Celedonia, F. Mejia, D. L. Low, and L. Park. 2007. Smallmouth bass and largemouth bass predation on juvenile Chinook salmon and other salmonids in the Lake Washington basin. *North American Journal of Fisheries Management* 27:1174–1188.
- Tatara, C. P., S. C. Riley, and J. A. Scheurer. 2009. Growth, survival, and habitat use of naturally reared and hatchery steelhead fry in streams: effects of an enriched hatchery rearing environment. *Transactions of the American Fisheries Society* 138:441–457.
- Tattam, I. A. 2006. Seasonal life history of *Oncorhynchus mykiss* in the South Fork John Day River basin, Oregon. Master's thesis. Oregon State University, Corvallis.
- Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* 12:581–599.
- U.S. Department of the Interior. 2008. Biological assessment on the continued long-term operations of the Central Valley project and the state water project. Bureau of Reclamation, Mid-Pacific Region, Sacramento, California.
- Via, S., R. Gomulkiewicz, G. De Jong, S. M. Scheiner, C. D. Schlichting, and P. H. Van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution* 10:212–217.
- Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1853–1858.
- Wentworth, R. S., and G. W. LaBar. 1984. First-year survival and growth of steelhead stocked as fry in Lewis Creek, Vermont. *North American Journal of Fisheries Management* 4:103–110.
- Williams, J. G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. *San Francisco Estuary and Watershed Science* [online serial] 4(3):article 2.