Age, Growth, and Life History of Steelhead Rainbow Trout (*Oncorhynchus mykiss*) in the Lower Yuba River, California

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Abstract.—Scale analysis was used to investigate the life history characteristics of wild steelhead rainbow trout (*Oncorhynchus mykiss*) in the lower Yuba River, California. Scale reading and quantitative measurements of scale features were used to interpret life history patterns and determine age, growth, and migratory history of steelhead rainbow trout. Scales from 787 juvenile and adult trout collected in the Yuba River from 1998 to 2007 revealed a predominantly resident or non-anadromous life history pattern. Limited sampling of migrating adults in the fish ladder at Daguerre Point Dam indicated that 14% of these fish were anadromous (steelhead), while only 1% of the fish caught by anglers were identified as steelhead. Application of standard back-calculation techniques revealed substantial variability in size at age but consistently high average freshwater growth rates of yearling and older trout comparable to those observed in highly productive spring-fed streams in California. Based on general life history theory and the known life history plasticity of *O. mykiss*, it is hypothesized that high, stable flows and cool temperatures resulting from summer and fall reservoir releases in the lower Yuba River support high growth, survival, and reproductive rates of steelhead rainbow trout that favor a resident life history strategy. The utility and potential application of scale analysis in future monitoring and research of Yuba River steelhead is discussed.

Introduction

Steelhead (*Oncorhynchus mykiss*) in California's Central Valley were listed in 1998 as a threatened species under the U.S. Endangered Species Act. Relatively little research and monitoring have been directed at Central Valley steelhead in the past and there is little current information on the biology, status, and life history of the majority of wild stocks. This has been attributed to several institutional and biological constraints, including the focus of fisheries monitoring programs on Chinook salmon, general assumptions regarding the benefits of salmon management actions on steelhead, flow-related difficulties in monitoring adult steelhead during their migration and spawning periods, lack of a reliable method of adult population estimation, and low sampling efficiencies for juvenile steelhead compared to juvenile salmon (McEwan 2001). The complex life history patterns of steelhead, including variable freshwater and ocean residence periods, multiple age classes of returning adults, and potential for multiple life history forms contribute to the difficulties in studying and managing wild steelhead rainbow trout populations.[1]

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[1] This paper uses the term steelhead rainbow trout to encompass all life history forms potentially expressed by the species *O. mykiss*. Steelhead or anadromous rainbow trout refer to sea-run adults while resident or non-anadromous rainbow trout refer to fish that remain in freshwater for their entire lives.

A primary goal of the CALFED Ecosystem Restoration Program (CALFED ERP) is to achieve the recovery of at-risk native species dependent on the Sacramento-San Joaquin ecosystem. The CALFED ERP identified steelhead trout as a the priority species because of major declines in their range and abundance, their present status as threatened under the federal Endangered Species Act, and their recreational importance in the Central Valley. One of ERP's priority actions for steelhead recovery is to support additional research to address large deficiencies in baseline information on their status, life history, distribution, and habitat requirements. Such information is needed to identify key stressors on steelhead populations and ensure the success of restoration actions by eliminating or reducing these stressors and restoring steelhead habitat and ecosystem processes that maintain these habitats. A major gap currently limiting the management and recovery of Central Valley steelhead is the scarcity of information on the structure and life history of wild populations and the relationship between resident and anadromous life history forms (Lindley et al. 2007). Consequently, a high priority has been placed on developing and improving methods for determining the age composition, growth, life history, and origins of existing populations.

Analysis of the growth patterns reflected in fish scales and otoliths has proven to be an effective method for determining the age structure, life history characteristics, and origins of fish populations, as well as analyzing relationships between growth, life history variation, and subsequent recruitment. Davis and Light (1985) developed criteria for determining freshwater age, ocean age, and spawning history of steelhead based on examination of scales and otoliths from known-age coded-wire tagged fish. Quantitative differences in scale growth patterns have been used to discriminate between wild and hatchery stocks in mixed high-seas samples (Bernard and Myers 1996) and in mixed-stock fisheries in Lake Michigan tributaries (Seelbach and Whelan 1988). Otolith growth patterns were used to determine the age and length of steelhead smolts migrating from mid-Columbia River Basin tributaries, and to investigate the effects of growth and body size on smoltification (Peven et al. 1994). Through back-calculation techniques, scales were used to assess differences in smolt-to-adult survival and recruitment in relation to smolt size in the Keogh River, British Columbia (Ward et al. 1989).

The Yuba River provides a unique setting to investigate the life history attributes and population structure of a Central Valley steelhead population. Historically, the Yuba River supported large numbers of steelhead and today is recognized as one of the largest remaining wild populations in the Central Valley. Although hatchery steelhead were formerly planted in the lower Yuba River, the river has been managed for natural steelhead production since the 1980s and currently supports one of the most popular wild steelhead rainbow trout fisheries in California.

Objectives

The purpose of this study is to address the need for information on the population structure and life history of Central Valley steelhead in support of ecosystem restoration and species recovery efforts under CALFED's ERPP, USFWS's Anadromous Fish Restoration Program, the federal ESA, and other state and federal steelhead conservation and recovery programs. The primary objectives of this study were to use scale analysis to describe the age, growth, and life history of

Yuba River steelhead rainbow trout; assess the relative contributions of steelhead and non-anadromous rainbow trout to this population; and evaluate scale analysis as a potential tool for future research and monitoring of steelhead.

Study Area

The Yuba River is a tributary of the Feather River, a tributary of the Sacramento River in the northern Central Valley of California. The Yuba River drains 3480 km^2 of the western slope of the Sierra Nevada from elevations of 2,775 meters above sea level to approximately 10 meters above mean sea level at its confluence with the Feather River (Moir and Pasternack 2008). The North, Middle, and South Yuba Rivers flow from steep mountainous headwaters to their confluence in the Sierra Nevada foothills upstream of Englebright Reservoir. Englebright Dam discharges into the lower Yuba River, which flows approximately 38 km to its confluence with the Feather River on the valley floor (Figure 1). Annual precipitation ranges from >150 cm in the headwaters to 50 cm on the valley floor, with approximately 85% falling between November and April. Much of the precipitation in the upper elevations falls as snow that contributes to spring runoff in April-July (Moir and Pasternack 2008).

The hydrology of the Yuba River has been altered by a series of reservoirs and water conveyance facilities that are operated for water supply, hydropower production, and flood control. New Bullards Bar Reservoir, constructed on the North Yuba River in the late 1960s, is the principal water storage reservoir in the watershed. This reservoir is operated for flood control, power generation, irrigation, recreation, and protection and enhancement of fish and wildlife. Since 1970, operation of New Bullards Bar Reservoir has modified the seasonal distribution of flows in the lower Yuba River by reducing spring flows and increasing summer and fall flows. However, the Yuba River below Englebright Dam still experiences a dynamic flood regime because of frequent uncontrolled winter and spring flows (Moir and Pasternack 2008).

Historically, the Yuba River supported large numbers of spring-run Chinook salmon, fall-run Chinook salmon, and steelhead. Extensive hydraulic mining in the late 1800s resulted in the massive influx of mining sediments that filled the lower river valleys and profoundly changed the physical character of the lower Yuba River (Moir and Pasternack 2008). The resulting habitat degradation followed by the construction of a series of impassable debris dams from the early to mid-1900s likely caused major reductions in salmon and steelhead populations in the Yuba River basin. Loss of access to much of their historic spawning and rearing habitat in the upper basin likely had particularly severe impacts on spring-run Chinook salmon and steelhead populations, which depended on the upper basin for successful summer holding and rearing (Yoshiyama et al. 1998, 2001). Daguerre Point Dam, constructed in 1910, was reported to be a partial or complete barrier to salmon and steelhead for many years because of the lack of functional fish ladders. Englebright Dam, completed in 1941, restricted all salmon and steelhead to the lower Yuba River, and is currently the upstream limit of salmon and steelhead migration.

The California Department of Fish and Game (DFG) estimated that about 200 steelhead spawned annually in the lower Yuba River before the completion of New Bullards Bar Reservoir in 1970 (Wooster and Wickwire 1970). Although no definitive population estimates exist, DFG reported that steelhead fishing improved considerably after New Bullards Bar Reservoir was completed because of higher, cooler summer flows resulting from operation of the reservoir and a hatchery stocking program that began in 1971 (Rogers, DFG file memorandum). Rogers stated that an annual run size of about 2,000 steelhead seemed reasonable based on angler catch data collected in the lower Yuba River in 1975-1977. During the fall and winter of 1976-1977, operation of a weir and trap in the lower river and an angler tag-recovery program resulted in an estimate of 400-500 steelhead, although run size was expected to be low that year because of severe drought conditions. The current abundance of this population is unknown, but it appears to be stable and supports a significant sport fishery (McEwan and Jackson 1996). The Yuba River is currently managed for natural steelhead production (California Department of Fish and Game 1991).

Methods

Scale Sources

Scales from 787 juvenile and adult steelhead rainbow trout were collected in the Yuba River from 1998 to 2007. The dates of capture, collection methods, numbers of fish, and sources are presented in Table 1. Most fish were collected by trapping, angling, and electrofishing. Trapping of upstream migrating trout was conducted in the north fish ladder at Daguerre Point Dam from November 11, 2000 through March 12, 2001 using a gated trap with a moveable floor that could be raised to allow netting of fish. Fish ladder trapping was originally intended to serve as the primary sampling method for this study but was suspended because of permitting delays and ultimately abandoned because of the installation of a fish counting system in the fish ladders in 2003. The remainder of the fish sampling efforts was conducted by hook-and-line angling on an opportunistic basis from 2004 to 2007 with the assistance of volunteer anglers from a local fly fishing club. Additional scale samples were provided by J. Kozlowski from juveniles and adults collected by electrofishing and angling in 1999-2000 (Kozlowski 2004). Juvenile and adult scale samples were also provided by R.Titus, California Department of Fish and Game, from fish collected by angling and rotary screw trapping in 2002, 2003, and 2005.

Field Data Collection

Steelhead rainbow trout captured by trapping and angling were anaesthetized with sodium bicarbonate, inspected for marks or tags, and photographed. Each fish was measured to the nearest millimeter fork length (FL) and weighed to the nearest 0.1 gram by placing the fish in a net suspended from a spring scale. A knife was used to remove 10-15 scales from the left side of the fish between the dorsal fin and lateral line as recommended by Maher and Larkin (1955). The scale sample was placed in a coin envelope labeled with an identification number.

Scale Preparation, Reading, and Measurements

Scales from individual fish were mounted between glass slides and visually examined at magnifications of 2× to 6.3× under a stereo microscope. The highest quality scales were photographed using a digital camera and computer imaging software (Spot Insight 3.5®). Printed copies of these images were used for subsequent scale interpretations. Two scale readers worked independently to mark the location of freshwater annuli, ocean annuli, and spawning checks using standard criteria for interpretation of steelhead and rainbow trout scales (Maher and Larkin 1955). Readers then worked collaboratively to review their interpretations, resolve discrepancies, and select a set of reference scales for which a high degree of confidence could be assigned. Quantitative measurements from these scales (e.g., distance and number of circuli to the first and second annulus) were then used by the author to conduct a final review of scale interpretations.

Scale features were measured from digital scale images using a computer and AutoCAD software. Measurements were taken along a standard axis (20^{o} and ventral to the anterior-posterior scale axis) extending from the focus to the edge of the scale (Figure 2 and 3). Measurements were taken from the focus to the first circulus, the focus to each successive annulus or check, and the focus to the edge of the scale (i.e., scale radius). Annuli and other major checks were measured from the focus to the anterior or outer margin of the annulus or check. Measurements were made to the nearest micrometer using a calibrated micrometer scale for each magnification power.

Back-Calculation Procedures

The Fraser-Lee technique was used to back-calculate lengths of individual fish at previous annuli based on scale measurements (Busacker et al. 1990). This technique assumes that scale radius and body length are proportional and that the regression between scale radius and body length has a non-zero intercept. Only non-regenerated scales with little or no scale erosion were used to develop this relationship. Because of the apparent non-linear relationship between fork length and scale radius (Figure 4), transformation of fork length and scale radius to natural logs was performed to improve linearity and satisfy the assumption of proportionality (Mottley 1942, Hooton et al. 1987). Following transformation of these variables, standard regression techniques were used to compute the y-intercept for use in the Fraser-Lee equation. The following modification of the Fraser-Lee equation was used for back-calculating the length of individual fish at previous ages (annuli):

$$\ln L_i = ((\ln L_c + 0.252) \ln S_i / \ln S_c) - 0.252$$

where ln = natural logarithm, L_i = length of fish at annulus i, L_c = length of fish at capture, S_i = scale radius at annulus i, and S_c = scale radius at capture.

Annual growth rates or increments were estimated by subtracting the back-calculated lengths of individual fish at a given annulus from the back-calculated length at the next consecutive annulus. Analysis of variance (ANOVA) was used to compare the mean sizes at age and annual growth rates of individual year classes of steelhead rainbow trout.

Results

Length-Frequency Distribution

Scales were taken from 142 age 0+ and age 1+ steelhead rainbow trout collected by electrofishing in July-September 1999 and July-August 2000. Sampled fish averaged 107 mm FL and ranged from 68 to 198 mm FL (Figure 5).

Scales were taken from 467 juvenile and adult steelhead rainbow trout collected by angling between September 1998 and June 2007 (Figure 5). Angler-caught fish averaged 321 mm FL and ranged from 85 to 559 mm FL. Based on scale analysis, nearly all fish had spent 1 to 4 winters in freshwater with no evidence of ocean residence. Only four fish were identified as steelhead ranging in length from 438 to 559 mm FL.

Scales were taken from 71 juvenile and adult trout trapped in the fish ladder at Daguerre Point Dam from November 1, 2000 through March 28, 2001 (Figure 5). Trapped fish averaged 401 mm FL and ranged from 220 to 720 mm FL. Sixty one were identified as age 2+ and older non-anadromous fish ranging in length from 220 to 660 mm. The oldest and largest non-anadromous fish was an age-6+ fish measuring 635 mm FL. Ten fish were identified as steelhead ranging in length from 453 to 720 mm FL.

Length-Weight Relationship

The relationship between body weight and fork length for 610 steelhead rainbow trout (68-720 mm FL) is shown in Figure 6.

Size at Age and Growth

Back-calculation was performed on the scales of 560 age 1+ to age 4+ steelhead rainbow trout using the Fraser-Lee method. Means and standard deviations of back-calculated fork lengths at successive freshwater annuli for each year class are presented in Table 2. Excluding estimates based on less than 10 individuals, mean fork lengths ranged from 98-118 mm at annulus 1, 261-268 mm at annulus 2, and 321-341 mm at annulus 3. With one exception, no significant differences in mean length at annulus formation were detected among year classes (ANOVA, $p>0.05$). The only exception was the 1999 year class, which had a significantly smaller mean length (98 mm FL) at annulus 1 than other year classes. Pooling all year classes, the back-calculated estimates of mean length (± 1 standard deviation) at the end of the first, second, third, and fourth winters were 108 mm (±28), 265 mm (±43), 338 mm (±28), and 387 mm (±8) (Figure 7).

Mean annual growth increments for each year and age class, derived from back-calculated lengths of individual fish at annulus formation, are presented in Table 3. Excluding estimates based on less than 10 individuals, mean annual growth increments ranged from 141-158 mm between annulus 1 and 2 and 65-78 mm between annulus 2 and 3. No significant differences in mean annual growth increments were detected among year classes (ANOVA, $p>0.05$). Pooling all year classes, mean annual freshwater growth increments following the first, second, and third winters were 146 mm (±28), 73 mm (±28), and 47 mm (±3).

Figure 8 presents the average growth trajectory of steelhead rainbow trout from age 0+ to age 4+ based on the measured lengths of individual fish in each age class and back-calculated lengths at winter annulus formation. These data are representative of the freshwater growth of juvenile and pre-spawning adults from year classes 1997 to 2005. The average ocean growth trajectories of an age-2/1 (age-3) and age 3/1 (age-4) steelhead is shown for comparison. The completion of winter annulus formation is assumed to occur in late winter (March 15) based on the location of the annulus and the amount of intermediate scale growth observed in fish captured on different dates throughout the year.

Steelhead Adults

Scale samples were taken from a total of 10 adult steelhead trapped at Daguerre Point Dam between November 2000 and March 2001, and 4 steelhead caught by anglers in February 2000, December 2004, December 2005, and May 2007 (Table 4). Twelve of these fish were identified as wild origin and two were identified as hatchery origin based on the presence or absence of an adipose fin and the distinctive first-year scale growth pattern of hatchery fish. Wild adults ranged from 438 to 638 mm FL representing at least four age categories (1/1, 2/1, 2/2, and 3/1), having spent 1, 2, or 3 years in freshwater and 1 or 2 years at sea before returning to spawn.

Five wild steelhead adults (all age 3/1) had scales that were suitable for back-calculation of lengths at annulus formation and ocean entry (Table 4). Scale measurements indicated that these fish averaged 125 mm FL at annulus 1, 275 mm FL at annulus 2, and 375 mm FL at ocean entry. These fish grew an average of 179 mm during their one-year residence in the ocean.

Size and Age at Spawning

Evidence of spawning was observed in non-anadromous trout at ages of 2 and older and sizes of 285 mm FL and larger. Based on the presence of one or more spawning checks, the majority of non-anadromous fish reach sexual maturity at ages 3 or 4. The frequency of spawning checks increased from approximately 10% for fish 280-300 mm FL to approximately 85% for fish 440-460 mm FL. Wild steelhead adults returning to spawn ranged in age from 2 to 4 years and size from 438 to 638 mm FL. Two of the 10 wild steelhead were on their second spawning migration at the time of capture (age 2/1S1) as indicated by a spawning check between the first and second ocean growth zones.

Discussion

Analysis of scales from 787 steelhead rainbow trout collected in the Yuba River between 1998 and 2007 revealed a predominantly resident or non-anadromous life history pattern.
Sampling of upstream migrants in the fish ladder at Daguerre Point Dam indicated that 14% of these fish were anadromous adults (steelhead), while only 1% of the fish caught by anglers were

identified as steelhead. Although potentially biased by the limited duration of trapping, the estimated proportion of steelhead among upstream migrants is generally consistent with the results of recent otolith microchemistry studies, which indicated that 10-15% of a sample of age-0+ to age-4+ fish from the Yuba River were offspring of a sea-run female parent (Zimmerman et al. 2009). In addition, based on nearly continuous infrared and video imaging of fish ascending the ladders at Daguerre Point Dam in 2007 and 2008, fish within the predominant steelhead size range (>460 mm FL) comprised approximately 5% of the total number of fish classified as *O. mykiss* in 2007 and 14% of the total number of fish classified as *O. mykiss* in 2008 (unpublished data, D. Massa, Pacific States Marine Fisheries Commission).

Back-calculation of fork length at previous ages revealed substantial variability in size and growth of individual steelhead rainbow trout. Variability in size at winter annulus formation reflects differences in individual growth rates as well as variability in the timing of hatching and emergence, which can extend for several months based on the presence of age 0+ fry (<35 mm) through late summer (Kozlowski 2004). Fry that emerge in late summer experience a reduced growing season and minimal growth through the remainder of the year, resulting in some fish that are substantially smaller (<70 mm FL) than average (108 mm FL) at the end of their first winter. Conversely, fry that emerge in early spring have a much higher growth opportunity, with some reaching sizes in excess of 180 mm FL by the end of winter.

Following their first winter in freshwater, age 1+ juvenile rainbow trout in the Yuba River experience rapid growth based on measured lengths through the summer and fall and back-calculated lengths at the end of their second winter. On average, age 1+ juveniles grew 146 mm in length, reaching an average fork length of approximately 265 mm by the end of their second winter. During this period of rapid growth, scale growth patterns (as indicated by circuli spacing) indicate a general seasonal pattern of growth characterized by an acceleration of growth in the spring, peak growth rates in the summer, and a deceleration of growth in the fall and winter associated with annulus formation. This pattern is evident in the annual growth zones of other age classes but is most discernable during the second year of life. Following their second winter in freshwater, steelhead rainbow trout in the Yuba River exhibit a slowing of total annual growth in length (reaching an average of 338 mm FL at age 3) but continued growth in mass as fish mature and reach reproductive age.

The freshwater growth rates of yearling and older steelhead rainbow trout in the Yuba River appear to be substantially higher than those estimated for lower Sacramento River and Klamath River steelhead, and comparable to growth rates of resident fish in highly productive spring-fed streams in the upper Sacramento River (e.g., Hat Creek, Fall River) (Figure 9). Moyle (2002) notes the high variability of juvenile steelhead growth in freshwater, but states that sizes of 100-120 mm FL at the end of the first year and 160-170 mm at the end of the second year are fairly typical in larger streams where food is abundant. In small California streams with lower summer flows, juveniles are usually 50-90 mm at the end of their first summer and 100-160 mm at the end of their second summer. In contrast, juveniles may reach 100-200 mm in their first year if summer flows are higher and food is abundant (Moyle 2002).

Examination of scales of the small numbers of adult steelhead collected in the Yuba River revealed the presence of at least four age categories (1/1, 2/1, 2/1S1, and 3/1) representing fish that spent 1, 2, or 3 years in freshwater and 1 or 2 years at sea before returning to spawn. Two of the 14 steelhead were returning to spawn for the second time (2/1S1). These age categories are generally consistent with the dominant life history patterns reported for wild steelhead in this portion of their range. In California, juveniles typically emigrate to the ocean after 1 to 3 years in freshwater, with the majority emigrating at age 2. For example, Hallock et al.'s (1961) examination of scales from adult steelhead returning to the Sacramento River indicated that 29% had spent one year, 70% had spent two years, and 1% had spent three years in freshwater before emigrating to the ocean. In Waddell Creek, the estimated proportions of age 1-, 2-, and 3-year-old smolts were 10%, 69%, and 19%, respectively (Shapovalov and Taft 1954). Although the relative contribution of smolts of different ages cannot be reliably inferred from the small sample of steelhead collected in the Yuba River, the relatively high proportion of age-3/1 steelhead suggests that fish spending up to three years in freshwater may be an important component of the run.

There is little historical data on the relative abundance of anadromous and non-anadromous life history forms in Central Valley rainbow trout populations. Hallock et al. (1961) reported evidence of a sizeable population of non-anadromous rainbow trout 14 to 20 inches in length in the upper Sacramento River, which he attributed to the presence of resident trout and/or trout that had not yet gone to sea. Current understanding of the relationship between steelhead and rainbow trout suggests that these two general life history forms can occur as a result of fixed differences between sympatric but reproductively isolated populations or as alternative life history strategies expressed among individuals within the same population (Zimmerman and Reeves 2002). Recent otolith microchemistry studies of the maternal origins of *O. mykiss* in several steelhead rainbow trout populations in the Central Valley (including the Yuba River) suggest that both resident and anadromous rainbow trout can be produced by either life history form (Zimmerman et al. 2009).

O. mykiss is characterized by a wide range of life history strategies that enable the species to persist in highly variable environments. Based on current life history theory, expression of resident and anadromous life history strategies is a consequence of both genetic and environmental factors operating on both short- and long-term time scales. Although the life history traits are heritable, much of the variability observed within and among populations (and between generations) can be explained by phenotypic plasticity in life history response to the environment. Models simulating the effect of the environment on physiology and growth of individual fish and subsequent effects on life history pathways have been developed for Atlantic salmon (Thorpe et al. 1998). Satterthwaite et al. (2009) proposed a similar model for steelhead trout that predicts alternative life history strategies based on genetically determined "decision" rules related to size, age, and growth during specific seasonal windows. Based on general model predictions, relatively high growth rates tend to favor earlier ages at smolting but can alternatively lead to high rates of freshwater maturation when coupled with high freshwater survival rates (relative to survival rates of anadromous fish), large adult size in freshwater, and relatively high post-spawning survival. Under some conditions, increased survival and large maximum size in freshwater may favor delayed smolting at larger sizes if this strategy offers a sufficient survival and reproductive advantage over other life history pathways.

These modeling predictions offer a potential explanation for the high incidence of freshwater maturation and associated growth rates of steelhead rainbow trout in the lower Yuba River. Growth rates are heavily influenced by climate and local habitat conditions. In Mediterranean climates, high, stable year-round flows coupled with mild winters and moderate summer water temperatures support the highest growth rates in steelhead (Hayes et al. 2008). In the Yuba River, it is hypothesized that relatively high, stable summer flows combined with apparent high rates of food production and suitable water temperatures throughout the year consistently support high growth and survival rates of juvenile rainbow trout, allowing a large proportion to successfully reach maturity and achieve large sizes in freshwater. Although these conditions appear to favor a resident or non-anadromous life history strategy, the presence of a small but significant sea-run component suggests that the population still retains the capacity to produce anadromous fish.

Monitoring and Research Implications

In the present study, scale analysis provided an effective method for investigating the age, growth, and life history of steelhead rainbow trout in the Yuba River. Scale analysis allows relatively rapid assessment of the age and growth history of large numbers of fish without the cost and preparation time associated with other structures (e.g., otoliths). In addition, scales can be quickly removed in the field with little risk of injury and, most importantly, without the need to sacrifice fish. However, several uncertainties and potential sources of error exist when reading scales and applying standard back-calculation techniques to estimate the lengths of fish at previous ages. These include variation in the seasonal timing of annulus formation, occurrence of missing or false annuli, and the absence or resorption of annuli in the scales of older fish (Beamish and McFarlane 1983). Although considerable effort was made to establish consistency and repeatability in the interpretation of scale characteristics, no independent means of confirming the age determinations or back-calculated lengths were available. Otoliths can be used in tandem with scales to increase confidence in scale interpretations (especially in older fish) but true validation requires mark-recapture studies or use of known age fish (Beamish and McFarlane 1983).

An important consideration for future applications of scale analysis in monitoring and assessment efforts is the inherent sampling biases associated with different types of fishing gears. For example, differences in proportions of steelhead adults collected by angling (1%) and trapping (14%) likely reflect differences in the size composition of the migratory and non-migratory components of the population as well as size-related differences in the capture efficiency of these gear types. These estimates may have also been biased by the unequal and limited distribution of sampling effort within the study period. This was especially true of the trapping data, which was limited to a five-month period. An additional concern with regard to the use of angler-caught fish for age and growth studies is the size selectivity of hook-and-line sampling and the potential for anglers to catch the largest, fastest-growing individuals of a particular age class (Hayes et al. 1996). In the present study, an attempt was made to minimize these potential biases by targeting a broad range of fish sizes using electrofishing, angling, and trapping.

An expanded trapping effort and analysis of scales of migrating adults is needed to improve our current understanding of the population and life history attributes of Yuba River steelhead. Year-round, systematic collection of scale and size data in conjunction with infrared and video imaging at Daguerre Point Dam would provide a comprehensive understanding of steelhead age structure and life history, and provide important information for developing and refining current size and morphological criteria for identifying anadromous and non-anadromous adults based on imaging data. Potential benefits to future population monitoring and assessment efforts include improved reliability in the estimation of annual run size and the relative contributions of different year classes, life history types, and origins to the adult population. Trapping at Daguerre Point Dam would also facilitate the tagging of juvenile and adult steelhead rainbow trout for ongoing telemetry studies as described below.

While scale analysis provides an effective means of determining age, growth, and major life history patterns (freshwater versus ocean residency) of steelhead rainbow trout, a current limitation of this method is an inability to correlate these patterns with the movements and distribution of fish over smaller spatial and temporal scales. Because of the variable migratory behavior of *O. mykiss* and the potential for complex patterns of freshwater, estuarine, and ocean residency, the lack of such knowledge represents a significant impediment to the development of effective restoration and conservation actions for this species. This research need is being addressed through an acoustic tagging program currently being conducted in the Yuba River and other Central valley rivers to track juvenile and adult steelhead rainbow trout, and investigate the relationships between movements and survival in relation to hydrologic, water temperature, and other environmental variables (pers. comm., R. Bloom, California Department of Fish and Game).

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Table 1. Sampling periods, methods, and numbers of scale samples collected from juvenile and adult steelhead rainbow trout in the Yuba River

Year	Months	Method	Number	Source
1998	Sep-Dec	Angling	18	J. Kozlowski
1999	Jul-Sep	Angling Electrofishing	218	J. Kozlowski
2000	Feb, May, Jul-Dec	Angling Electrofishing Trapping	162	J. Kozlowski This study
2001	Jan-Mar	Trapping	67	This study
2002	Jul-Sep	Angling[1]	11	DFG
2003	Jul, Aug, Oct	Angling[1]	49	DFG
2004	Jan, Mar, Jun-Sep, Dec	Angling	70	This study
2005	Jan-Jul, Nov-Dec	Angling[1]	178	This study DFG
2006	Dec	Angling	5	This study
2007	Apr-Jun	Angling	8	This study

[1] Some scale samples obtained from DFG were from fish collected by rotary screw trap

Table 2. Means (±1 SD) of back-calculated freshwater lengths (mm FL) of steelhead rainbow trout representing year classes 1995-2004

Year Class[1]	Annulus 1	Annulus 2	Annulus 3	Annulus 4
1995	115 (±13) N=2	200 (±21) N=2	328 (±21) N=2	—
1996	110 (±21) N=17	268 (±42) N=17	321 (±16) N=11	382 (—) N=1
1997	118 (±26) N=42	261(±45) N=39	341 (±27) N=29	—
1998	107 (±30) N=144	267(±47) N=54	—	—
1999	98 (±28) N=97	285(—) N=1	348(—) N=1	393(—) N=1
2001	115 (±21) N=22	262(±38) N=22	339 (±30) N=18	—
2002	112(±26) N=49	268 (±43) N=31	356 (±41) N=6	—
2003	111(±26) N=36	261(±37) N=23	323 (±8) N=2	—
2004	109(±22) N=8	300(±20) N=3	347 (±23) N=3	—

[1] Year class refers to the year of hatching and emergence; lengths at each annulus represent the mean length at the end of each successive winter following hatching and emergence; fish representing year class 2000 were not sampled

Table 3. Means (±1 SD) of annual growth increments (mm) of steelhead rainbow trout representing year classes 1995-2004

Year Class	Ann 1-Ann 2	Ann 2-Ann 3	Ann 3-Ann 4
1995	85 (±8) N=2	129 (±1) N=2	—
1996	158 (±37) N=17	65 (±23) N=11	49 (—) N=1
1997	141 (±38) N=39	78 (±26) N=29	—
1998	145 (±38) N=54	—	—
1999	154 (—) N=1	63 (—) N=1	45 (—) N=1
2001	147 (±31) N=22	72 (±30) N=18	—
2002	149 (±35) N=31	74 (±24) N=6	—
2003	147 (±33) N=23	54 (±14) N=2	—
2004	174 (±10) N=3	47 (±3) N=3	—

Table 4. Age and lengths of steelhead adults collected in the Yuba River

Capture Date	Capture Method	Origin	Age	Length at Age in Freshwater (mm)			Length at Ocean Entry (mm)	Length at Capture (mm)
				Age 1	Age 2	Age 3		
02/25/00	Angling	Hatchery	1/1S	–			–	559
11/01/00	Trap	Wild	2/1S1	–	–		–	570
01/17/01	Trap	Wild	2/1S	–	–		–	453
020/2/01	Trap	Hatchery	1/2	–			218	720
02/12/01	Trap	Wild	3/1	116	224	–	348	540
02/28/01	Trap	Wild	3/1	139	312	–	379	555
03/05/01	Trap	Wild	2/1S1	–	–		–	638
03/09/01	Trap	Wild	3/1	113	288	–	381	572
03/12/01	Trap	Wild	3/1	170	307	–	385	535
03/19/01	Trap	Wild	3/1	85	243	–	382	566
03/19/01	Trap	Wild	3/1	–	–	–	–	545
12/10/04	Angling	Wild	2/1	–	–		–	468
12/01/05	Angling	Wild	1/–	–			–	464
05/25/07	Angling	Wild	1/1S	–			–	438

Note: A dash indicates that age or back-calculated length could not be determined because of significant scale resorption, regeneration, or absence of distinct scale check(s)

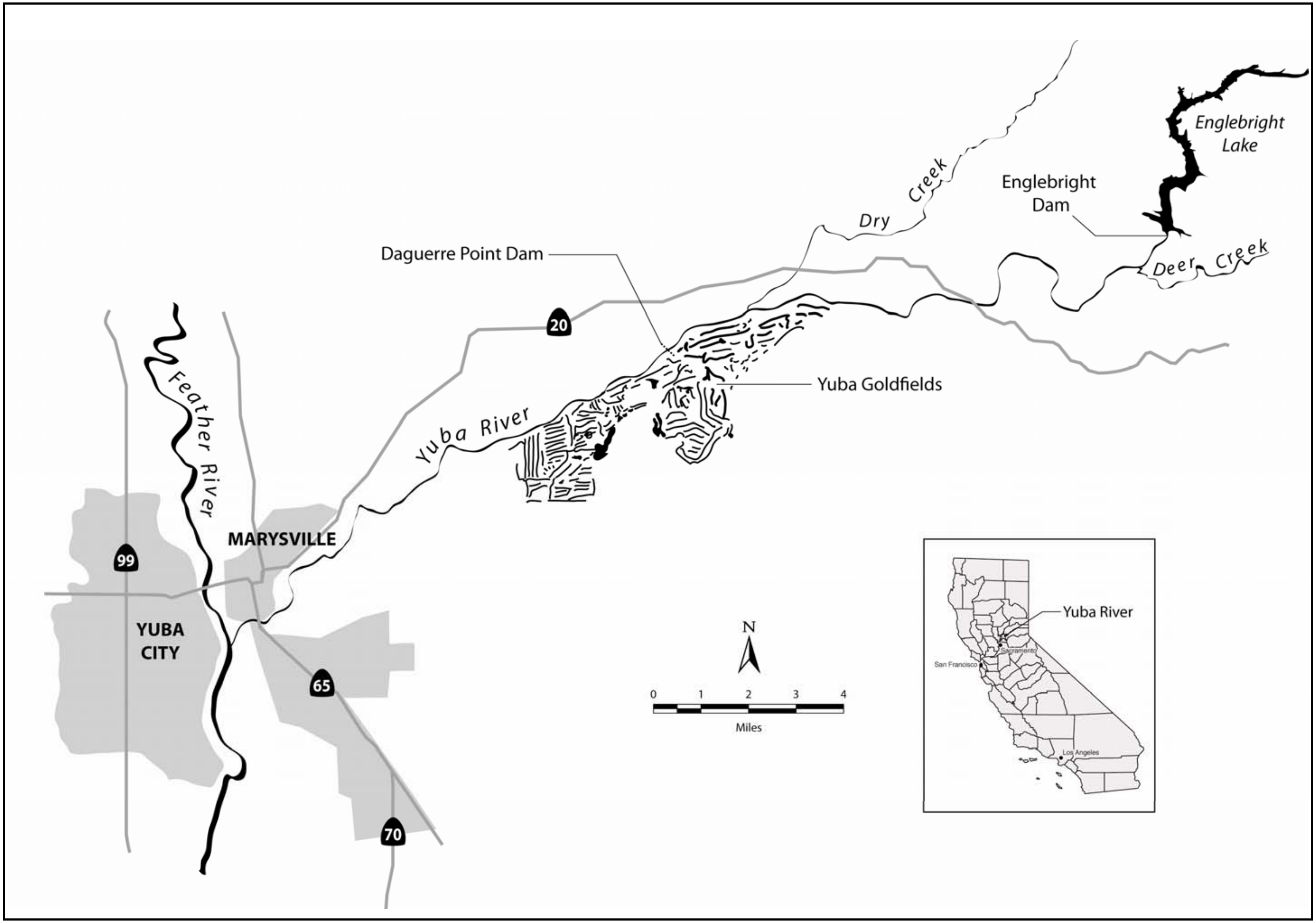

Figure 1
Map of the lower Yuba River

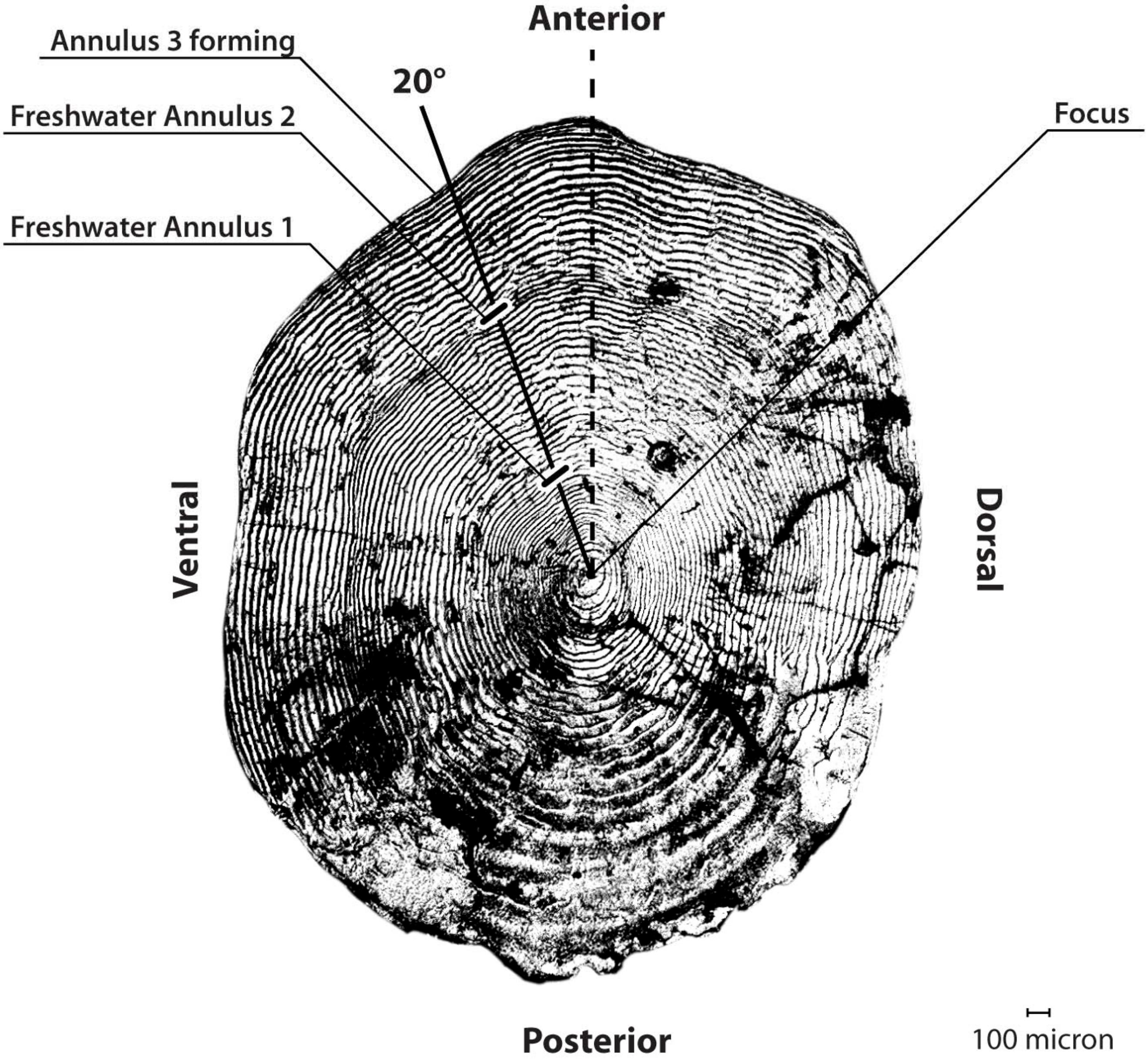

Figure 2
Scale from steelhead rainbow trout (410 mm FL) with three-year freshwater growth pattern. This fish was trapped at Daguerre Point Dam on March 14, 2001.

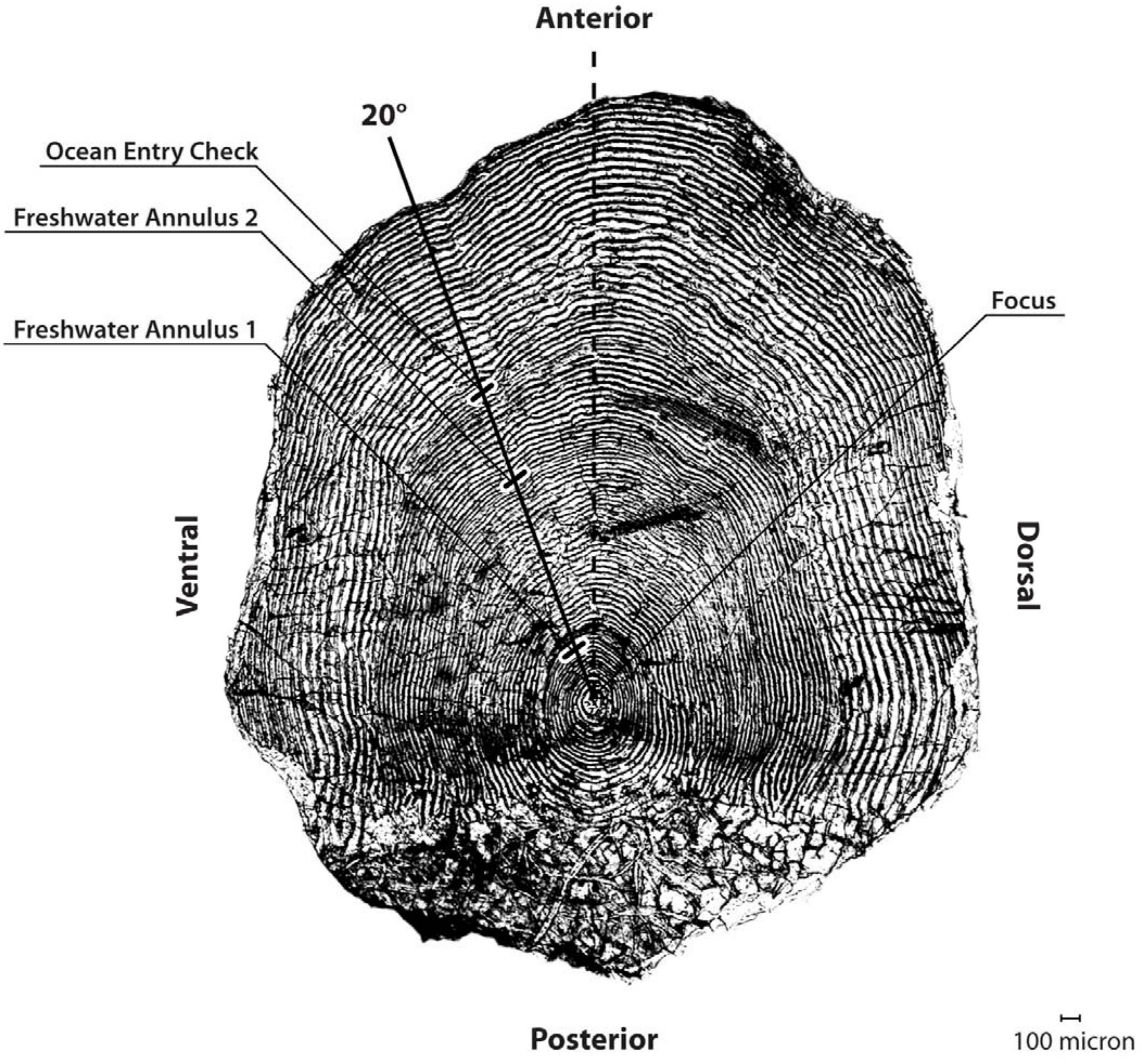

Figure 3
Scale from adult steelhead (572 mm FL) with three-year freshwater and one-year ocean growth pattern (age 3/1). This fish was trapped at Daguerre Point Dam on March 9, 2001.

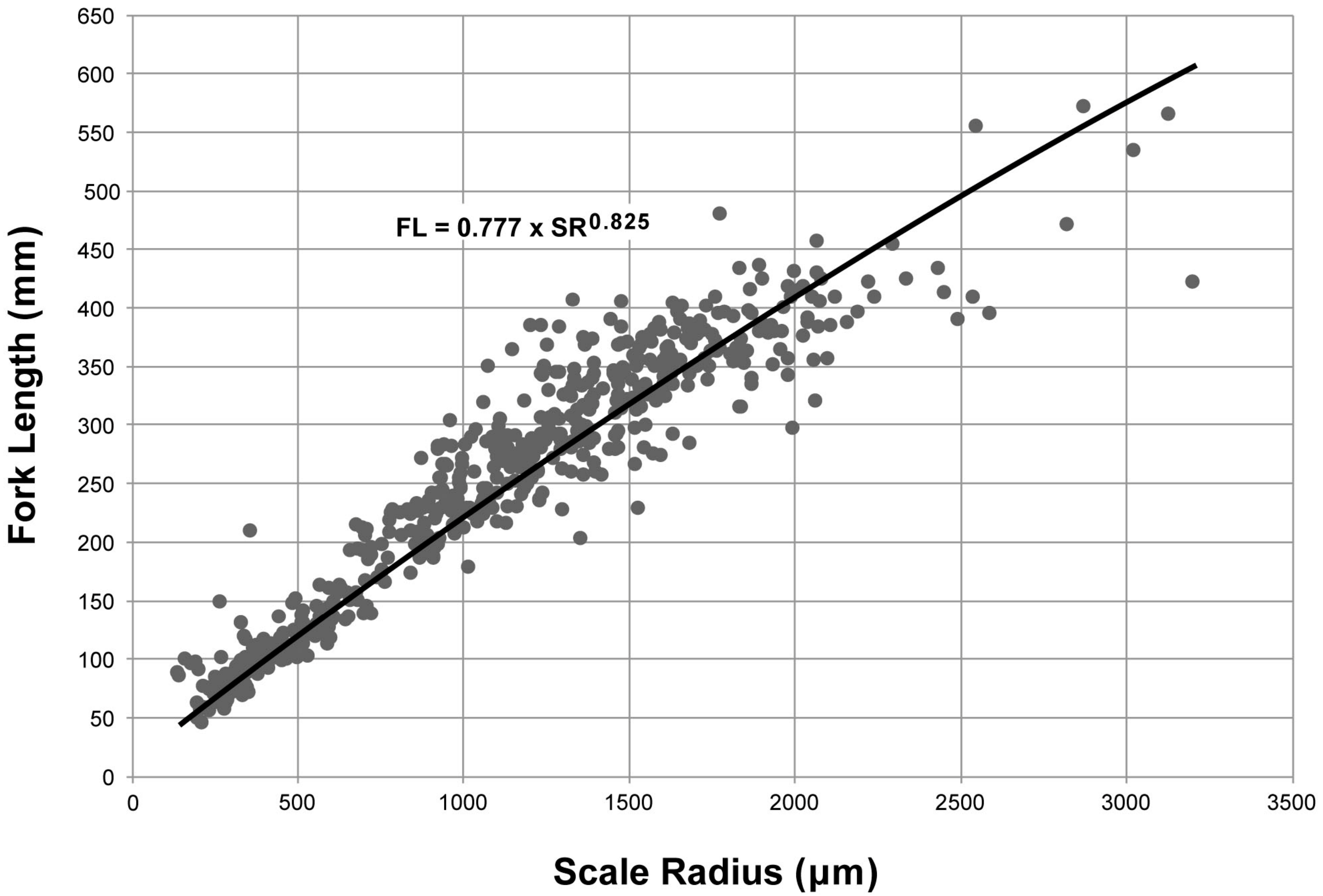

Figure 4

Relationship between scale radius (SR) and fork length (FL) of juvenile and adult steelhead rainbow trout from the lower Yuba River, 1999-2007.

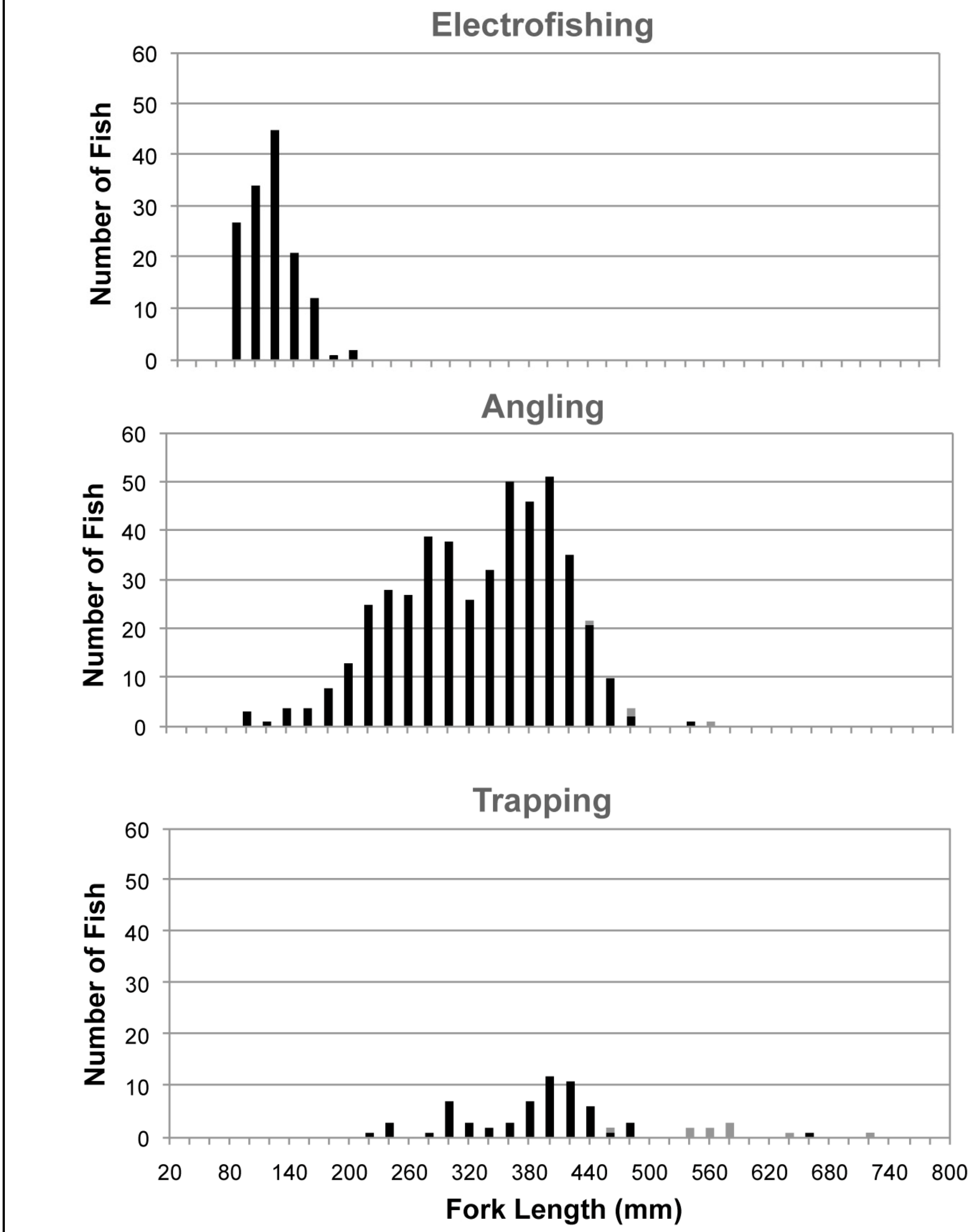

Figure 5

Length-frequency distribution of steelhead rainbow trout collected by electrofishing, angling, and trapping in the lower Yuba River, 1998-2007. Gray bars denote fish identified as steelhead (sea-run).

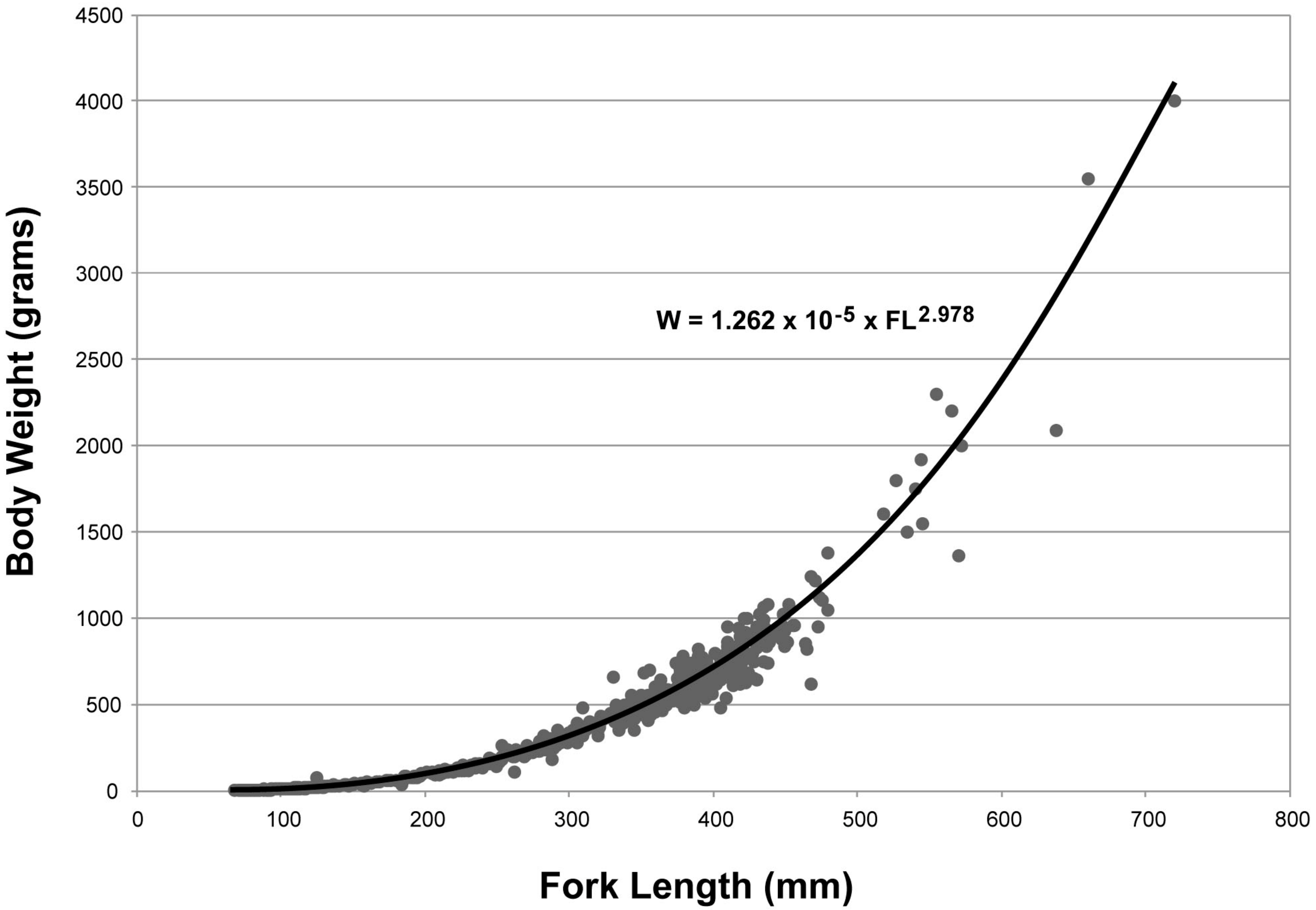

Figure 6

Relationship between body weight (W) and fork length (FL) of steelhead rainbow trout from the lower Yuba River, 1998-2007.

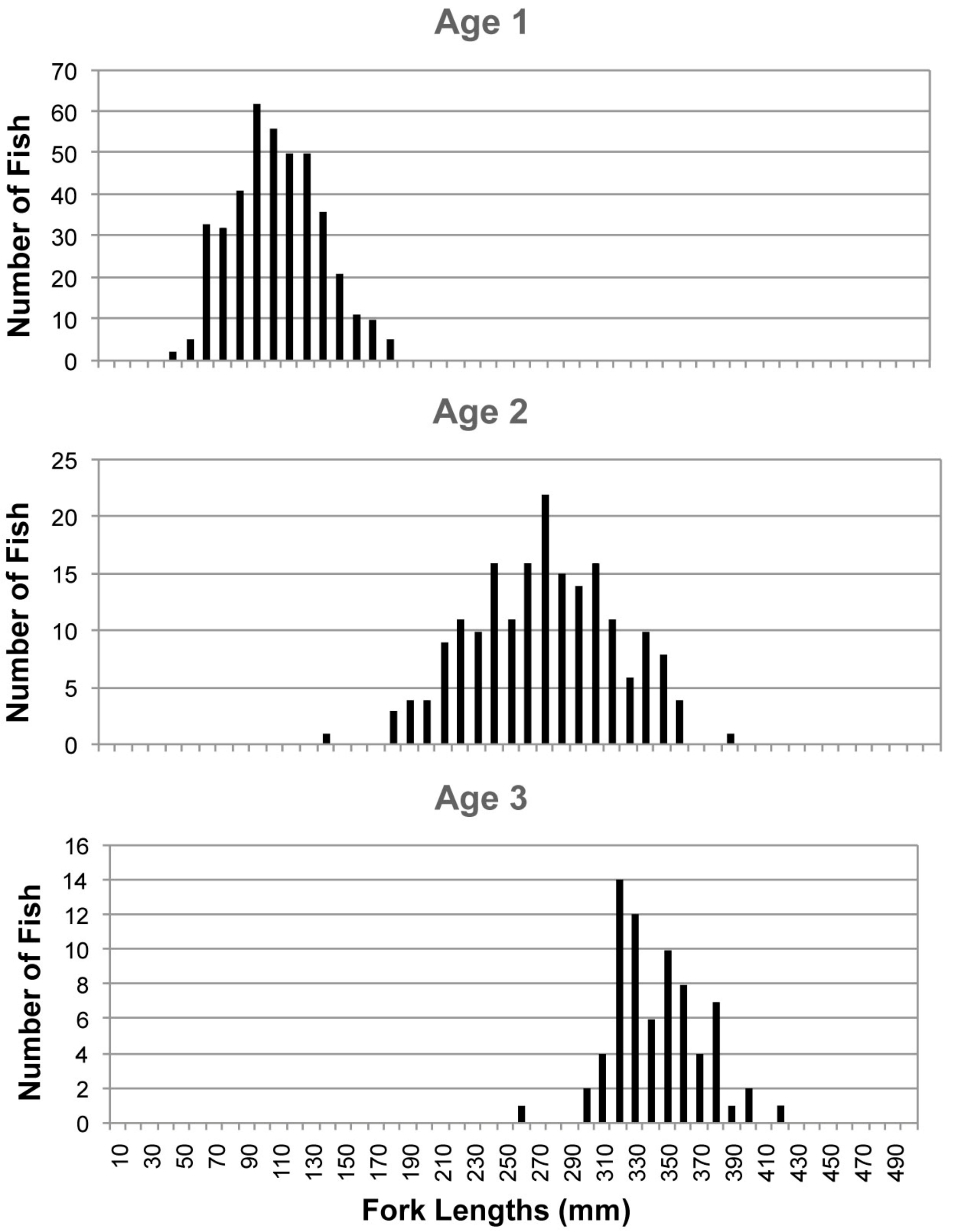

Figure 7

Frequency distribution of back-calculated lengths of steelhead rainbow trout at the end of their first, second, and third winters in freshwater (annulus 1, 2, and 3).

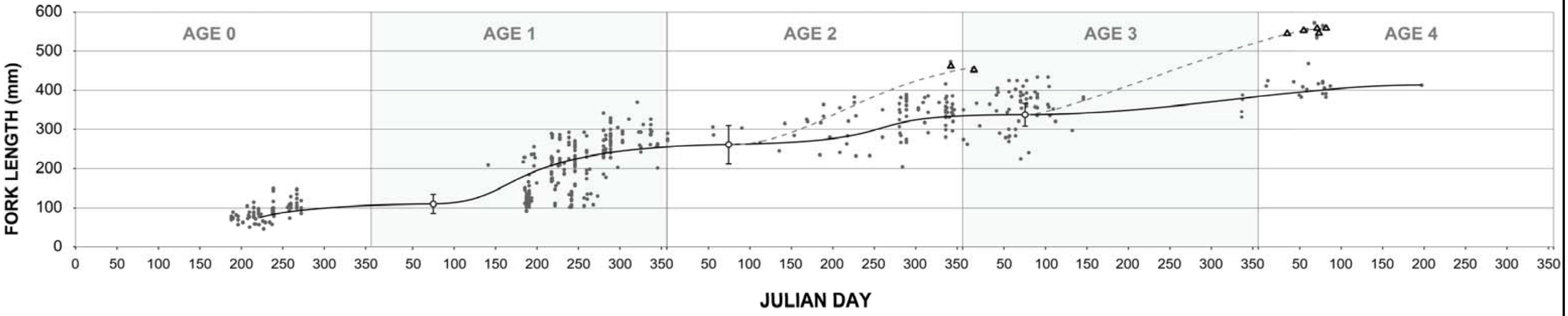

Figure 8

Average freshwater and marine growth trajectories of steelhead rainbow trout based on measured lengths (individual points) and back-calculated mean lengths at annulus 1, 2, and 3. Marine growth trajectories (dashed lines) based on measured lengths of ages 2/1 and 3/1 steelhead adults (open triangles).

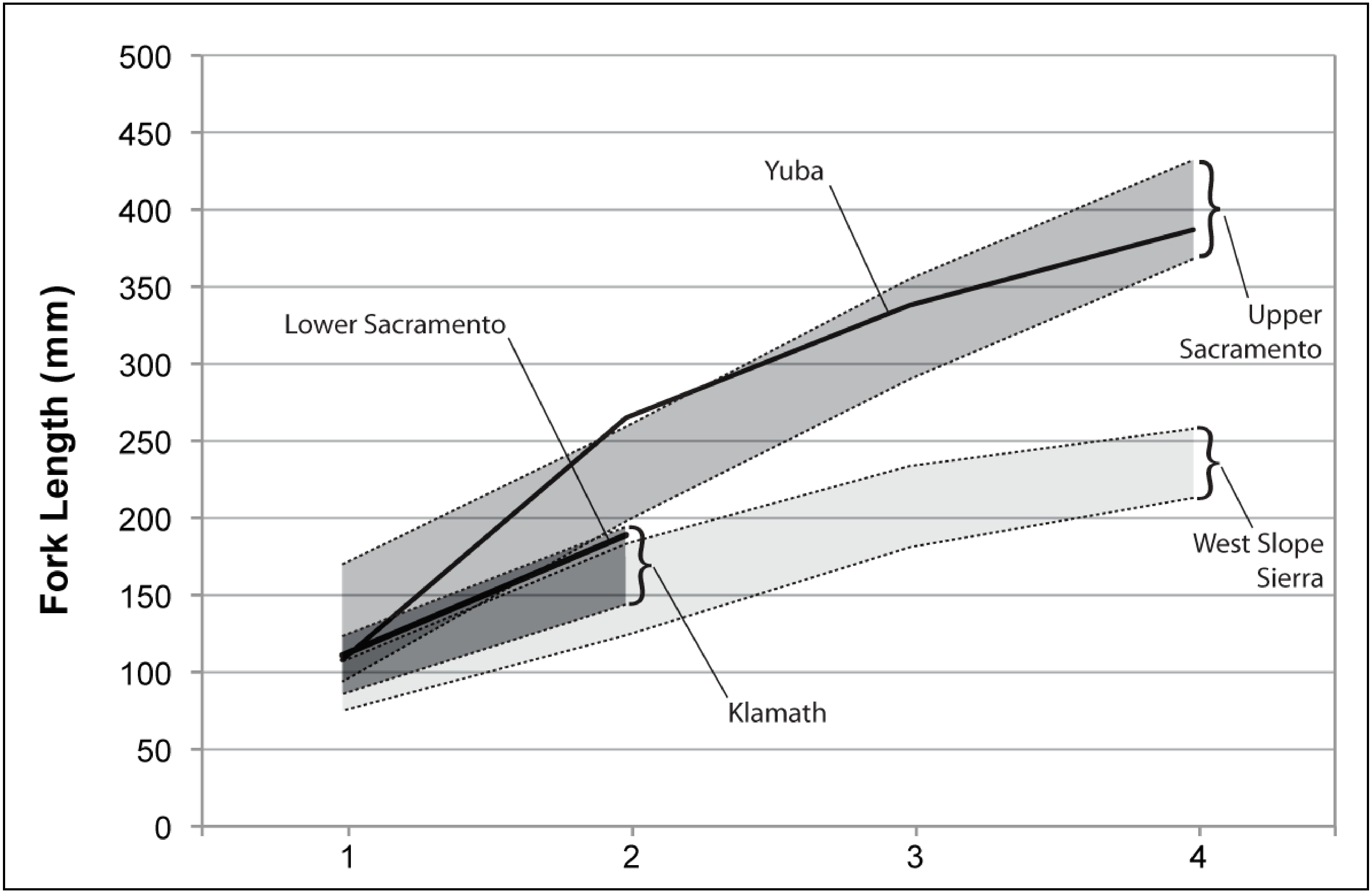

Figure 9

Comparison of growth and size at age (back-calculated lengths at annulus formation) of *O. mykiss* in the lower Yuba River and several other geographic regions and streams of California. Upper Sacramento River streams include McCloud River, Hat Creek, and Fall River; West Slope Sierra Nevada streams include North Fork Yuba River, North Fork American River, and Middle Fork Feather River; Klamath River streams include Klamath and Trinity River mainstem and tributaries; Lower Sacramento are back-calculated lengths of steelhead adults trapped in the lower Sacramento River above the Feather River (Sources: Hallock et al. 1961, Kesner and Barnhart 1972, Snider and Linden 1981, Hopelain 1998).