

## Steelhead Growth in a Small Central California Watershed: Upstream and Estuarine Rearing Patterns

SEAN A. HAYES,\* MORGAN H. BOND, CHAD V. HANSON, AND ELLEN V. FREUND

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,  
Fisheries Ecology Division, Southwest Fisheries Science Center,  
110 Shaffer Road, Santa Cruz, California 95060, USA

JERRY. J. SMITH

Department of Biological Sciences, San Jose State University,  
1 Washington Square, San Jose, California 95192, USA

ERIC C. ANDERSON, ARNOLD J. AMMANN, AND R. BRUCE MACFARLANE

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,  
Fisheries Ecology Division, Southwest Fisheries Science Center,  
110 Shaffer Road, Santa Cruz, California 95060, USA

**Abstract.**—We monitored growth and life history pathways of juvenile steelhead *Oncorhynchus mykiss* and compared growth rates between the upper watershed and estuary in Scott Creek, a typical California coastal stream. Growth in the upper watershed was approximately linear from May to December for age-0 fish. For passive integrated transponder (PIT) tagged, age-1+ fish, growth transitioned to a cyclic pattern, peaking at 0.2% per day during February–April, when maximum flows and temperatures of 7–12°C occurred. Growth of PIT-tagged fish then slowed during August–September (0.01% per day), when temperatures were 14–18°C and flows were low. During each spring, smolts (mean fork length [FL] ± SE = 98.0 ± 1.2 mm) and fry migrated to the estuary; some fish remained there during summer–fall as low flows and waves resulted in seasonal sandbar formation, which created a warm lagoon and restricted access to the ocean. Growth in the estuary–lagoon was much higher (0.2–0.8% per day at 15–24°C). Our data suggest the existence of three juvenile life history pathways: upper-watershed rearing, estuary–lagoon rearing, and combined upper-watershed and estuary–lagoon rearing. We present a model based upon the above data that reports size at age for each juvenile life history type. The majority of fish reaching typical steelhead ocean entry sizes (~150–250 mm FL; age 0.8–3.0) were estuary–lagoon reared, which indicates a disproportionate contribution of this habitat type to survival of Scott Creek steelhead. In contrast, steelhead from higher latitudes rear in tributaries during summer, taking several years to attain ocean entry size.

Growth rates, associated environmental influences, and subsequent effects on life history decisions have been extensively studied in Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* in both the laboratory and the field by means of classical periodic sampling and more recently passive integrated transponder (PIT) tag recaptures (e.g., Elliott 1975; Thorpe 1977; Jones and Hutchings 2001; Jones et al. 2002; Arnekleiv et al. 2006; ). Comparatively little data exist for Pacific salmonids in the field, and most work is limited to studies of coho salmon *Oncorhynchus kisutch* (Parker and Larkin 1959; Breuser 1961; Chapman 1962; Bustard and Narver 1975; Fransen et al. 1993; Peterson et al. 1994; Bilby et al. 1996). Because Pacific salmon populations exist across broad

latitudinal ranges (reviewed in Quinn 2005), it is likely that juvenile growth and life histories vary in response to environmental differences and may have subsequent effects on marine survival and ultimately adult returns. Variation in juvenile growth and life history among populations of steelhead *O. mykiss* is typically evaluated in terms of size and age at ocean entry, measured either directly from smolts or more often estimated from analyses of scales from returning adults (Busby et al. 1996). It is suspected that the amount of time required to reach the size threshold for marine survival depends upon the length of the summer growing season and may take several years in northern latitudes (Withler 1966; Narver 1969; Narver and Andersen 1974; Busby et al. 1996). However, only limited data exist on year-round growth or habitat use for juvenile steelhead across their range, 34–60°N (Hartman 1965).

Environmental conditions may affect seasonal patterns of growth in ways that are not understood,

\* Corresponding author: sean.hayes@noaa.gov

Received February 26, 2007; accepted July 29, 2007  
Published online January 8, 2008

possibly having both positive and negative effects in the southern part of the steelhead range where many populations are listed under the Endangered Species Act as endangered or threatened (NMFS 2006). Steelhead growth rate varies across temperature and probably among populations, but optimal growth is thought to occur between 15°C and 19°C and lethal temperatures are between 27.5°C and 29.6°C for one southern population (Wurtsbaugh and Davis 1977b; Railsback and Rose 1999; Myrick and Cech 2005). While little is known about steelhead growth in the wild, the longer growing season associated with mild climates at the southern portion of their range may enable the fish to reach smolt stage within a shorter period of time (Withler 1966; Busby et al. 1996). Connolly and Peterson (2003) proposed that overwintering survival might be especially tenuous for larger age-0 steelhead in warmer climates due to the “challenges” of the winter climate—specifically, elevated metabolic rate and limited food. Alternatively, winter conditions may be superior, potentially providing better growing conditions than those in northern-latitude streams due to mild temperatures and better food production. The real challenges faced by southern populations may be associated with summer, when warm temperatures may increase metabolic rates while extremely low flows result in reduced aquatic invertebrate production and terrestrial insect drift in upper watersheds. In fact, growth conditions for some southern populations have been reported as poor during summer and fall, causing scale annulus formation in September (Shapovalov and Taft 1954; Railsback and Rose 1999).

While estuarine use has been studied within the central and northern portions of Pacific salmonid ranges (e.g., Healey 1982; Levings et al. 1986; Tschaplinski 1987; Miller and Sadro 2003; Bottom et al. 2005), limited research exists on the use of coastal estuaries by southern salmonids and the associated effects on growth. Many coastal California streams have estuaries that lose surface connectivity with the ocean during the summer months, forming lagoons (Shapovalov and Taft 1954; Schwarz and Orme 2005). Temperatures in these estuaries and lagoons can range from 15°C to 24°C or more during summer months. Juvenile steelhead are known to use these estuaries, but the effects of estuarine rearing on steelhead growth and survival have been reported only rarely in peer-reviewed literature (e.g., Smith 1990; Cannata 1998).

In this study, we report growth rates of juvenile steelhead from emergence to ocean entry in a typical small stream along the central California coast and we provide a comparative analysis of upstream and estuarine rearing by similarly aged fish. From these

results, we describe the associated habitat use patterns and construct growth models for the various life history paths followed by fish before reaching the ocean. Finally, we address how the southern environmental conditions affect steelhead growth and compare our results with the limited growth data available from the remainder of the species' range.

### Study Area

Scott Creek is a small, 70-km<sup>2</sup> coastal watershed located 100 km south of San Francisco in central California. Anadromous fish can access approximately 23 km of stream between the estuary and natural upstream barriers of the main stem and the three main tributaries, Little, Big, and Mill creeks (Figure 1). The upper portion of the watershed consists of high-gradient stream dominated by a thick canopy of coastal redwoods *Sequoia sempervirens*. The main stem below the major tributary confluences tends to be characterized by a low gradient, a lower density overstory cover primarily produced by alders *Alnus* spp., and an understory dominated by willows *Salix* spp. A small estuary at the bottom of the watershed can become a freshwater lagoon during summer and fall when a sandbar builds up at the creek mouth, isolating the stream from the ocean. During the last two decades, natural and anthropogenic influences often interfered with lagoon formation (e.g., artificial breaching, water diversions, and drought; J.J.S., unpublished data). Stream width varies from approximately 40 m in the estuary when closed to about 10 m on the main stem, to less than 1 m in the upper tributaries. While the lagoon area and depth varied during the course of this study, measurements made in November 2003 at a typical size indicated an approximate surface area of 18,435 m<sup>2</sup>, mean depth of 0.72 m, and a maximum depth of 2.1 m.

### Methods

*Environmental measurements.*—Flows were measured on a cross section of the main stem downstream of major tributaries with a portable flowmeter (Marsh-McBirney, Inc., Frederick, Maryland; Model 2000 Flo-Mate). It was not possible to enter the stream at high-flow events (>~8 m<sup>3</sup>/s), and flows were estimated from cross-sectional area measurements of peak flow and approximated velocity measurements after flow subsided. Water temperatures were measured on an hourly basis upstream and at the estuary (Figure 1); we initially used IB-Cod temperature loggers (Alpha Mach, Mont St. Hilaire, Quebec; May 2002–June 2003) at both sites and then switched to Onset Tidbits (Onset Computer Corp., Pocasset, Massachusetts) in the upper watershed and YSI 600 XLM data loggers

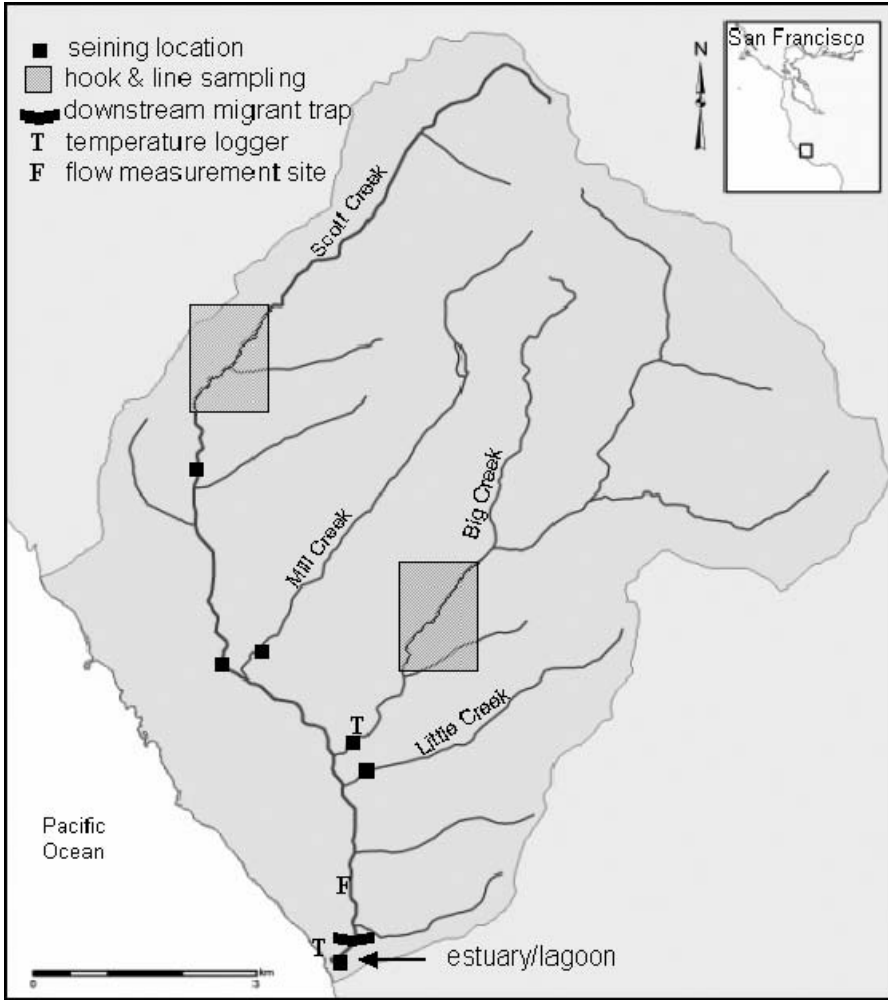


FIGURE 1.—Map of the Scott Creek watershed, California, showing locations where juvenile steelhead were sampled for a study of growth and rearing patterns.

(YSI, Inc., Yellow Springs, Ohio) in the estuary (July 2003–January 2005).

*Fish sampling.*—Sampling involved multiple methods and age-classes and was conducted in the upper watershed and estuary during May 2002 through

November 2006. Specific time frames and methods are summarized in Table 1. Fish were sampled monthly at multiple locations throughout the upper watershed in pools with a 3.0 × 1.5-m beach seine (0.32-cm square mesh) and by hook and line (Figure 1). Downstream-

TABLE 1.—Summary of sampling effort used to determine growth and life history patterns in Scott Creek, California, juvenile steelhead, by age-class, location, tag type applied, collection method, and date range.

Age	Location	Tag type	Collection method	Date range
0	Upper watershed		Seine	May 2002–Dec 2004
0	Upper watershed	Elastomer	Seine	Jun 2003–Dec 2003
1+	Upper watershed	PIT	Seine, hook and line	May 2003–Oct 2004
All	Upper watershed		Electrofisher	Oct 2002–2004
All	Estuary	PIT	Seine	May 2003–Nov 2006
1+	Head of estuary	PIT	Hoop net (smolt trap)	Jan 2003–Nov 2005

migrating fish were trapped at the head of the estuary by means of a two-chambered hoop net (0.635-cm square mesh) with wings extending to each bank. The trap was operated 3 d/week throughout the year except during exceptionally high flows associated with winter storms. Fish in the estuary (downstream of the migrant trap) were captured with a  $30 \times 2$ -m beach seine (wings: 0.950-cm square mesh; bag: 0.635-cm square mesh).

Fish were handled according to the methods of Hayes et al. (2004). Specific details for this study are as follows. Up to 20 age-0 fish were randomly sampled for fork length (FL) and mass measurements at each seining site in the upper watershed. To determine whether (1) age-0 fish were remaining at the sample sites and (2) our assessments of age-0 growth by repeated sampling of untagged fish was accurate, we injected 200 age-0 steelhead (between 25 and 65 mm FL) with an elastomer dye (Northwest Marine Technology, Shaw Island, Washington) that was color coded to indicate 5-mm-FL bins. Elastomer injections took place during the second week of June 2003. All fish collected in the upper watershed that exceeded 65 mm FL received a PIT tag (Allflex, Boulder, Colorado; FDX-B Glass Transponder, 11.5 mm) injected intraperitoneally with a 12-gauge needle and were scanned for previously implanted PIT tags. Scale samples were taken from every PIT-tagged fish just posterior and ventral to the dorsal fin on the left side. The PIT tags were also implanted in fish caught at the downstream migrant trap and in the estuary. All collected fish were scanned for previously implanted PIT tags. A subset of untagged fish was sampled and tagged during each collection effort. All recaptured tagged fish were measured for FL and mass, and additional scale samples were taken from the right side of the fish.

In addition to our sampling efforts, relative abundance of juvenile fish was assessed each fall by one of us (J.J.S., unpublished data). Briefly, 12–14 reaches were blocked off and sampled with two passes of a backpack electrofisher (Smith-Root, Inc., Vancouver, Washington; Type 7, smooth pulse) to estimate the number of steelhead and coho salmon per unit length of stream.

*Scale analysis.*—Scales were flattened between two microscope slides and digitally photographed. Scale images were then analyzed using OPTIMAS software (Media Cybernetics, Silver Springs, Maryland) to measure scale radius, number and location of annuli, and number and distance between circuli. Where age information is reported in the text, a “+” sign is used to indicate all year-classes equal to or greater than the number given (e.g., age 1+).

*Growth rate.*—Fork lengths of age-0 fish (newly hatched fry to parr stage) were measured repeatedly at five upstream locations on a monthly basis. Growth rates were calculated by determining the temporal change in mean FL. Specific growth rate (SGR) could not be calculated for this size-class, since the calculation is most accurately done with repeated measures on known individuals and age-0 fish were too small to mark with unique identifiers such as PIT tags. During the late summer and fall months, fast-growing age-0 fish began to overlap in size with some age-1 fish. Scale analysis was used to distinguish between individuals in their first and second year. The general linear models (GLM) procedure in SYSTAT version 11 was used to test for significant differences in growth rate among different cohorts of age-0 steelhead and between elastomer-tagged and untagged age-0 steelhead. Hereafter, all means are reported with SEs.

For fish greater than 65 mm FL, SGR in mass and FL was calculated (Busacker et al. 1990) based upon the measured changes in mass and FL of recaptured – PIT-tagged individuals. Growth rate was then applied to the date intermediate between capture events. Only recaptures obtained 7–120 d after the previous capture were used in the analysis. Fish sampled in the upstream habitat were analyzed separately from those in the estuary. Growth rates between habitats and seasons were tested using analysis of variance (ANOVA) in SYSTAT 11. Only one recapture event per individual was used, and all recaptures between upstream and estuarine habitats were excluded.

Estuarine population size was estimated each year (2002–2005) with PIT tags and the Petersen mark–recapture method. After sandbar closure, we tagged a subset of the fish caught in the newly formed lagoon. Seining surveys were repeated each month until winter rains made seining of the estuary impossible. Population size and variance for each month after the initial survey was estimated using equations 3.5 and 3.6, respectively, from Ricker (1975).

It was not possible to quantify mortality due to handling and predation between seining efforts, and we assumed mortality of tagged and untagged fish was equal. In years when multiple samplings were done, estimates were pooled and mean values were used. Mark–recapture methods were not used to estimate population size before sandbar closure because of the possibility of individuals entering the ocean and leaving the population during that time. In addition, the rate of downstream migration drops rapidly after June and we assumed addition of new migrants to be negligible (Hayes et al. 2004). There may have been some movement from the estuary back upstream, which would result in an overestimation of the

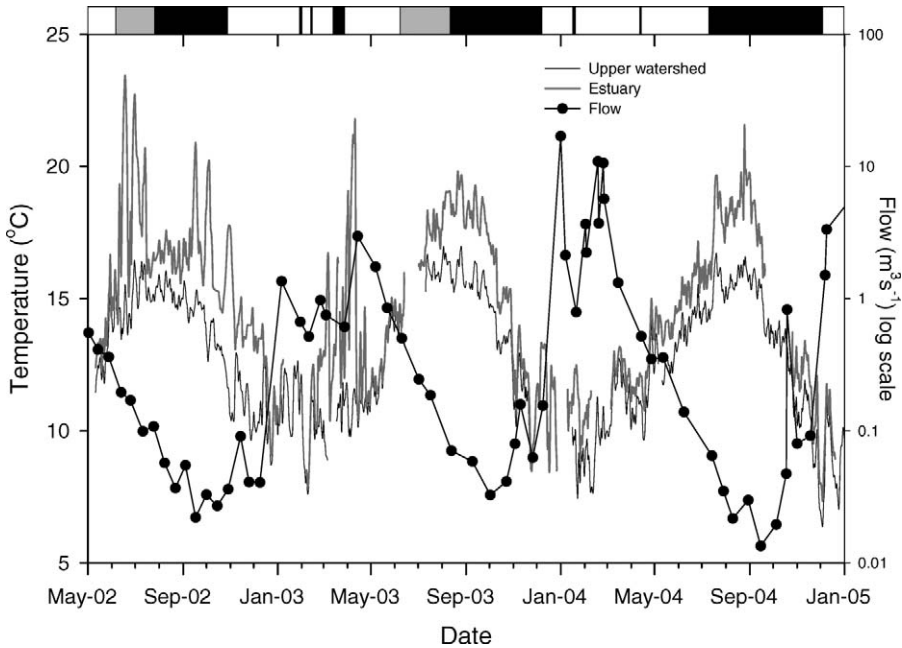


FIGURE 2.—Mean daily water temperature at upper and estuarine sites in the Scott Creek watershed, California (primary y-axis), and biweekly flow in the lower main stem (secondary y-axis) from May 2002 to January 2005. Shading in top bar represents estuarine status (white = open; gray = partially closed by sandbar; black = closed).

population, but this was assumed to be consistent across years.

Growth rate data were used to construct growth trajectories for various juvenile life history pathways. Initial age-0 growth rates were drawn from FL regressions developed from the results of upper-watershed growth. Confidence intervals (90% CIs) of the regressions were used to represent upper and lower growth curves. On this growth trajectory, age-0 fish were large enough to be PIT-tagged by the end of year 1. The SGR data from PIT tag recaptures were used to represent upstream growth (after December 31 of year 1) and estuarine growth. To obtain a daily estimate of growth, all intervals between successive recapture events greater than 7 d and less than 120 d from a given habitat were pooled, regardless of the number of recaptures per individual. Each interval spanning a particular day was interpreted as a growth rate observation on that day. Each day was spanned by a variable number of growth rate intervals (upstream mean = 15.7 d; estuarine mean = 34.1 d). We used a nonparametric smoother (Friedman 1984) to infer the central tendency of growth rate as a function of time. A 90% CI around this growth rate function was obtained by bootstrapping. Each bootstrap replicate was obtained by sampling with replacement from the pool of observed recapture intervals; the bootstrap intervals

were converted as above to daily observations and a new growth-rate curve was estimated with the Friedman smoother for each bootstrap replicate. Two-hundred bootstrap replicates were made. For each day, the lower (upper) endpoint of the 90% CI for growth rate was the smoothed value for the 10th smallest (largest) of the 200 bootstrap-estimated growth rates. Bootstrapping and smoothing were done using the software package R (Ihaka and Gentleman 1996). Growth trajectories were completed by adding each day's growth to the sum of all previous days' growth. To portray these trajectories graphically, a base trajectory representing 4 years of growth in the upper watershed was plotted, and estuarine growth trajectories diverging from the upper-watershed line each summer were used to represent growth potentials of fish that migrated to the estuary.

**Results**

*Environmental Data*

Streamflow along the main stem varied by more than three orders of magnitude, from 0.013 m<sup>3</sup>/s to over 17 m<sup>3</sup>/s (Figure 2). Daily mean temperatures for the study period ranged from 5.6°C to 19°C in the upper watershed, and the overall mean was 10.3 ± 1.4°C. Daily mean temperatures in the estuary ranged from 7.4°C to 23.5°C and averaged 15.3 ± 3.1°C (Figure 2).

TABLE 2.—Growth rate estimates ( $\pm$ SE) for age-0 steelhead in Scott Creek, California, and multiple comparison test results for differences among years.

Year	Intercept Jan 1 (mm)	Growth rate (mm/d) <sup>a</sup>	R <sup>2</sup>	n	Mean FL (mm) <sup>b</sup>	Date range
2002	20.73 $\pm$ 1.39	0.112 $\pm$ 0.006	0.203	1,370	46.12 $\pm$ 0.31	Jun–Nov 2002
2003	16.51 $\pm$ 1.63	0.139 $\pm$ 0.007	0.303	795	46.38 $\pm$ 0.45	Jun–Nov 2003
2004	22.32 $\pm$ 2.16	0.129 $\pm$ 0.010	0.280	471	50.72 $\pm$ 0.61	Jun–Nov 2004
Combined years	20.54 $\pm$ 0.72	0.119 $\pm$ 0.003	0.313	3,024	46.23 $\pm$ 0.23	Mar–Dec

<sup>a</sup> Multiple comparison tests: 2002 vs. 2003,  $P = 0.004$ ; 2002 vs. 2004,  $P = 0.101$ ; 2003 vs. 2004,  $P = 0.417$ .

<sup>b</sup> Multiple comparison tests: 2002 vs. 2003,  $P = 0.878$ ; 2002 vs. 2004,  $P = 0.001$ ; 2003 vs. 2004,  $P = 0.001$ .

During this study, a warm, relatively deep lagoon typically formed during summer (partially closed and closed; see Figure 2) when a sandbar formed at the mouth of the stream. However, the timing of formation varied from year to year. Except for occasional large wave events that pushed salt water over the sandbar and created haline stratification in deeper basins, the lagoon was primarily freshwater during summer and fall months.

*Upstream Growth: Age-0 Fish*

Newly emerged fry were observed between March and June of each year. We compared differences in growth rates for age-0 steelhead sampled at the upstream survey sites during June through November 2002–2004 (data were not consistently collected for all

3 years before June or after November; Table 2; Figure 3). Growth rates were approximately linear during the first 10 months of growth. Growth rates differed among the 3 years (heterogeneity of slopes test:  $F = 4.288$ ,  $P = 0.014$ ). A comparison of mean FLs revealed significant differences among years ( $F = 26.309$ ,  $P < 0.001$ ) as did comparisons using the Tukey post hoc analysis (Table 2). Mean growth rate per year was potentially influenced by several variables, including flow, temperature, age-0 coho salmon density, and age-0 steelhead density for each year (Table 3). Because only 3 years of data were available, no correlation analyses were performed and only raw data are presented.

We compared growth rates between untagged and elastomer-tagged individuals present at the same sites during June through November 2003. No significant

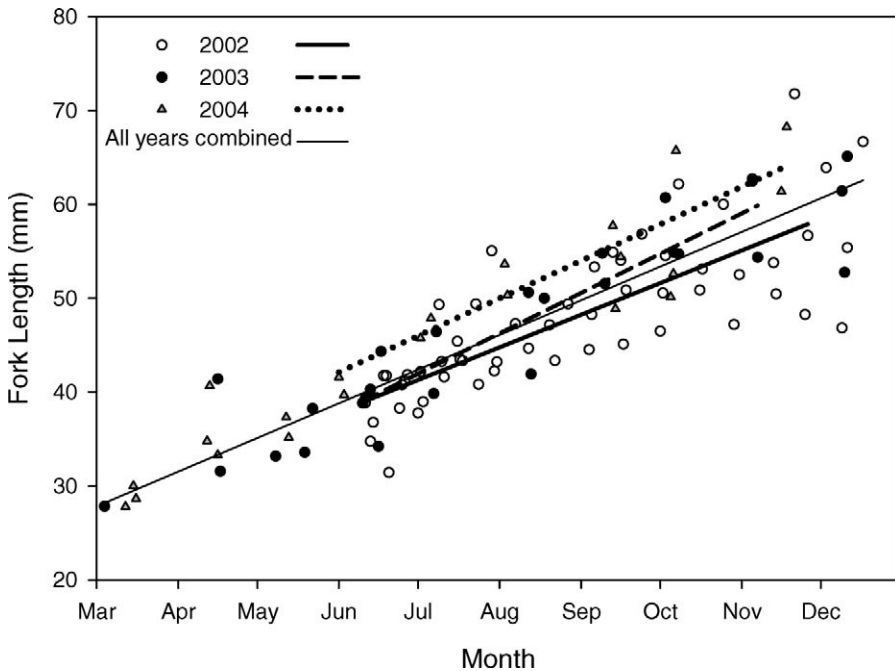


FIGURE 3.—Age-0 steelhead fork length (FL) over time in the upper Scott Creek watershed, California, 2002–2004. Symbols represent mean FL ( $n \approx 20$  fish) at each of five age-0 sample sites. Linear regressions were calculated from raw data (not means) and are described in Table 2.

TABLE 3.—Age-0 steelhead growth rates relative to means of several biotic and abiotic variables measured in Scott Creek, California. Fish density is given as number of age-0 fish per 30.5 m.

Year	Growth rate (mm/d)	FL (mm)	Mass (g)	Water temperature (°C) (Jun–Nov)	Flow (m <sup>3</sup> /s)	Coho salmon density	Steelhead density
2002	0.112	46.2	1.34	13.80	0.074	79.2	35
2003	0.139	46.4	1.63	14.44	0.132	1.5	55
2004	0.129	50.8	1.79	13.70	0.089	8.6	37

differences in growth rate between tagged and untagged fish were detected (heterogeneity of slopes test:  $F = 0.953, P = 0.329$ ). The elastomer tagging of fish in June 2003 confirmed that many individuals remained at their original tagging sites and that growth measurements were at least partially based upon repeated captures of the same individuals.

*Upstream Growth: Age-1 and Older Fish*

We deployed 611 PIT tags in the upper watershed. We recaptured 114 fish at least once and several individuals were recaptured multiple times, yielding a total of 196 recaptures in the upper watershed between May 2003 and November 2004. The mean time

interval between recapture events used in seasonal analysis was  $55.3 \pm 2.7$  d ( $n = 106$ ). At initial capture, mean FL was  $104.3 \pm 2.8$  mm ( $n = 106$ ) and mean mass was  $15.6 \pm 1.2$  g ( $n = 103$ ). With the onset of winter rains, mean individual growth rates increased, peaking at around 0.160% per day in April and then declining to less than 0.014% per day by August. Growth remained slow in the upper watershed until November. To compare growth rates for different times of year, data were binned into seasonal categories (fall = August–October; winter = November–January; spring = February–April; summer = May–July). Growth rates differed significantly among seasons for FL ( $F = 12.5, df = 4, n = 106, P < 0.001$ ) and mass ( $F = 8.4, df = 4, n = 99, P < 0.001$ ; Figure 4). Significance values for Tukey post hoc analysis of seasonal SGR differences in FL and mass are presented in Table 4.

*Estuarine Growth*

We deployed 1,498 PIT tags in fish caught while seining the estuary or in the smolt trap at the head of the estuary between February 2003 and December 2004. Of these, 378 fish were recaptured at least once and some individuals were recaptured up to five times over the course of a year, resulting in a total of 994 recaptures in the estuary between May 2003 and December 2004 (mean recapture interval =  $41.7 \pm 1.6$  d,  $n = 311$ ). Mean FL at initial capture was  $126.23 \pm 2.0$  mm ( $n = 311$ ). Mean mass at initial capture was  $28.4 \pm 1.6$  g ( $n = 306$ ). To compare growth rates for different times of year, data were binned into the same seasonal categories defined above. Specific growth rates differed significantly among seasons for both FL ( $F = 27.1, df = 6, n = 311, P < 0.001$ ; Figure 4) and mass ( $F = 23.2, df = 6, n = 311, P < 0.001$ ). Results of Tukey post hoc analysis of seasonal SGR differences in FL and mass are presented in Table 5.

Mean SGRs (FL) in the estuary for summer and fall 2003 ( $n = 147$ ), 2004 ( $n = 104$ ), 2005 ( $n = 87$ ), and 2006 ( $n = 47$ ) were calculated and plotted against the number of fish in the estuary after the time of closure (Figure 5). This was accomplished by the PIT tagging of additional fish ( $n = 1,205$ ) between January and November of 2005 and 2006. The difference in

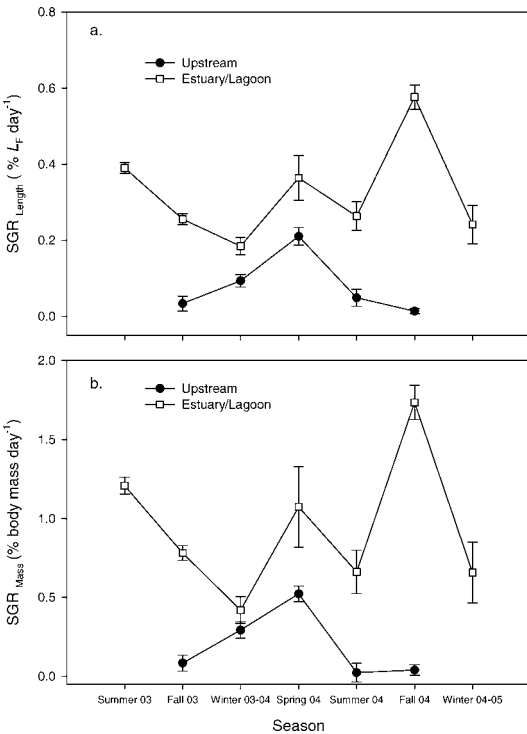


FIGURE 4.—Mean ( $\pm$ SE) specific growth rates (SGRs) of PIT-tagged steelhead recaptured in upper and estuary–lagoon habitats of the Scott Creek watershed, California, 2003–2005: (a)  $SGR_{FL}$  and (b)  $SGR_{mass}$ .

TABLE 4.—Results of Tukey post hoc analysis testing for significant differences in juvenile steelhead growth between seasons in upstream habitat within Scott Creek, California. Bold type indicates *P*-values less than 0.05.

Season and year	Winter 2003–2004	Spring 2004	Summer 2004	Fall 2004
<b>FL (mm)</b>				
Fall 2003	0.178	< <b>0.001</b>	0.955	0.823
Winter 2003–2004		<b>0.012</b>	0.502	<b>0.018</b>
Spring 2004			< <b>0.001</b>	< <b>0.001</b>
Summer 2004				0.399
<b>Mass (g)</b>				
Fall 2003	0.115	<b>0.001</b>	0.905	0.944
Winter 2003–2004		0.295	<b>0.022</b>	<b>0.017</b>
Spring 2004			< <b>0.001</b>	< <b>0.001</b>
Summer 2004				0.999

estuarine growth rate among years is at least partially explained by differences in steelhead population size among years; there was a negative relationship between estuarine population size and growth ( $R^2 = 0.9895$ ,  $P = 0.005$ ), as described by the equation:

$$SGR_{FL} = -0.0002(\text{population size}) + 0.8389. \quad (1)$$

Mean FL of smolts in the lagoon during the last fall sampling event was compared for 2003–2006 to determine whether length at the end of the summer–fall growing season varied between years. A significant difference was observed ( $F = 29.3$ ,  $df = 3$ ,  $n = 526$ ,  $P < 0.001$ ). However, Tukey post hoc analysis revealed that this effect was driven by 2003, which was the only year that differed; fish were significantly longer during that year than in the other 3 years ( $P < 0.001$  for each comparison with 2003; Figure 5).

*Comparisons of Estuarine versus Upstream Growth*

Fish grew much faster in the estuary than upstream (Table 6; Figure 4). Coho salmon were typically absent from the estuary and were present in very low densities

during the time upstream steelhead growth measurements were made with PIT tag recaptures. Summer temperatures in the upstream habitat were 14–18°C, while estuary–lagoon temperatures were warmer (from 15°C to  $\geq 24^\circ\text{C}$ ).

Condition factor ( $\text{mass}/[\text{length}^3]$ ) varied primarily as a function of season ( $F = 14.26$ ,  $df = 6$ ,  $n = 1,204$ ,  $P < 0.001$ ) and did not vary significantly between the two habitats ( $F = 0.001$ ,  $df = 1$ ,  $n = 1,204$ ,  $P = 0.971$ ). In general, the lowest condition factors in both habitats were observed in the spring and were presumably associated with smoltification (Hoar 1976).

*Timing of Life History Decisions and Growth Trajectories*

Most of the fish in this watershed migrate during the spring after their first or second winter, as shown in Figure 6, which provides the size frequency distribution of downstream migrants during spring 2004. Based on scale analysis ( $n = 185$ ), fish under 120 mm FL were less than 2 years old. Once fish have begun the downstream migration, the tendency to

TABLE 5.—Results of Tukey post hoc analysis testing for significant differences in juvenile steelhead growth between seasons in the Scott Creek estuary, California. Bold type indicates *P*-values less than 0.05.

	Fall 2003	Winter 2003–2004	Spring 2004	Summer 2004	Fall 2004	Winter 2004–2005
<b>FL (mm)</b>						
Summer 2003	< <b>0.001</b>	< <b>0.001</b>	0.999	<b>0.012</b>	< <b>0.001</b>	<b>0.039</b>
Fall 2003		0.583	0.557	1.000	< <b>0.001</b>	1.000
Winter 2003–2004			0.081	0.598	< <b>0.001</b>	0.949
Spring 2004				0.703	<b>0.007</b>	0.609
Summer 2004					< <b>0.001</b>	1.000
Fall 2004						< <b>0.001</b>
<b>Mass (g)</b>						
Summer 2003	<b>0.002</b>	< <b>0.001</b>	0.995	<b>0.001</b>	< <b>0.001</b>	<b>0.024</b>
Fall 2003		0.137	0.818	0.981	< <b>0.001</b>	0.993
Winter 2003–2004			0.059	0.743	< <b>0.001</b>	0.885
Spring 2004				0.538	<b>0.028</b>	0.645
Summer 2004					< <b>0.001</b>	1.000
Fall 2004						< <b>0.001</b>



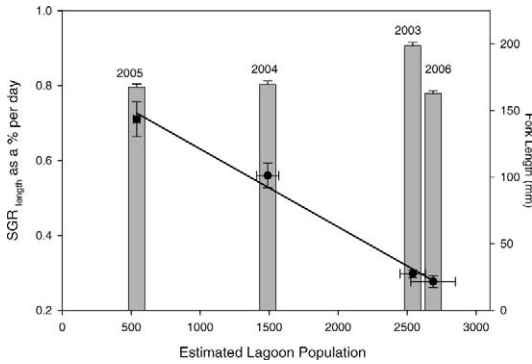


FIGURE 5.—Estimated annual lagoon population sizes and mean growth rates from 2003 to 2006 (left y-axis) The bar graph (right y-axis) represents mean fork length of fish sampled in the estuary in late fall of each year just before winter storm season and lagoon opening. Years match points within labeled columns. All data are means  $\pm$  SE,  $R^2 = 0.99$ ; regression  $P = 0.005$ .

remain in the estuary or go to sea appears to be influenced by the timing of lagoon formation, which typically occurs sometime between May and August (Figure 2). In years when the lagoon forms later, juvenile steelhead densities are much lower, as many of the age-1+ downstream migrants appear to have left the watershed. Recruitment of age-0 steelhead to the estuary after the smolt run ends presumably occurs in response to reduced competition and predation from older fish in the lagoon or may simply be due to higher flows in wetter years, which contribute to delayed lagoon formation. These differences in density and age of recruitment to the estuary were observed during this study. The lagoon formed early (June) and recruitment was high (~2,540 fish) in 2003, whereas the lagoon formed later (July) and recruitment was much lower

TABLE 6.—Results of two-way ANOVA of the effect of habitat type (estuary and upstream) and season (fall 2003, winter 2003–2004, and spring–fall 2004) on juvenile steelhead specific growth rates (SGR) in Scott Creek, California (SS = sum of squares; MS = mean squares).

Factor	df	SS	MS	F	P
<b>SGRFL</b>					
Habitat	1	3.031	3.031	106.336	<0.001
Season	4	1.465	0.366	12.848	<0.001
Habitat $\times$ season	4	2.382	0.595	20.892	<0.001
Error	303	8.637	0.029		
<b>SGRmass</b>					
Habitat	1	24.392	24.392	72.095	<0.001
Season	4	16.368	4.092	12.095	<0.001
Habitat $\times$ season	4	22.587	5.647	16.691	<0.001
Error	296	100.144	0.338		

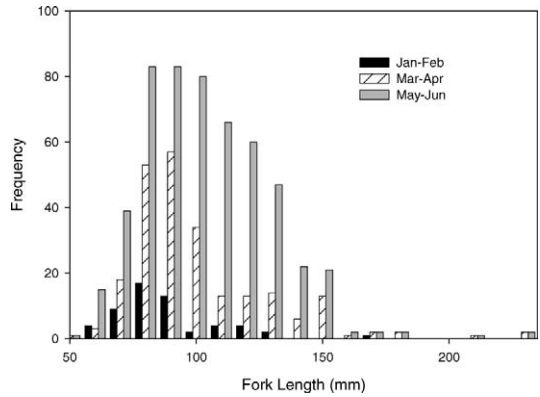


FIGURE 6.—Fork length frequency distribution (10-mm bins) for downstream-migrating steelhead in Scott Creek, California, during spring 2004. Data are grouped by 2-month intervals.

(~1,489 fish) in 2004. In addition, estuarine fish were significantly older ( $t = 2.23$ ,  $P < 0.002$ ,  $n = 28$ ) and larger ( $t = 2.04$ ,  $P < 0.001$ ,  $n = 124$ ) at the time of recruitment in 2003 (mean age = 1.52 years; mean FL = 152 mm) than in 2004 (mean age = 0.57 years; mean FL = 93 mm), confirming the large proportion of age-0 fish in 2004. This trend continued into 2005 (Figure 5), when the lagoon formed even later (August 26) and recruitment was limited to about 540 fish. In 2006, lagoon formation began in early June and followed a pattern similar to that in 2003. It is unlikely that recruitment to the lagoon was strongly influenced by total number of smolts. Although good estimates of smolt abundance among years were not available due to varying trap efficiency, the age-0 steelhead densities from the electrofishing surveys in the previous fall (Table 3) showed no relationship with lagoon population size observed during the subsequent summer.

In this watershed, juvenile steelhead exhibit three life history pathways before ocean entry. The first pathway is direct recruitment to the estuary after spending only a few months in the upper watershed (Figure 7, pathway A). The second pathway is to spend 1–2 years rearing in the upper watershed, migrate downstream to the estuary, and remain there for an additional 1–10 months before ocean entry (Figure 7, pathway B). The third is to spend one or more years rearing in the upper watershed, migrate downstream, and enter the ocean (Figure 7, pathway C). Alternatively, fish exhibiting pathway C might never migrate and instead will carry out their life cycle in freshwater as residents. Based upon the growth rate data from this study, it is possible to model fish demonstrating different life history pathways and compare those with observations of the population at a given time. After

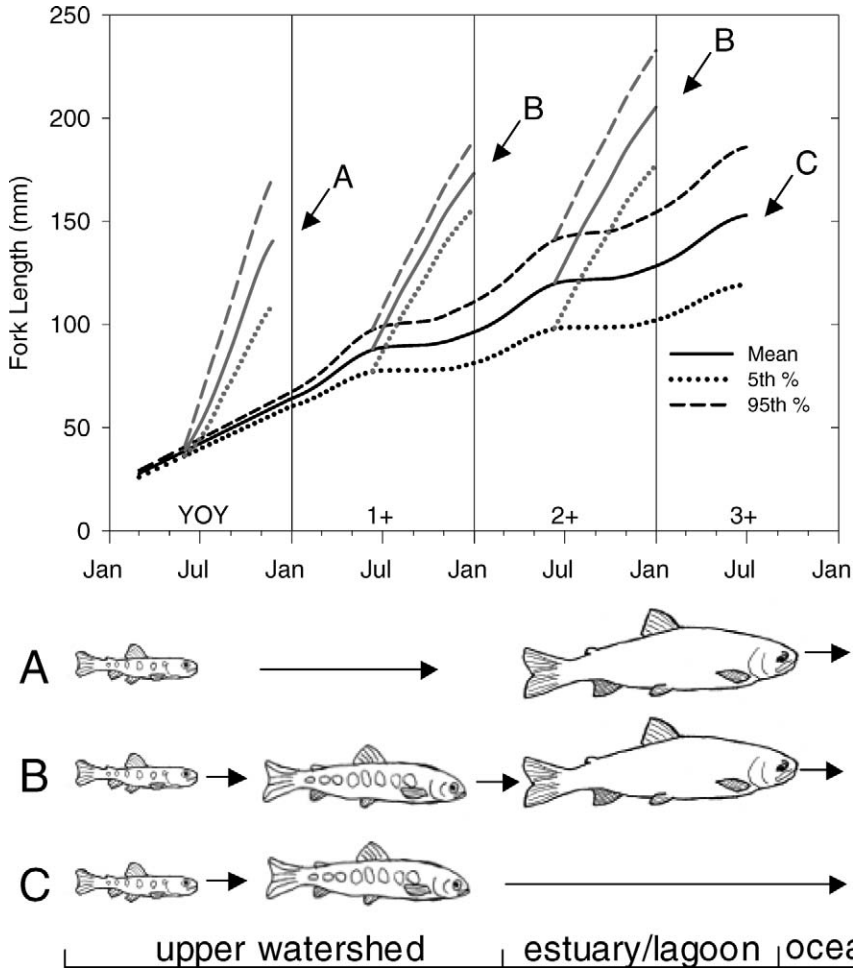


FIGURE 7.—Upper panel: growth trajectories of juvenile steelhead in the Scott Creek watershed, California, showing observed changes in FL determined from resampling of age-0 fish during the first 8–10 months and larger PIT-tagged individuals (ages 1–3 and older) that were recaptured in the upper watershed (black lines) or estuary (gray lines). All PIT tag recaptures were pooled within each habitat and were bootstrap sampled to determine central tendencies. Lower panel: the three freshwater life history pathways corresponding to A–C in the upper panel are illustrated (from left to right, size-classes are fry–age-0, parr, and estuary–lagoon residents). The question mark at the end of pathway C indicates the possibility that fish remain as residents in the creek.

hatching in the spring (Table 2), steelhead fry could migrate to the estuary during the summer (pathway A) and switch to an estuarine growth trajectory based on low densities (using data from summer 2004) or they could remain in the upper watershed, where growth is slower (see Table 2), and would reach 65 mm by the end of their first year. As fish entered their first winter, our measurements of growth transitioned from population means to measurements of known individuals (identified by PIT tags). Data collected from fish that were PIT-tagged in the upper watershed can approximate the size of fish during the subsequent May (the peak of the spring downstream migration). At this

point, fish either spend another year in the upper watershed or begin their spring downstream migration. The predicted size range after 1–2 years of upstream growth (Figure 7) corresponds well with the observed downstream migrant sizes at ages 1 and 2 in this population (mean FL =  $96.8 \pm 1.1$  mm,  $n = 641$ ; Figure 6). After downstream migration, fish remaining in the estuary would probably follow a growth trajectory similar to that observed in the summer of 2003, when the lagoon began forming in June. While timing of lagoon formation tends to influence recruitment and growth rate, as the two are inversely related, the end result is that fish are of similar size by late fall

(Figure 5). Some larger downstream migrants may also depart the estuary before lagoon formation with only 1–2 months of additional growth.

### Discussion

In this study, we reported growth rates of wild, free-ranging juvenile steelhead from the time of emergence to ocean entry in both upstream and estuarine habitats in a small stream along the central California coast. Growth rates were heavily influenced by local habitat and seasonal climate patterns. Specifically, growth in the upper watershed was limited and somewhat out of seasonal phase (mild winter, dry summer) with what would be expected from populations at higher latitudes or elevations, where fish exhibit slow growth during harsh winter periods (Chapman and Bjornn 1969; Wurtsbaugh and Davis 1977b). Estuarine growth, which has not been reported for steelhead previously, was much higher overall than growth in the upper watershed. Finally, growth patterns and movement suggest that steelhead pursue one of three life history pathways while rearing in various combinations of upper watershed and estuarine habitats. From the data collected, we were able to construct a growth model showing size at age for each freshwater life history pathway observed.

Growth of age-0 fish was measured over 3 years and varied significantly. While 3 years was insufficient to compare mean annual trends, several potential influences were apparent. For instance, age-0 steelhead growth was negatively associated with juvenile coho salmon density, which varied dramatically among years in this watershed due to the near extirpation of two year-classes (Hayes et al. 2004). This result was not surprising (Fraser 1969; Hearn 1987), and the reverse effect (i.e., steelhead density affecting coho salmon growth) has also been observed in other populations (Harvey and Nakamoto 1996). In addition, age-0 growth was positively associated with mean annual flow and mean summer–fall temperature in the upper watershed.

Growth of age-1+ fish in the upper watershed was slowest during the summer and fall, and in some cases individual fish actually decreased in FL. Age-0 steelhead densities were typically an order of magnitude higher than those of all older age-classes combined (J.J.S., unpublished data). Also, the majority of surviving fish migrated downstream after their first winter (Figure 6). In combination, these results indicate that the upstream watersheds are not very productive, presumably because of the low-flow environment and a low nutrient input under redwood canopies (Romero et al. 2005). This pattern of accelerated growth in the winter and spring (0.3–0.6% per day) and limited

growth in the summer (0–0.2% per day) has been reported for foothill streams of the Sierra Nevada Mountains (Railsback and Rose 1999; Merz 2002) and other coastal California streams (Harvey et al. 2005), where growth rates were only 10–20% of potential maxima of 2.5–3.0% per day (Wurtsbaugh and Davis 1977b; Myrick and Cech 2005). These patterns are confounded by the fact that growth was slowest when temperatures were near the thermal optimum. While not quantified in this study, low summer flows in the upper tributaries may contribute to reduced wetted surface area for aquatic invertebrate production and terrestrial invertebrate drift, resulting in less food during a time when warmer temperatures are increasing metabolic rates of fish. Limited growth data exist across the latitudinal range of *Oncorhynchus* spp.; however, similar growth patterns were observed for coho salmon in coastal streams in Oregon and Washington (Breuser 1961; Bilby et al. 1996).

In comparison with upstream growth, growth rates in the estuary were much higher, which is probably due in part to the warmer summer and fall temperatures and differences in food availability as was reported for Atlantic salmon (Cunjak 1992). In Scott Creek, coho salmon did not use the estuary, presumably due to thermal preferences or tolerances (Stein et al. 1972); however, temperatures were at the thermal optimum for steelhead (17–19°C; Wurtsbaugh and Davis 1977b; Myrick and Cech 2005). Competition with coho salmon was probably not a major influence on differences in age-1+ steelhead growth between upstream and estuarine habitats, since the steelhead were larger than coho salmon fry and growth upstream was measured during a period of low coho salmon density. The estuary seemed to be a very productive habitat, particularly when in a lagoon state. Seining efforts were often difficult due to the large volumes of freshwater algae growing there and marine algae that were deposited by waves. Large numbers of invertebrates (amphipods *Eogammarus* spp. and *Corophium* spp.; shrimp *Neomysis* spp.; and isopods *Gnorimosphaeroma* spp.) were regularly observed in association with the algae. While comprising less than 5% of the total stream area, the estuary may be the most important habitat for steelhead growth in this watershed.

Estuarine growth rates were among the fastest reported for wild steelhead in the literature (1–2% per day), but did not reach the maximum (2.5–3.0% per day) observed in captivity for this species (Wurtsbaugh and Davis 1977b; Myrick and Cech 2005). Growth rates in the estuary varied among years and appeared to be density dependent: fish grew much faster in the estuary during years when recruitment was lower.

Recruitment was related to the timing of lagoon formation, when water began backing up behind a sandbar on the beach, forming a warm deep environment. Among years, the timing of sandbar formation varied by several months. The earlier the lagoon formed, the greater the population size. Although the growth rate was lower in these years, the longer growing season appeared to compensate for this, and fish were the same size or larger by the end of the season (Figure 5). In addition, short-term recruitment periods on the order of weeks to a couple of months have been observed in Scott Creek and other coastal California watersheds, wherein steelhead take advantage of a brief growth period and enter the ocean before sandbar formation (Smith 1990; Bond 2006).

A secondary issue explaining differences in estuarine growth rates among years relates to the age of fish recruiting to the estuary. In years when the lagoon formed late, age-0 fish recruited to the lagoon in higher proportions than in years when it formed early. In the laboratory, small fish grow faster than large fish under similar ration levels (Wurtsbaugh and Davis 1977a; Connolly and Peterson 2003). The age-0 steelhead that reared in the estuary entered the ocean 6–10 months after recruitment at a greater size with potentially greater chances of marine survival than the age-1+ fish that left before lagoon formation.

The high-resolution growth data collected over the entire juvenile life history cycle in this study enabled the construction of growth trajectories for this population. While not discussed here, it should be acknowledged that the decision to follow a particular pathway is probably due in large part to individual fish behavior and this system is more complex than fish simply growing in response to basic habitat conditions. The scope of this paper was to describe the common trajectories observed in this system. Independent confirmation of these trajectories was provided by data collected on the size and age of downstream migrants in the population (Figure 6), which were not used in creating the trajectories but match the predictions in Figure 7. These trajectories led to several different life history pathways. While such data have been collected for Atlantic salmon (Arnekleiv et al. 2006) and brown trout (Ombredane et al. 1998), comparable data sets are not common for Pacific salmon, presumably due to harsh winters that make the logistics of monitoring growth on a year-round basis more challenging.

In general, it appears that juvenile steelhead from this population migrate downstream before age 2, as very few fish greater than 150 mm or older than age 2 are observed among smolts. While the fish are still relatively small in size, their strategy is to take advantage of lagoon growth opportunities; overall,

these fish probably enter the ocean within 6–10 months, and a majority enter the ocean before age 3. Detailed estimates of the relative proportion of fish following each strategy were beyond the scope of this study. In general, the distribution of size and age for downstream migrants was consistent between years (Bond 2006) and the age of fish recruiting to the estuary–lagoon was probably influenced by the timing of lagoon formation and varied between years. Withler (1966) and Busby et al. (1996) reviewed steelhead smolt age along the West Coast of North America and indicated that there is a general cline in freshwater residence time; steelhead from Alaska and British Columbia stay in freshwater for 3 years, whereas fish from Washington, Oregon, and California typically remain for 2 years and the frequency of 1-year-old smolts increases in southern parts of the range. It is unknown whether fish in southern populations are truly younger at ocean entry than those from northern populations. Fish in Scott Creek migrate downstream or undergo parr–smolt transformation at a younger age but then often spend additional time rearing in the estuary before ocean entry, an observation possibly missed by previous studies due to location of smolt traps upstream of the estuary (Shapovalov and Taft 1954), a lack of additional annulus formation, or both, as emigrating smolts transition from peak upper-watershed growth rates to even faster estuarine growth rates.

Marine survival measured in the Scott Creek watershed and across the steelhead range appears to be influenced by size at ocean entry, and generally fish smaller than 150 mm are unlikely to survive (Ward et al. 1989; Bond 2006). The southern coastal estuaries that form lagoons provide the opportunity for fish to achieve the necessary size for marine survival, which heavily influences adult escapement and possibly defines adult production from the watershed. However, it is not known how coastal California steelhead achieve sufficient size for marine survival in watersheds where upstream growth is limited and where estuaries do not form summer lagoons, either due to natural geological and hydrological processes or anthropogenic processes (e.g., water consumption, stream mouth modifications, artificial breaching of sandbars). Even if very few adults are produced from systems without lagoons, there may still be sufficient numbers available in most years to replenish the stream with juveniles. At Scott Creek, lagoons suitable for rearing have been absent in many years over the last two decades due to artificial sandbar breaching, water diversion, and drought. However, juvenile abundance upstream was fairly consistent from 1988 to 2007 (J.J.S., unpublished data), possibly buffered by the

iteroparous nature of steelhead. Alternatively, it may be that without a reliable presence of lagoons from year to year, populations may not be able to maintain anadromy. We could expect to see a higher proportion of fish pursuing resident life history paths in southern populations from systems where estuaries are lacking or have been compromised by development. Finally, estuaries in many systems also provide important growth opportunities for out-migrating smolts and brackish areas for the fish to adjust to salt water (Healey 1982); this would improve the ocean survival of the relatively small smolts reared in some watersheds like Scott Creek.

The steelhead population in this study and most California coastal stocks are federally listed as threatened under the Endangered Species Act, and stocks situated farther south are listed as endangered. As flows in these watersheds are at constant risk of being reduced even more by human consumption demands, this has become a critical management issue that will probably only increase in importance over time. In addition to the challenges of low flows in the upper watershed, there is a need to maintain connectivity with the estuary. Fish may need to take refuge from the estuary by moving upstream during periods of extreme temperature or low oxygen levels. In addition, summer flows must be low enough for sandbars to build up (thus forming the lagoon) but high enough that the lagoon does not leach through the sand bar (thus leaving only a shallow or dry creek bed).

Presumably, with increasing flows and nutrient contributions from marine (salmon carcasses) and terrestrial sources, upper-watershed habitats will become more productive as one moves north, trading off the loss of coastal summer lagoons as flows become too high for sandbars to close off streams. In addition, winter temperatures become limiting in the north, while summer temperatures are near the growth optimum (Hartman 1965). Therefore, fish in high-altitude or high-latitude river systems will probably grow better in summer than in winter and will follow different growth trajectories from those reported here.

#### Acknowledgments

Funding for this study was provided by the National Marine Fisheries Service, the Central Coast Salmon Restoration Program, and the Fisheries Restoration Grant Program. Constructive reviews were provided by Steve Lindley and Dave Rundio, several anonymous reviewers, and the associate editor. Field assistance was provided by Corey Phillis, Megan Atchenson, Ryan Weidling, Joanne Wong, Devon Pearse, Jeff Harding, and Jeff Perez. Landowner access was provided by Big Creek Lumber Company and California Polytechnic

State University's Swanton Pacific Ranch. Animal studies were carried out according to and approved by the University of California–Santa Cruz Animal Use Committee based on National Institutes of Health guidelines.

#### References

- Arnekleiv, J. V., A. G. Finstad, and L. Ronning. 2006. Temporal and spatial variation in growth of juvenile Atlantic salmon. *Journal of Fish Biology* 68:1062–1076.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:164–173.
- Bond, M. H. 2006. The importance of estuarine rearing to central California steelhead (*Oncorhynchus mykiss*) growth and marine survival. Master's thesis. University of California, Santa Cruz.
- Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. Report NMFS-NWFSC-68.
- Breuser, R. N. 1961. Foods and growth of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), and Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) in certain Oregon streams. Master's thesis. Oregon State University, Corvallis.
- Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.
- Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 32:667–680.
- Cannata, S. 1998. Observations of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*) and water quality of the Navarro River estuary/lagoon May 1996 to December 1997. Draft report prepared for the Humboldt State University Foundation, Arcata, California.
- Chapman, D. W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Research Board of Canada* 19:1047–1080.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams with special reference to food and feeding. Pages 153–176 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. Institute of Fisheries, University of British Columbia, Vancouver.
- Connolly, P. J., and J. H. Peterson. 2003. Bigger is not always better for overwintering young-of-year steelhead. *Transactions of the American Fisheries Society* 132:262–274.
- Cunjak, R. A. 1992. Comparative feeding, growth and movements of Atlantic salmon (*Salmo salar*) parr from

- riverine and estuarine environments. *Ecology of Freshwater Fish* 1:26–34.
- Elliott, J. M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. *Journal of Animal Ecology* 44:805–821.
- Fransen, B. R., P. A. Bisson, B. R. Ward, and R. E. Bilby. 1993. Physical and biological constraints on summer rearing of juvenile coho salmon (*Oncorhynchus kisutch*) in small western Washington streams. Pages 271–288 in L. Berg and P. W. Delaney, editors. *Coho salmon workshop*. Canadian Department of Fisheries and Oceans, Nanaimo, British Columbia.
- Fraser, F. J. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream channels. Pages 253–256 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. Institute of Fisheries, University of British Columbia, Vancouver.
- Friedman, J. H. 1984. A variable span scatterplot smoother. Laboratory for Computational Statistics, Stanford University, Technical Report 5, Stanford, California.
- Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 22:1035–1081.
- Harvey, B. C., and R. J. Nakamoto. 1996. Effects of steelhead density on growth of coho salmon in a small coastal California stream. *Transactions of the American Fisheries Society* 125:237–243.
- 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, 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(Supplement A):101–121.
- Healey, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315–341 in V. S. Kennedy, editor. *Estuarine comparisons*. Academic Press, New York.
- Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. *Fisheries* 12(5):24–31.
- Hoar, W. S. 1976. Smolt transformation—evolution, behavior, and physiology. *Journal of the Fisheries Research Board of Canada* 33:1233–1252.
- Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5:299–314.
- Jones, M. W., and J. A. Hutchings. 2001. The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. *Heredity* 86:675–684.
- Jones, W., W. S. C. Gurney, D. C. Speirs, P. J. Bacon, and A. F. Youngson. 2002. Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. *Journal of Animal Ecology* 71:916–924.
- Levings, C. D., C. D. McAllister, and B. D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia (Canada), by wild and hatchery-reared juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1386–1397.
- Merz, J. E. 2002. Seasonal feeding habits, growth, and movement of steelhead trout in the lower Mokelumne River, California. *California Fish and Game* 88(3):95–111.
- Miller, B. A., and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* 132:546–559.
- Myrick, C. A., and J. J. Cech. 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.
- Narver, D. W. 1969. Age and size of steelhead trout in the Babine River, British Columbia. *Journal of the Fisheries Research Board of Canada* 26:2754–2760.
- Narver, D. W., and B. C. Andersen. 1974. Fish populations of Carnation Creek and other Barkley Sound streams—1970–1973: data record and progress report. Fisheries Research Board of Canada Manuscript Report 1303:115.
- NMFS (National Marine Fisheries Service). 2006. Endangered and threatened species: final listing determinations for 10 distinct population segments of West Coast steelhead. *Federal Register* 71:3(5 January 2006):834–862.
- Ombredane, D., J. L. Bagliniere, and F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. *Hydrobiologia* 372:99–106.
- Parker, R. R., and P. A. Larkin. 1959. A concept of growth in fishes. *Journal of the Fisheries Research Board of Canada* 16:721–745.
- Peterson, N. P., E. F. Prentice, and T. P. Quinn. 1994. Comparison of sequential coded wire and passive integrated transponder tags for assessing overwinter growth and survival of juvenile coho salmon. *North American Journal of Fisheries Management* 14:870–873.
- Quinn, T. J. 2005. *The behavior and ecology of Pacific salmon and trout*. University of Washington Press, Seattle.
- Railsback, S. F., and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. *Transactions of the American Fisheries Society* 128:241–256.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletins of the Fisheries Research Board of Canada* 191:382.
- Romero, N., R. E. Gresswell, and J. L. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1797–1807.
- Schwarz, K. M., and A. R. Orme. 2005. Opening and closure of a seasonal river mouth: the Malibu estuary barrier lagoon system, California. *Zeitschrift fuer Geomorphologie Supplementband* 141:91–109.
- Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and

- silver salmon (*Oncorhynchus kisutch*). California Department of Fish and Game, Fish Bulletin 98.
- Smith, J. J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell and Pomponio Creek estuary/lagoon systems, 1985–1989. Report prepared by San Jose State University under Interagency Agreement 84-04-324 for the California Department of Parks and Recreation, Sacramento, California.
- Stein, R. A., P. E. Reimers, and J. D. Hall. 1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall Chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. *Journal of the Fisheries Research Board of Canada* 29:1737–1748.
- Thorpe, J. E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *Journal of Fish Biology* 11:175–184.
- Tschaplinski, P. J. 1987. The use of estuaries as rearing habitats by juvenile coho salmon. In T. W. Chamberlin, editor. Pacific Biological Station. Proceedings of the workshop: applying 15 years of Carnation Creek results. Pacific Biological Station, Nanaimo, British Columbia.
- 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.
- Withler, R. E. 1966. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. *Journal of the Fisheries Research Board of Canada* 23:365–393.
- Wurtsbaugh, W. A., and G. E. Davis. 1977a. Effects of fish size and ration level on the growth and food conversion efficiency of rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* 11:99–104.
- Wurtsbaugh, W. A., and G. E. Davis. 1977b. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. *Journal of Fish Biology* 11:87–98.