AGE AND GROWTH OF STEELHEAD RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) IN THE BIG SUR RIVER

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Master of Science in Biological Sciences

by

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Title: Age and Growth of Steelhead Rainbow Trout (*Oncorhynchus mykiss*) in the Big Sur River

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ABSTRACT

Age and Growth of Steelhead Rainbow Trout (*Oncorhynchus mykiss*) in the

Big Sur River

Cynthia Collin

Steelhead trout (*Oncorhynchus mykiss*) numbers have been on a steady decline for at least the last thirty years. The Department of Fish and Game is mandated to restore steelhead populations to twice their current numbers by *The Salmon, Steelhead trout and Anadromous Fisheries Program Act of 1988.* There is thought to be different evolutionary significant units (ESU's) of steelhead separated geographically into northern, central, and southern locations. Little is known about the southern ESU life history traits. This study characterized age and length at spawning, age and length at smolting, and range and frequency of adult sizes of the Big Sur River steelhead population. These characteristics were then compared to other coastal populations north of Big Sur River. Comparisons were made between populations from the big Sur River and several other populations including Waddell Creek (Santa Cruz County), Garcia River (Mendocino County), Gualala River (Mendocino County), Jacoby Creek (Humboldt County), the Mad River (Humboldt County), and the Alsea River (Lincoln County, Oregon). Smolts are significantly larger in Big Sur River as compared to populations at a more northerly latitude. There is a higher proportion of one year old smolts in the Big Sur River when compared to northern populations. First spawners found in the Big Sur River were not significantly different from the Waddell Creek first spawners in length, however, as the

comparison was extended up the coast to more northerly populations, Big Sur River fish were significantly smaller than first spawners of other populations. Fish seemed to mature earlier in this southern portion of the steelhead range. This could be due to warmer water temperatures causing higher primary productivity and, therefore, higher growth rates.

ACKNOWLEDGMENTS

I wish to express thanks to many people who helped me get through this project. Dr. Rob Titus, California Department of Fish and Game, brought me into the project, provided trap designs, materials, field support, data analysis, and provided financial support. This project would not have been possible for me without his guidance and help. Dr. Royden Nakamura, my advisor on this project, helped with the data analysis, field set up, and without his support this project would not have gotten off the ground. I would also like to extend thanks to my committee members Dr. Roger Gambs and Dr. Dennis Frey who have supported me throughout my education and this project and provided me with an example of excellence. I would like to extend sincere thanks to Dr. Robert Smidt, a statistician, who not only helped me to analyze this data in using valid and robust techniques, but whose example of hard work and excellence will not be forgotten by me. I want to thank the Monterey Salmon and Trout project who loaned me the weir panels for the trap. Without these panels, the project would have been put on hold for another year while we built them ourselves, and I am very thankful for their generosity. Jennifer Nelson, Monterey office of California Department of Fish and Game, needs to be thanked again and again for her on-call help. She was my on-site field help, and without her this project never would have happened. She helped with the trap designs, building the traps, storage space, trap installation, walking and snorkeling the river for fish, and she allowed her scientific aid to assist in the project for many hours among other things. Twyla Anderson was Jennifer Nelson's scientific aid who offered many hours to this project. Jeremy Brown also helped build and install the traps. Most of all I would like to thank Allen Clausen, my soon to be husband, for his support throughout this project and for help on the river at odd hours and days when no one else was available.

My parents, John and Edith Collin have given quiet support of my education from the very beginning. They have shown support for the project and encouraged hard work throughout my life. I thank you for giving so much so that I could gain the experience and education that I have. I love you.

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Introduction

The family Salmonidae is made up of salmon and trout. Salmonids are the dominant fishes in the cold-water streams and lakes of North America and Eurasia, where they support major sport and commercial fisheries (Moyle and Cech, 1988). The family is recognized by its streamlined body, forked tail, adipose fin, axillary process by the pelvic fins, large number of pyloric ceca, and a large number of branchiostegal rays (Moyle and Cech, 1988). Steelhead trout are an anadromous form of rainbow trout. Most species of salmonids undergo a spawning migration and possess a series of distinctive life history stages which are modified in sea-run (anadromous) populations. The eggs may be laid in a depression (redd) dug in the gravel in freshwater habitats. The eggs are buried in the redd. The egg develops into an alevin or sac fry, a newly hatched fish which still possess a yolk sac. As the yolk sac is absorbed and the alevins emerge from the gravel, they become fry. The fry eventually develop a series of bars on their sides (parr marks) when they are a few centimeters long and are then called parr, a stage which may last a few months or years. Stream fish may retain the parr marks throughout their life. In anadromous populations, parr transform into smolts and migrate to the sea (Moyle and Cech, 1988). This transition includes profound changes in morphology, physiology, and behavior (Hoar, 1976). In the ocean, smolts mature into adults and eventually return to their home streams for spawning (Moyle and Cech, 1988).

The rainbow trout (*Oncorhynchus mykiss*) is a highly polymorphic species and its sea-going form (steelhead) is one of California's most important anadromous fishes (McEwan et al., 1996). Populations of *O. mykiss* may be anadromous, resident, or a mixture where the two forms interbreed. The two different forms have different names: the anadromous form is called steelhead whereas the resident form is simply called rainbow trout (Titus et al., in prep). Both forms may exist in the same stream system and in some instances they are physically separated from one another due to an impassable barrier to upstream migration, such as a waterfall (Titus et al., in prep).

Steelhead trout were once abundant in California's coastal and Central Valley rivers and streams, however, like many of California's anadromous fish resources, steelhead numbers have been declining for a long time and continue to do so. Crude estimates place the total statewide population at about 250,000, probably less than half of the population of 30 years ago (McEwan, 1996). Restoration of California's anadromous fish populations is mandated by *The Salmon, Steelhead Trout, and Anadromous Fisheries Program Act of 1988* which states that it is a policy of the State to significantly increase the natural production of salmon and steelhead by the end of the century. SB 2261 directs the California Department of Fish and Game to develop a program that strives to double naturally spawning anadromous fish populations by the year 2000 (McEwan and Jackson, 1996). Information on fresh water and ocean life history, behavior, habitat requirements, and other aspects of steelhead biology is needed to develop and implement steelhead conservation (McEwan and Jackson, 1996).

Studies on steelhead trout in Central and Southern California have been limited, and generally they attribute to steelhead many of the same anadromous traits as Pacific salmon (*Oncorhynchus spp.*). The general life history pattern of pacific salmonids is as follows. After a period of two years in a stream (Moyle and Cech, 1988) the juvenile form migrates to the ocean, where it lives for two to three years until reaching maturity; then it returns to its home stream to reproduce and die (Shapavalov and Taft, 1954; Briggs, 1953; Gidley, 1982). Some straying from home streams by returning pacific salmonids occurs, but is not thought to be significant (Shapavalov and Taft, 1954).

Unlike some pacific salmon, steelhead spawning runs are composed of individuals having different combinations of years in fresh water and the ocean (Gidley, 1982). Steelhead from the same brood can migrate to the ocean at different ages and times within a season. They may spend different amounts of time in the ocean and return over protracted periods in a season (Gidley, 1982). Unlike Pacific salmon steelhead are iteroparous (capable of spawning more than once), precocious males have been known to spawn before their first migration to the ocean (i.e. male parr), and are capable of remaining in fresh water if conditions demand it for their entire lives (Gidley, 1982). Shapavalov and Taft (1954) found that fish which spawned once, and returned to the ocean, may skip the next spawning season, and return after two years to spawn again.

South of San Francisco Bay, steelhead are winter-run fish. Entry into freshwater is dependent upon breaching of a sandbar at the stream mouth following the onset of the winter rainy season (Titus et al., in prep). The most comprehensive life history investigation on steelhead was conducted in Waddell Creek in Santa Cruz County (Shapovalov and Taft, 1954). Most upstream movement in Waddell Creek occurred during December - April with the heaviest movement being December - February (Shapovalov and Taft, 1954). These fish spawn during the same spawning season, normally within four months of entering the stream. The migratory stimulus is environmentally controlled by increasing flow and/or temperature (Briggs, 1953). Shapovalov and Taft found that males dominate the early portion of the run; whereas females dominate the latter portion of the run. In addition, younger fish arrive earlier as is typical of other salmonids (Shapovalov and Taft, 1954).

The female chooses the redd site, constructs the nest, and covers the eggs after fertilization (Shapovalov and Taft, 1954). Additional redds may be constructed. After spawning is complete, most fish move immediately downstream towards the ocean (Gidley, 1982). At Waddell Creek Shapovalov and Taft (1954) found that most downstream movement was during March - July, but some fish remained in large pools after spawning (Shapovalov and Taft, 1954). Males may spend a longer period in fresh water than females perhaps in order to mate with more than one female. Males spending longer periods in freshwater may become more susceptible to diseases, parasites, predation, fishing pressure, and other factors which lead to a higher mortality in males than females. This difference in freshwater occupancy could account for the observation that a higher percentage of females are repeat spawners (Chapman, 1958).

The time interval between fertilization and hatching is temperature dependent in all salmonids and may also vary with population (Wagner et al., 1963). Hatching occurs after about 19 days at an average temperature of 15.5 degrees Celsius and 80 days at 4.5 degrees Celsius (Wales, 1941). After emergence, juveniles take one to three years to reach migration size (Wagner et al., 1963). Average migration size according to Wagner et al. (1963) was 16 cm. irrespective of age.

As parr transform into smolts they become more streamlined in shape, take on a silvery appearance, show an increase in activity, and become adapted to saline conditions (Hoar, 1976). The body shape is measured by a length - weight relationship and is associated with a fall in total body lipids (Hoar 1939, Martin 1949, Fessler and Wagner 1969) . Silvering is due to deposition of purine layers, specifically guanine, beneath the scale layer and deep in the dermis adjacent to the muscle. Related to this purine deposition is an increase in the ratio of guanine and hypoxanthine during smoltification which are also found in the same layers (Johnston and Eales, 1967). Salinity resistance involves active transport of salt across the gills fueled by ATP causing an increase in Na+ - K+ ATPase activity during the spring. As fish increase in size they also mature physiologically in preparation for the saline ocean environment. Salinity resistance increases as fish increase in size. Thus, for a given age, larger fish are more resistant to increased salinity. These changes during smolt development fall into two categories. Fish kept under lab conditions undergo changes when they reach a certain size, but unless photoperiod changes are introduced, complete transformation will not take place. Therefore, some changes are size dependent (e.g. silvering and body shape) while others are dependent on environmental factors such as salinity resistance. Photoperiod is the main environmental factor influencing salinity resistance (Conte and Wagner, 1965). Data from steelhead indicate that the smolt change is transient and if the fish is retained in freshwater for several weeks after the usual time of migration, they lose this high salinity resistance and revert back to the physiology of a fresh-water fish (Conte and Wagner, 1965).

Within and between population variation in physiology and certain life history traits is not well documented for California steelhead especially south of San Francisco Bay (Titus et al., in prep). According to Nielsen (1994) all forms of *O. mykiss* in the same drainage are more closely related to each other than they are to *O. mykiss* from another drainage. For example, steelhead are more closely related to resident rainbow trout in the same drainage than they are to steelhead from another drainage (Nielsen, J., et al., 1994). This pattern suggests interbreeding between steelhead and rainbow trout (Titus et al., in prep). Shapovalov and Taft's (1954) comprehensive study provides general baseline information upon which comparisons can be made.

Generally, little is known about individual stocks of southern steelhead from specific drainages; consequently management decisions are based on the "generic" ecological and life history characteristics of the better known northern steelhead populations (McEwan, 1996). Recent information strongly suggests that many anadromous fish population characteristics vary from drainage to drainage (Nielsen, et al., 1994). Such variability in population characteristics indicates that data on southern populations of steelhead trout are needed to properly manage these resources.

The specific objectives of this study were to determine selected life history characteristics of Big Sur River steelhead as representative of coastal populations south of San Francisco Bay. This included determining the age at smolting, size at smolting, the age at first spawning, the size at first spawning, and the range and frequency of adult and smolt sizes. Then these characteristics were compared to the Waddell creek study and other coastal steelhead populations on the western coast to evaluate possible latitudinal trends.

Methods and Materials

Study Area

The Big Sur River, Monterey County, (Figure 1 and 2) was selected by CDFG as a study site because it is relatively pristine, offers good accessibility, and has a viable steelhead trout population. Only the lower 12 km of the river is available to steelhead for spawning purposes. Access to the upper river is blocked by a natural bedrock waterfall. Above this bedrock waterfall, the river flows through the Ventana Wilderness within the Los Padres National Forest. Pfeiffer Big Sur State Park is located directly downstream from the falls. The lowermost 6.4 km is included in Andrew Molera State Park. Redwoods (*Sequoia sempervirens*) dominate the riparian zone while the upper hill slopes are dominated by grassland, chaparral, and oak woodland communities (California Department of Fish and Game, 1994).

For purposes of this study, the accessible lower portion of the river was divided into three main study reaches divided by physical characteristics of the channel such as stream gradient, channel morphology, substrate composition, and riparian vegetation (CDFG, 1994).

The uppermost reach is designated as the 'gorge reach.' It extends from the barrier bedrock falls to just above the Pfeiffer Big Sur State Park campground area. This reach is characterized by high gradients in a steep, dry, rocky canyon, a confined channel with no floodplain development, substrate dominated by large cobbles, boulders, and bedrock, and relatively low retention of sediments. The habitat in this reach consists of a series of step runs and pools (CDFG, 1994).

The middle reach is designated as the 'campground reach' which begins at the bottom of the gorge in the upper part of the campground where the stream gradient decreases abruptly. The middle reach extends to the upstream boundary of Andrew Molera State Park. It is characterized by a well developed riparian redwood forest, moderate floodplain development; and the average substrate particle size decreases to cobbles. This reach consists of a series of riffles and runs (CDFG, 1994).

The lower reach is designated as the 'Molera reach' and extends downstream from the upper Andrew Molera State Park boundary. The reach terminates in the Pacific Ocean, but the lowest 1.6 km portion of the reach becomes a brackish lagoon during the dry season when a sandbar accumulates restricts flow to the ocean. The lower reach is characterized by the lowest stream gradient, greatest floodplain development, and the substrate is dominated by large gravel and cobbles. The mixed riparian forest gradually diminishes into a narrow, dense willow-dominated riparian border. This reach also consists of a series of riffles and runs (CDFG, 1994).

Two tributaries enter the Big Sur River within the study area. Juan Higuera Creek is the largest perennial tributary to the lower Big Sur River, and enters the river in the lower half of the campground reach (CDFG, 1994). Post Creek is a smaller tributary, which shows intermittent flow in some summers. Post Creek enters the Big Sur River in the upper campground reach. Both tributaries have lower and upper reaches that are divided by an impassable fish barrier and both creeks offer some spawning and nursery grounds for steelhead (CDFG, 1994).

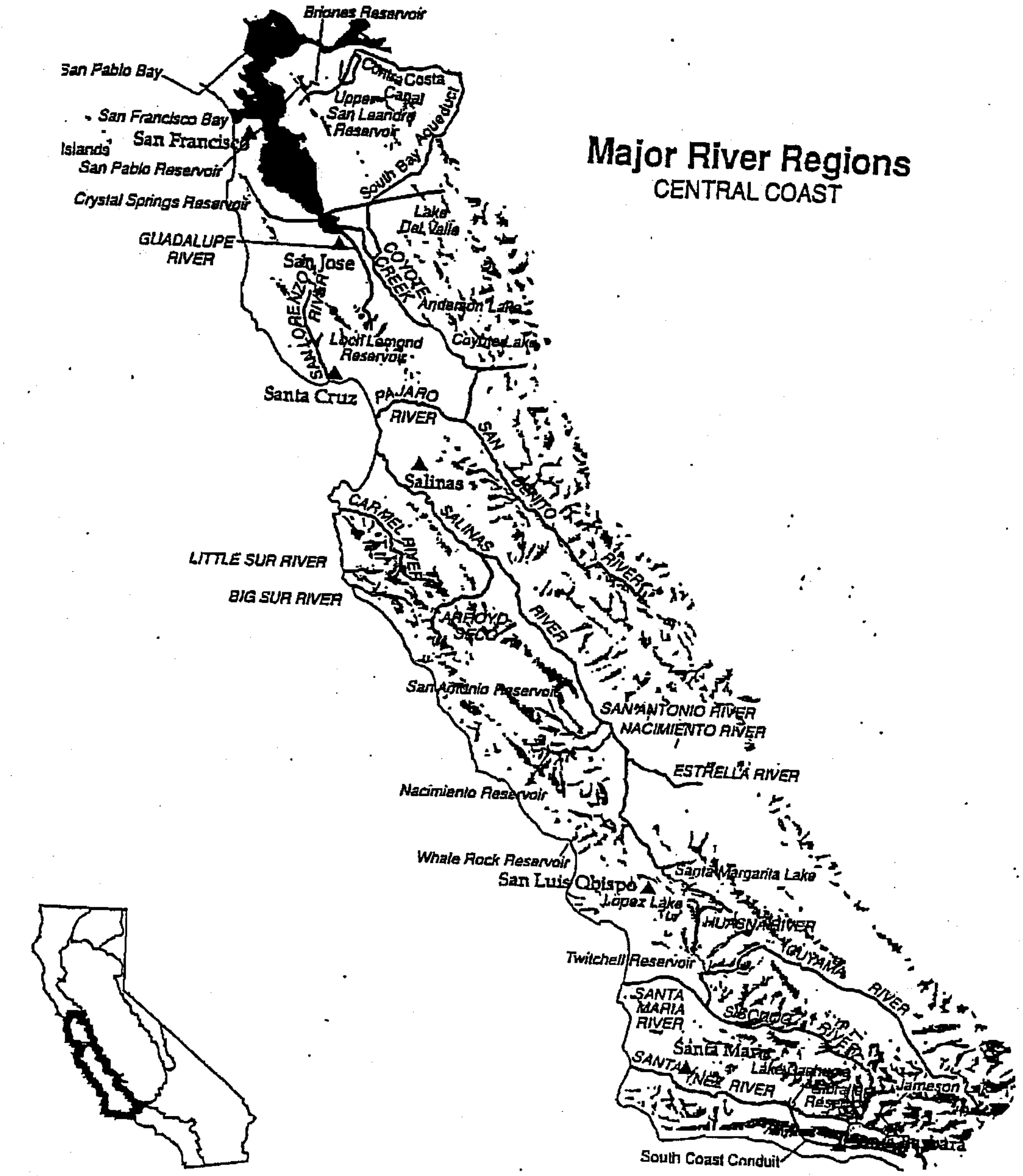

Figure 1

Map of the Big Sur River in the Central Coast Region of California (Chatfield et al., 1993)

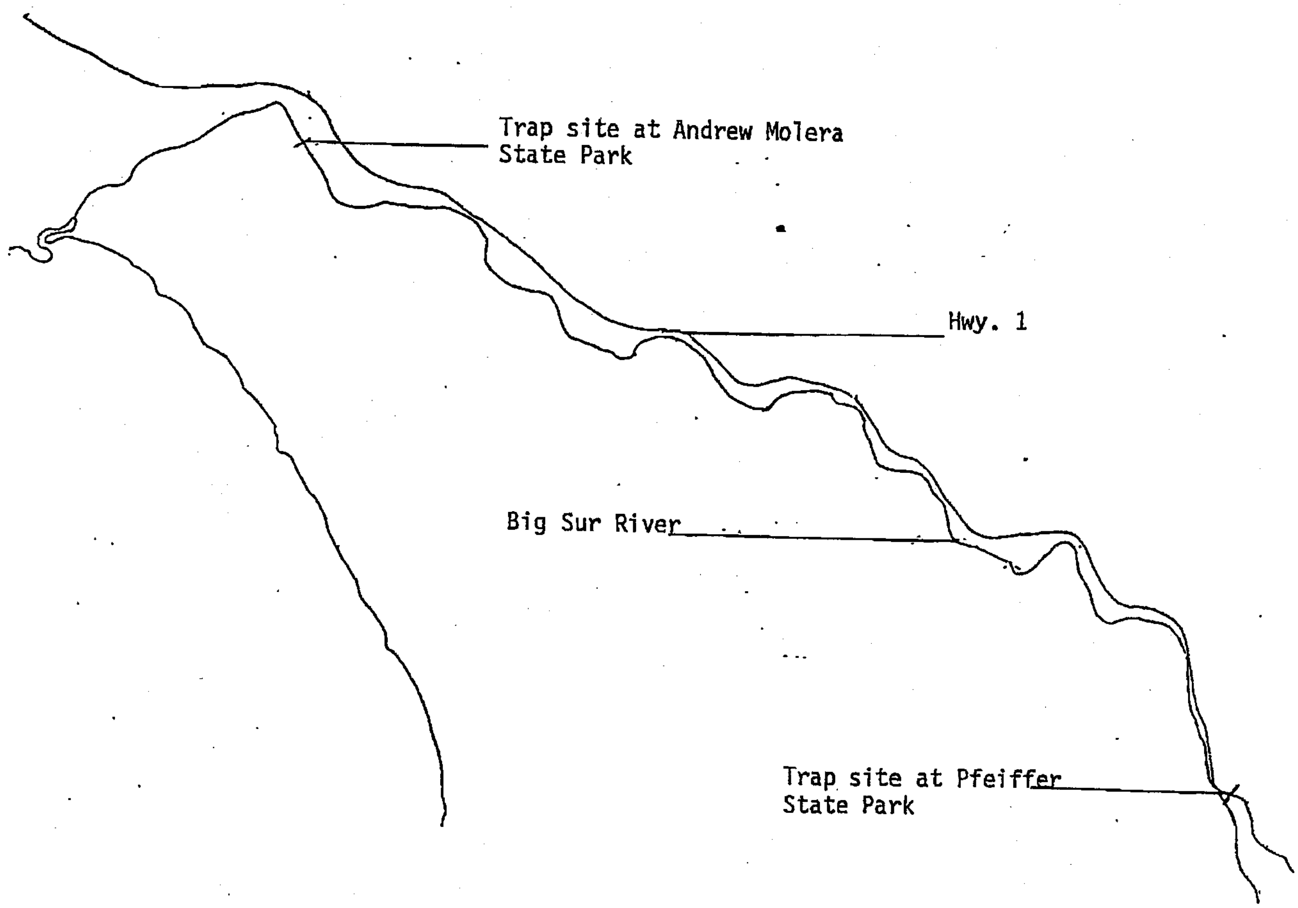

Figure 2

Big Sur River, Monterey County

Preliminary Field Work

During 17-20 September 1992 a California Department of Fish and Game reconnaissance electrofishing survey of the lower Big Sur River revealed the presence of juvenile steelhead/rainbow trout throughout the lower river and Juan Higuera Creek. The main river and tributary reaches were also identified at this time. Distinct habitat units (riffles, runs, pools, and cascades) from each reach were chosen for the study. Overall 19 distinct habitat units were identified for study throughout the three reaches (CDFG, 1994). The four defined habitat units are described as follows. A pool is generally deeper and wider than the average width and depth of the stream, the velocity within it is slower than that upstream or downstream from it, and hiding places for the fish are more extensive in it than in adjacent parts of the stream (Lagler, 1952). Also, the slope in a pool area approaches 0%. A riffle area has a higher water velocity because of the increased slope. Some surface white water may be apparent and water is generally shallow compared with the average depth of the system. A run has a similar slope to a riffle, however the water is deeper and there is no apparent white water in these habitat types. A cascade is a habitat defined by sections containing a higher slope than the other habitat types previously discussed where water is falling from small waterfall to small 'pools' and the gradient is noted from the bottom of the section to the beginning of the first upstream waterfall.

During 13 October - 6 November 1992, 881 juvenile steelhead/rainbow trout were anesthetized, marked with alcian blue dye on the ventral surface, a scale sample was taken, and fish were released. All fish marked with the alcian dye had their adipose fin clipped. Therefore, all of these fish were identifiable as a recapture by the adipose clip even if the dye marks have faded (CDFG, 1994). Dye marks were applied to different parts of the ventral surface to distinguish habitat unit and size of fish. Three age classes were identified. The first age class included large young-of-the-year fish (0+), the second included smaller young-of-the-year fish (0+), and the third included all other fish. The results of this marking session showed that the mainstem population structure was clearly dominated by young-of-the-year steelhead (0+). A small proportion of fish were one year old (1+), two years old (2+), and older fish. Fish were found in all habitat units identified and in both reaches of Juan Higuera Creek.

In 1993 a second marking survey was done from 23 August - 24 September and 1068 juvenile steelhead/rainbow trout were sampled in the same manner as 1992. Trout occurred in 17 of the habitat units from the gorge through the Molera reach.

Three pipe traps were installed to monitor downstream migration and collect data on smolt lengths (CDFG, 1994) (Figure 3). The first pipe trap was installed on 2 April 1993. It was located in the lower Molera reach, adjacent to the walk-in campground in Andrew Molera State Park. Many downstream migrants were captured, but very few were marked. Young-of-the-year (0+) dominated numerically. The second pipe trap was installed near the downstream boundary of the campground reach on 10 August 1993. A third pipe trap was installed below the downstream boundary of the gorge reach, at the confluence with Post Creek, on 21 September, 1993.

In the fall of 1994 1,000 fish were marked with PIT (Passive Integrated Transponder) tags and released. PIT tags allowed fish to be distinguished so that its rearing habitat could be compared to sea growth and other life history traits provided that enough of these fish could be recaptured (CDFG, 1994).

Pipe traps were periodically monitored until January of 1995 when high flows blew the traps out. Lack of funding to continue this component of the project prevented follow-up work on the PIT tagged juveniles (CDFG, 1994).

Adult Steelhead Trout Data Collection

Two attempts to collect field data on adults steelhead were made during the 1996-1997 field season. (This is when the author became involved in the study). The first involved a migrant trapping effort for both upstream and downstream migrants. The second effort involved collecting scales and other information from the anglers in the Big Sur River. Both juvenile and adult scales were also obtained from the Sacramento office of the California Department of Fish and Game.

Coordinated Angler Collections (Creel Census)

On November 23, 1996 a meeting was held involving the local anglers in Big Sur, Rob Titus and the author. The purpose of this meeting was to ask for angler help in collecting data including scales and other parameters and to try and enlist their help during high flow situations when the trap set-up would need to be taken out of the river. The turnout was small, but there were representatives from the Carmel Steelheaders Association, Big Sur local anglers, and the Friend's of the Big Sur River. These representatives were receptive to both objectives of the meeting. We handed out instruction sheets for the data collection process and fielded any questions that arose. We collected the scale envelopes from the anglers through angler survey boxes installed in Fall of 1996 by the Monterey California Department of Fish and Game office. In this way relationships were established early. No

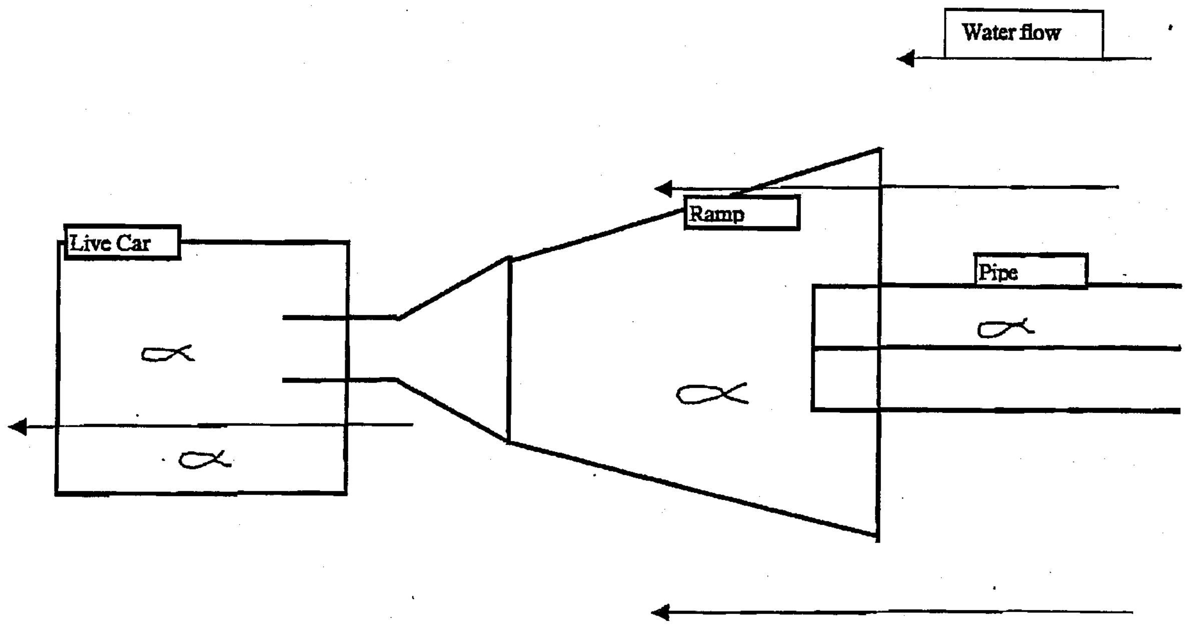

Figure 3

Pipe trap design used by the California Department of Fish and Game in the preliminary field work on the Big Sur River (Figure not to scale).

high flow events occurred after the installation of the trap.

Trap Construction and Upstream/Downstream Migrant Trapping Methods

Trap building started on November 19, 1996. Two live boxes were built on various days until their installation into the Big Sur River on February 20, 1997. The live cars were 1.8 meters long by .91 m. high by .91 m. wide (Figure 4). They were framed with plate steel slotted angles. The frame was surrounded by .64 centimeters mesh welded wire. The sides were supported by plate steel slotted flats placed around the middle of the box and cris crossed at the base of the trap. A hatch was cut in the top of the live car that was .91 meters by .91 m. to allow removal of fish. The fish entrance was funnel-shaped with a door at the base of the funnel. The door was 12.7 cm. wide by 15.2 cm. high in the upstream trap and 10.2 cm. wide and 12.7 cm. high in the downstream migrant trap. In the upstream migrant trap the water velocity kept the door shut behind any fish. In the downstream migrant trap the door was weighted so that the water velocity would not keep it open. Each live car had sun cloth on the top of the trap to reduce excessively high temperatures. Suncloth was also added on the upstream side of the upstream migrant trap to reduce water velocity in the live car.

Ten weir panels, 1.2 meters wide by .91 m. tall, were used to span the width of the river. The weir panels were framed with .64 cm. steel slates and had .64 cm. welded rebar running horizontally between the steel slates. Rebar was placed approximately 2.5 cm. apart and panels were installed by leaning them against the current and supporting them with struts. The rebar spacing on the weir would allow passage of all steelhead age classes except adults.

Installation of the weir and live boxes into the Big Sur River occurred on 20 February 1997. This was late in the spawning season, however, high flows precluded installation before this date (See figure 5 and 6). The traps were installed immediately below the Big Sur Lodge in Pfeiffer State Park. This site was upstream from the angler boundary which is the Hwy 1 crossing over the Big Sur River. The river was approximately 15.2 meters wide when traps were installed. The downstream live car was placed in the deepest, highest velocity area in the channel (the thalweg) in an effort to catch spent fish that may be drifting downstream in the current. Four 19 millimeter rebar pieces were driven into the channel and fastened to the live can with bailing wire. Weir panels were placed at an upstream angle across the river and the upstream migrant live car was placed just out of the high velocity zone of the main channel in an effort to minimize water velocity inside the trap. Weir panels were attached with bailing wire at two or three locations along each seam. Gaps between the bottom of the panels and the substrate were sealed with rocks and between the live cars and panels were sealed with hardware cloth. A staff gage to measure flow was installed in order to monitor flow at the site. A temperature logger was installed on the downstream trap to record water temperatures throughout the duration of the study. Weatherproof informational sheets about the project were made and installed on each bank for public awareness. Each live car was locked while I was not at the site to discourage poaching attempts. These traps were fished from Saturday mornings through Tuesday afternoons(three nights a week). On Tuesday afternoons the trap was closed by laying down three weir panels on the bottom of

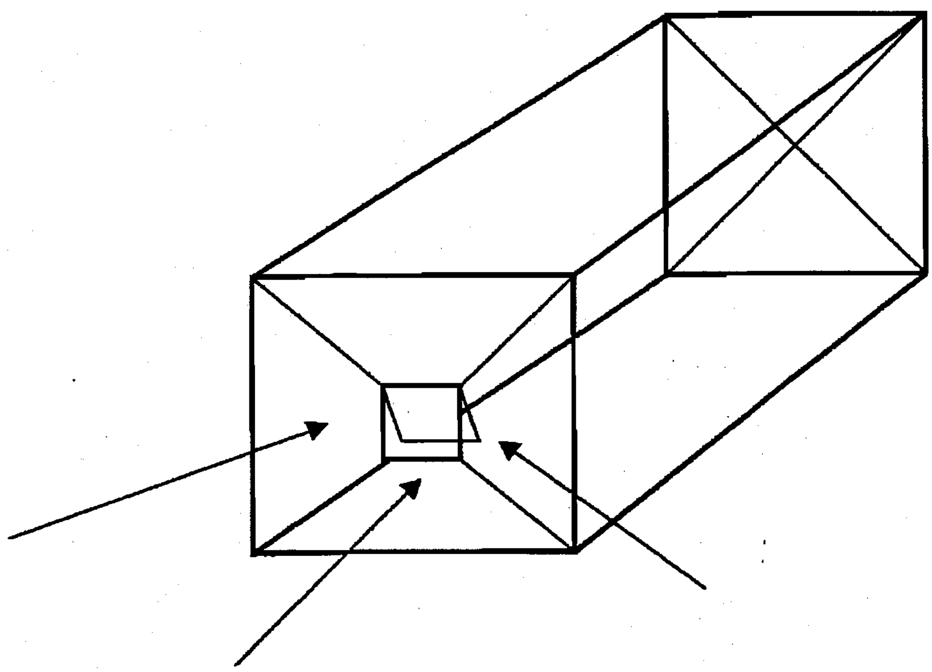

Figure 4

Box trap design used in this study for the collection of upstream and downstream steelhead trout migrants. (Measurements were 6 feet long by 3 feet wide by 3 feet tall. Figure not to scale.)

the river and securing the trap doors with bailing wire to prevent fish from entering boxes. On Saturday morning the trap doors were opened and the weir panels were set upright again. The traps were checked in the morning, afternoon, and evening so that fish were not held in the trap longer than overnight.

February through April, 1997, proved to be extremely dry months and flow rate steadily dropped through the spring monitoring period. Flow rate dropped so fast that the door of the upstream migrant live car was above the water level by the end of March. This site was above the angler boundary, but the fishing season had ended and there had been many fish sighted spawning downstream of the trap. Therefore, we moved the traps downstream to Andrew Molera State Park and installed them just below the parking lot on 26 and 27 March 1997. The river at this site was approximately 7.6 meters wide when traps were installed. The trap was fitted with an upstream live car as before, but this time a fyke net was used to catch downstream migrants. The mouth of the fyke net (Figure 7) was placed flush with the weir panels. The fyke net was tied to T-stakes driven in flush with the weir panels. The mouth of the fyke net measured 4 feet by 4 feet and length of the net was 18 feet. The end of the net funneled into a measured 2 feet by 2 feet by 4 feet box. The mouth of the fyke net was placed in the thalweg of a riffle in an effort to catch spent fish floating downstream in the current. The live car was positioned in a deep pool so that water velocity in the box was slow. Weir panels at this site were again fastened together with bailing wire and placed at an angle where both upstream and downstream fish were shunted by the panels towards the appropriate trap. This set up also included the temperature recorder, the staff gage, two informational signs, and locks on both the upstream and downstream live cars. This trap was monitored Thursday morning through Sunday afternoon (three nights a week). In order to close the downstream trap on Sunday afternoons, a weir panel was placed in front of the mouth of the fyke to exclude any adults from entry. Two weir panels were laid on the bottom of the river so fish could pass through the trap when it was not being monitored. The trap door of the upstream migrant trap was secured using bailing wire.

Scale Analysis

Scales collected from anglers and trapped fish were allowed to dry in the scale envelopes for at least one month. At least two scales were then mounted between two slides which were taped together and labeled. This produced slides permanent enough to work with, but also allowed the scales to be removed if necessary.

Scale Interpretation and Ageing Protocol

Standard ageing techniques involved counting annuli and taking measurements from the scales (Shapovalov and Taft, 1954). All scales were read at the same magnification, therefore, all readings could be compared. All measurements were taken along the anterior radius of the scale from the focus of the scale to the outer edge of each annulus (Figure 8). When possible, an average radius was calculated from three scales from each sample; sometimes an average radius was based on two or one scale when three were not available. Age was taken for both adult and juvenile scales. When reading adult scales, measurements were taken to each annulus and used in the back calculation process (described below) to arrive at a length for each fish at each age. Adult scales were read

Figure 5

Trap site above the Hwy 1 crossing and the angler boundary in the campground reach of the river.

Figure 6

Trap site above the Hwy 1 crossing and the angler boundary in the campground reach of the river.

Figure 7

Trap site in Andrew Molera State Park.

three times and the third reading was used for data analysis purposes. Protocols for scale analysis are described by Shapovalov and Taft (1954) and summarized as follows. A fish was considered to be in its first year of life from the time that it hatched until the beginning of formation of new scale growth following the completion of the first annulus. Fish in this age class were denoted as 0+ fish or simply by a +. A fish is in its second year (denoted 1+) includes the time after new growth begins after the first annulus until the completion of the second annulus and the beginning of new growth. In this way the number denoting a fish is the number of annuli present (Shapovalov and Taft, 1954). In order to incorporate some details of the life history when reading the scales the following system has been used by Shapovalov and Taft (1954). The sign '/' is used to separate life in fresh water from life in salt water. Thus, a fish which had spent two growing seasons in fresh water only would be represented by the formula 2/ and one that had migrated to sea in its first year and had spent its first two years at sea would be represented by the formula +/2. Continuing, the formula 2/1 represents a fish that had spent two years of stream life and one year of sea life. In the case of steelhead, a capital "S" is used to indicate a spawning, normally represented on the scales by a spawning mark. The S is not added until a fish has completed spawning. Thus, if a fish had spent two years of stream life and one year of sea life and had then entered fresh water and spawned it would by represented by the formula 2/1S. A period is used to separate years followed by a spawning from years not followed by a spawning. Consequently, if the same fish had not entered fresh water and spawned until the end of a second year of sea

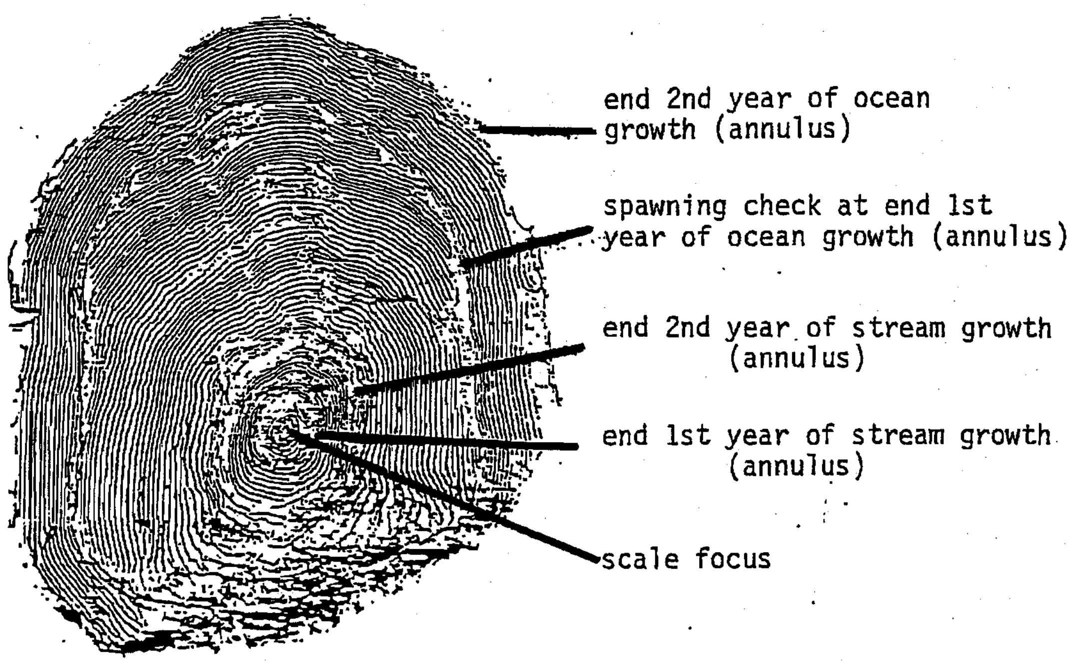

Figure 8

Adult steelhead trout scale with a 2/2S life history.

life it would be represented by the formula 2/1.1S. If instead the fish had spawned at the end of both its first and second years of sea life it would be represented by the formula 2/2S (Shapovalov and Taft, 1954).

Data Analysis

Multiple regression was used to develop a relationship between total scale radius and fish length and to bring out any differences between the juvenile relationship and the adult relationship of scale radius and total length. This relationship can not be plotted because there is more than one factor that bests predicts the value of total scale radius. The natural log was taken of total scale radius and fish length in order to get a linear relationship instead of a curvilinear one. The natural log of the total scale radius was best predicted by two variables; the natural log of fish length and the product between the natural log of fish length and a dummy variable differentiating juvenile fish and adult fish where 0=juvenile fish and 1=adult fish. The dummy variable itself was included in the model to begin, but proved to be insignificant in predicting the natural log of the total scale radius. The dummy variable by itself does not add any new information to the equation. The predictor of the product covers the information that the dummy variable brought to the equation. The regression equation used was $y = B0 + B1X1 + B2X2$ where y = the natural log of the total scale radius measurement, B0 was -3.3, B1 was 1.01, X1 was the natural log of fish length, B2 was .0393, and X2 was the product of the natural log of fish length and the dummy variable previously discussed. Because the dummy variable was 0 for juveniles and one for adults the additional slope was used for the adults and not used for the juveniles in the back-calculation of length at annulus formation, spawning check formation, or smolting. There was a slight difference in slope between the two relationships, but the y intercept was identical (3.3). Back-calculations were derived by using the predictive regression equation with a correction factor which forced the regression line through the origin (Ward and Slaney, 1989). This correction factor was 3.3 and was used so that scale growth was assumed to begin at fish length 0. Therefore, the complete equation used was $y = (B0 + B1X1 + B2X2) - 3.3$ (equation 1). Back-calculated fish lengths at each annuli were calculated using the derived predictive regression equation. The back-calculated lengths were then used in comparisons with other studies on more northerly populations of steelhead. The major comparison was made with the Waddell Creek study by Shapovalov and Taft (1954). Statistical comparisons were based on simple t-tests, chi-square tests, and normality plots using minitab software.

Results

Smolts

Smolt information was obtained from scales taken from 28 adult fish. Back-calculation of length at ocean entry was derived using equation 1 (previously described in methods). Twenty of the fish (71%) smolted after two years of fresh water growth and 8 (29%) smolted after one year of fresh water growth (Table 1). Mean length of age 2+ smolts was 199.6 millimeters at ocean entry. Mean length of age 1+ smolts was 157.0 millimeters at ocean entry. The average length at smolting was 188.4 millimeters (Table 2). The frequency distribution histogram of back-calculated smolt length shows an approximately normal distribution (Figure9).

Back calculations of smolt length and ranges of lengths of the three different first spawner categories is shown in Table 3. For the 1/1 age class the average back-calculated smolt length was 165.6 millimeters and the range was 109.1 - 224.7 millimeters. For the 2/1 age class the average back-calculated smolt length was 186.9 millimeters and the range was 149.0 - 259.8 millimeters. There was only one 2/2 first spawner observed and its back-calculated length was 209.7 millimeters. A sample of smolts was taken in downstream migration traps as part of an earlier study (1993) on steelhead in the Big Sur River by the California Department of Fish and Game. Data from these fish provided a frequency distribution of lengths shown in Figure 10. The CDFG sample is used to compare observed smolt lengths (OSL) to my back-calculated smolt lengths (BSL) (Table 4). Before comparing back-calculated smolt lengths to observed smolt lengths a normality test was run to make sure that the sample of 28 adults used in back-calculating came from

Table 1

The age of smolting steelhead inferred from the adult scales collected in the Big Sur River between 1994 and 1997.

Age at smolting	Total Number	Percent of Total Run
1	8	29
2	20	71

Table 2

Average smolt length broken down by age at smolting.

	Average Smolt total length (mm)
Total	188.4
At age 1+	157.0
At age 2+	199.6

a normal population. This was done because a sample of 28 fish is borderline between a large and small sample. In a two sample t-test both samples must either come from a large sample size or a normal population (Personal communication, R. Smidt, 1997). Total length in fish is usually a fairly normally distributed variable (Personal communication, R. Smidt, 1997), however, the data were plotted for confirmation (Figure 11). Figure 11 shows a scatterplot that is close to linear. This shows that approximately 95% of the data is within two standard deviations from the mean which is a normal distribution. The null hypothesis that the data does not differ from a normal distribution was accepted at the alpha =.05 level of significance. The CDFG sample was large enough, therefore, under the Central Limit Theorem (Moore, 1995) the data will act normal and the use of a two-sample t-test is valid (Moore, 1995). A standard two sample t-test was run to compare observed smolt length to back-calculated smolt length. The p-value for that test was .0001 (Table 4), therefore, the null hypothesis that there is no difference between mean length of calculated smolt lengths and observed smolt lengths is rejected at the alpha = .05 level of significance. The mean length for OSL was 145.7 millimeters which was a difference of 41.7 millimeters between OSL and BSL.

Comparison of smolt age

To test whether there was a difference in smolt ages between Big Sur River and Waddell Creek a Chi square test was performed on the number of 1/ and 2/ smolts counted in Waddell Creek, Santa Cruz County, and Big Sur River, Monterey County (Table 5). The observed and expected number of smolts of each age are shown in Table 5. Each expected value is greater than 5. This validates this analysis technique indicating

Table 3

Average back-calculated smolt length separated by age at first spawning.

Age Class	Number	Average back-calculated Smolt total length (mm)	Range Total length (mm)
1\1	7	165.6	109.1 - 224.7
2\1	8	186.9	149.0 - 259.8
2\2	1	209.7	--------

Table 4

Two sample t-test comparing observed smolt lengths from 1993 steelhead smolt sample from the Big Sur River and back-calculated smolt lengths from the 1997 Big Sur River adult steelhead sample.

Two sample t for observed smolt lengths vs. back-calculated smolt lengths

	Sample Size	Mean (mm)	St.Dev	SE Mean
Observed smolt lengths	44	145.7	34.2	5.2
Back-calculated smolt lengths	28	188.4	42.7	8.1

T-test sample average of observed smolts = sample average of back-calculated smolts (vs. not =): T = -4.35 P=.0001

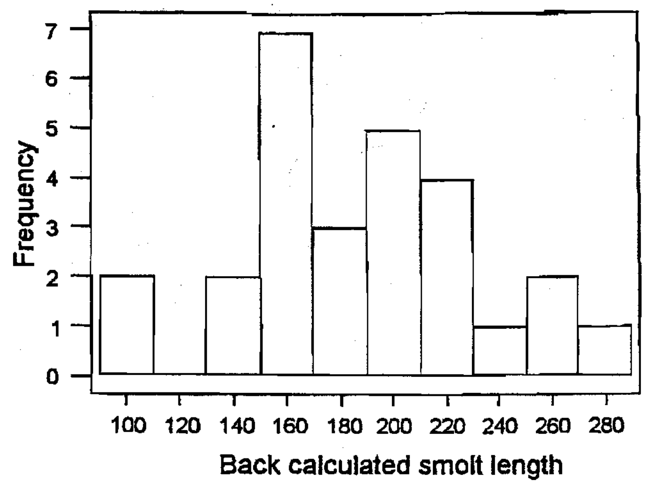

Figure 9

Length frequency histogram of back-calculated smolt length from 1997 Big Sur River adult steelhead sample.

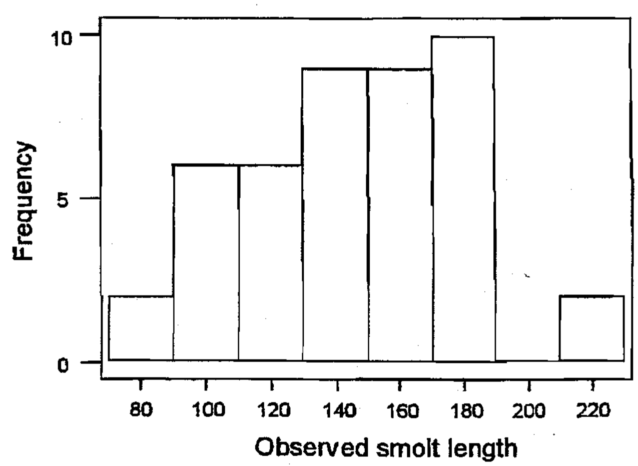

Figure 10

Length frequency histogram of observed smolt length from 1993 Big Sur River steelhead smolt sample.

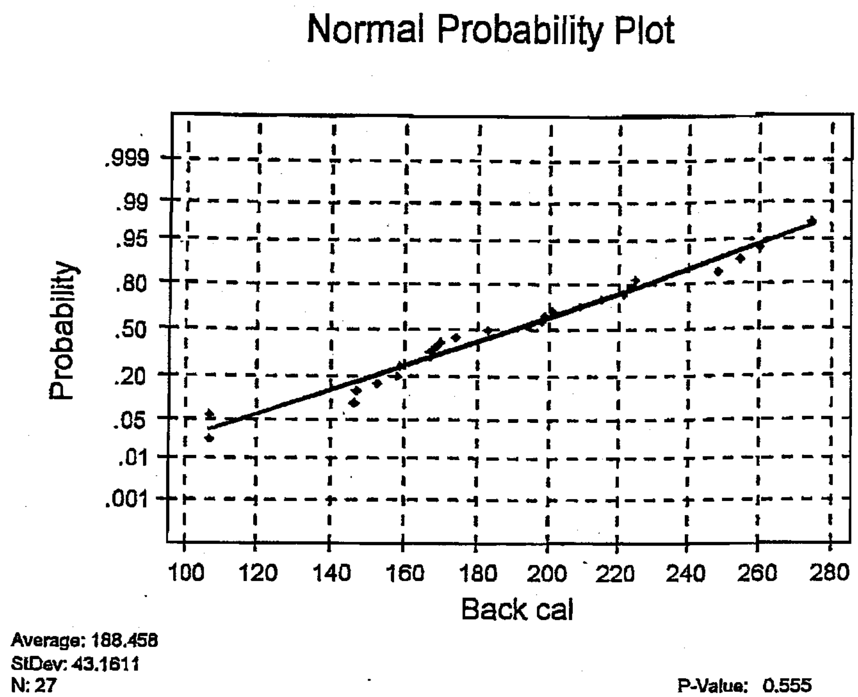

Figure 11

Normality Plot for back calculated Big Sur River smolt length.

sample sizes were large (Personal communication, R. Smidt, 1997). The p-value for this test was less than .05. The null hypothesis for no relationship between the ratio of 1/ and 2/ fish in the Big Sur River and Waddell Creek is rejected (alpha = .05). Therefore, to decipher which cells are contributing to the low p-value the outlying high values are found. In this case 6.38 and 13.49 are both high and contributing to the low p-value. Therefore, it can be inferred from this test that there is a higher proportion of 2/ smolts in Big Sur River compared to Waddell Creek and a lower proportion of 1/ smolts in the Big Sur River compared to Waddell Creek.

Comparison of smolt length

Comparisons of smolt length according to smolt age were made between Big Sur River and Waddell Creek. The mean total length of 14,707 smolts 1+ in age in Waddell Creek was 96.0 millimeters (Table 6). Because this sample size is so large a student t-hypothesis test can be used where 96.0 millimeters is used to represent the population mean. The null hypothesis for this test was that there was no difference between the smolt size of 1/ fish in Waddell Creek and the Big Sur River and the alternative hypothesis was that there was a difference in smolt size of 1/ fish between the two locations. The t-statistic value for this test was 4.49 and the p-value for the test was .0030. Therefore, the null hypothesis can be rejected at the alpha = .05 level of significance. 1/ smolts in the Big Sur River were significantly larger than 1/ smolts in Waddell Creek. The mean total length of 6,938 smolts 2+ in age in Waddell Creek was length of 164.0 millimeters (Table 6). Because this sample size is large, the average is used as the population mean and a t-test is

Table 5

Chi Square test comparing the number of 1/ and 2/ smolts in Waddell Creek and Big Sur River.

Age Group		Waddell Creek Shapovalov and Taft, 1954	Big Sur River	Total
1/	Observed	14707.0	8.0	14715
	Expected	14695.9	19.0	
	Chi square value	.008	6.377	
2/	Observed	6938.0	20.0	6958
	Expected	6949.0	8.9	
	Chi square value	.017	13.487	
	Total Observed	21645	28.0	21673

Chi Square summation = .008 + 6.377 + .017 + 13.487 = 19.89p = .000

d.f. = 1.0

used. The null hypothesis was that there was no significant difference between smolt length of 2\ smolts in Waddell Creek and the Big Sur River and the alternative hypothesis was that there was a significant difference in the length. The t-statistic for this test was 8.68 and the p-value was .0006 (Table 6). Therefore, the null hypothesis can be rejected at the alpha = .05 level of significance. 2/ smolts in the Big Sur River were significantly larger than 2/ smolts in Waddell Creek.

Comparisons also were made with two other locations on the western coast. The first was with Jacoby creek, Humboldt County in northern California. The sample size was not as large as the Waddell Creek sample, and the average smolt size was the only statistic available (Harper, 1980). The average smolt size in Jacoby creek was 164.3 millimeters regardless of age and the average smolt size in the Big Sur River was 188.4 millimeters regardless of age (Table 6). The null hypothesis was that there is no significant difference between the smolt length of fish in the Big Sur River and Jacoby Creek and the alternative is that there is a significant difference in smolt length. The mean smolt size for Big Sur River smolts was 187.4 millimeters (Table 6), the t-statistic for the test was -3.61 and the p-value was .0008 (Table 6). Therefore, the null hypothesis was rejected at the alpha = .05 level of significance. The Big Sur River smolts are significantly larger at smolting when compared to Jacoby Creek. The second comparison was made with the Alsea river, Lincoln County, central Oregon where the mean smolt size was 157.6 millimeters (Table 6). The test was run in the same manner, the t-statistic was 3.69 and the p-value was .0010 (Table 6). Therefore, the null hypothesis was rejected at the alpha = .05 level of significance. Big Sur River smolts are significantly larger at smolting than

Table 6

P-values for t-tests comparing the average total smolt length (mm) in the Big Sur River with other locations on the western coast of Oregon and California.

Comparison	Mean	P-value
Waddell Creek 1/ vs. Big Sur River 1/	96.0 157.0	.0030
Waddell Creek 2/ vs. Big Sur River 2/	164.0 199.6	.0006
Big Sur River average smolt size vs. Jacoby Creek	188.4 164.3	.0080
Big Sur River average smolt size vs. Alsea River	188.4 157.6	.0010

Alsea River smolts.

Adults

Adult steelhead were captured by anglers and trapped by the California Department of Fish and Game during 1994, 1995, and 1997 in the Big Sur River. A total of 28 fish were examined. The frequency distribution histogram for adult lengths is skewed to the left with larger sizes being more common (Figure 12).

Composition of Spawning Runs

Table 7 shows (57%) adult steelhead captured in the Big Sur River were on their first spawning run; whereas twelve (43%) of the adults captured were previous spawners. The number of previous spawners seemed high on the Big Sur River (43%) and is comparable to Gidley (1982) who found 38% previous spawners. For previous spawners on the Big Sur River the majority had only spawned once before (58%) and (42%) had spawned two times previously (Table 9).

The various age combinations for the Big Sur River are shown in Tables 8 and 9. The most common age group was the 2/1 category (29% of captures); the next most common was the 1/1 fish (25% of captures) (Table 8); followed by the 2/1S fish (18%) and the 2/2S (14%) (Table 9). These four age groups represent 84% of the fish captured.

The 2/1 age group had an average length of 571.6 millimeters and a fairly wide range (from 406 - 711 millimeters) (Table 8). Back-calculation of average length at annulus formation at the time of first spawning was 459.3 millimeters. The 1/1 age group had an average length of 468.3 millimeters and a wide range (from 335 - 686 millimeters).

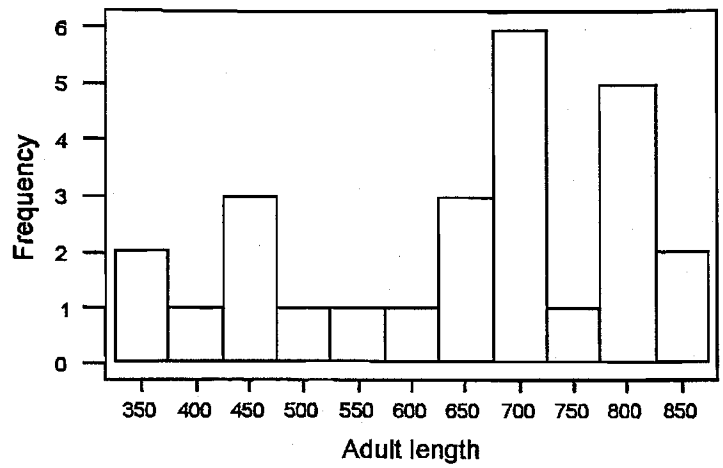

Figure 12

Length frequency distribution of Big Sur River adult steelhead.

Table 7

The number of adult steelhead captured in the Big Sur River between 1994 and 1997 including the number of first and previous spawners.

	Total Number	Percent of Sampled Run
Total number	28	100
First spawners	16	57
Previous spawners	12	43

Back-calculation of average length at annulus formation at first spawning was 428.5 millimeters. The 2/1S (Table 9) fish had an average length of 702.2 millimeters and a range of 640 - 812 millimeters. Back-calculation of average length at first spawning was 534.3 millimeters. The 2/2S fish had an average length of 818.8 millimeters and a range of 787 - 838 millimeters. Back-calculation of average length at first spawning as 438.4 millimeters. The other age groups that made up the remaining 16% of the run are 2/2 first spawners, 1/2S, 2/1.1S, and 2/1S1 previous spawners. Overall there were eight life history compositions found. Traditionally three measures of growth are taken and used for comparison purposes. The first is absolute growth which is expressed as a rate of growth such as millimeters per day or year. The second is the annual growth rate which expresses the percent change over time. The third is instantaneous growth which is the natural log of annual growth which is necessary to combine rate information from different cohorts or different time frames from the same cohort. The average size at first spawning for each first spawner age class, the average absolute yearly ocean growth, the annual growth, and instantaneous growth for fish before first spawning are shown in Table 10. The average spawning size for 1/1 fish was 468.3 millimeters. The average ocean growth during the one year spent in the ocean prior to spawning for this age class was 279.7 millimeters. The annual growth for 1/1 fish in the first ocean year is an increase of 1.49 and the instantaneous growth rate is .91. The average size at first spawning for 2/1 fish was 571.6 millimeters with an absolute ocean growth of 383.2 millimeters, an average increase of 2.03, and an instantaneous growth rate of 1.11. The size at first spawning for

Table 8

The number of steelhead first spawners captured in the Big Sur River between 1994 and 1997 separated by age class.

Age Class	Number	Percent Total Run	Average Length at Capture (mm)	Range of Lengths at Capture (mm)	Back-calc. length at last Annulus (mm)
1\1	7	25	468.3	335.0-686.0	428.5
2\1	8	29	571.6	406.0-711	459.3
2\2	1	4	775.0	--------	787.3

Table 9

The number of steelhead previous spawners captured in the Big Sur River between 1994 and 1997 separated by age class.

Age Class	Number	Percent Total Run	Average Length at Capture (mm)	Range of Lengths at Capture (mm)	Back-calc. length at first spawning (mm)
1\2S	1	4	650.0	--------	461.5
2\1.1S	1	4	813.0	--------	809.3
2\1S	5	18	702.2	640.0 - 812.0	534.3
2\1S1	1	4	749.0	--------	351.7
2\2S	4	14	818.8	787.0 - 838.0	438.4

the only 2/2 fish in the sample was 775.0 millimeters. The back-calculated length at the first ocean annulus was 567.7 millimeters. Absolute growth for the first ocean year was 379.3 millimeters and 206.3 millimeters for the second year. The annual growth for the first ocean year was 2.01 and for the second ocean year was .36. The instantaneous growth rate was calculated to be 1.10 for the first ocean year and .31 for the second ocean year (Table 10). The absolute growth calculations were all based on the average back-calculated smolt size which was 188.4 millimeters (Table 6).

Length at Age Comparisons

The first comparison made was length at first spawning where information was compiled from a literature review of several coastal creeks on the western coast of California that support steelhead populations (Shapovalov and Taft 1954, Forsgren, 1979, Harper 1980, and Gidley 1982) (Table 11). Length at first spawning for the different life history categories found in the Big Sur River were compared. These groups were 1\1 fish, 2\1 fish, and 2\2 fish; however the 2/2 first spawner life history category was left out of this comparison because of the small sample size (1). There were other age groups found in the different locations which were also left out of the comparison. Throughout the literature mean length at first spawning and age at first spawning were consistently given. However, standard deviations were not provided. Therefore, the sample mean is used here to represent the population mean and one sample t-tests were used. The comparison with Waddell Creek seems to be the most valid because the sample size for Waddell Creek is very large (n=3,888 adult fish). For the other studies the sample sizes did not approach this, but the assumption that the sample mean is an approximate predictor of the

Table 10

Yearly ocean growth for Big Sur River adult steelhead showing average length at capture, back-calculated length at time of annulus formation, absolute growth between years, annual growth, and instantaneous growth rates for each first spawner age class

	Age (Sample Size)		
	1/1 (7)	2/1 (8)	2/2 (1)
Average length (mm)			
First Annulus	468.3	571.6	567.0
Second Annulus			775.0
Absolute Growth (mm)			
Age 0-1	279.9	383.2	379.3
Age 1-2			206.3
Annual Growth			
Age 0-1	1.49	2.03	2.01
Age 1-2			.36
Instantaneous Growth Rate			
Age 0-1	.91	1.11	1.10
Age 1-2			.31

Calculated smolt average = 188.4

Table 11

Length at age information using total age for steelhead runs at different locations on the western coast of California.

Age Sur	Waddell Creek	Gualala River	Garcia River	Mad River	Jacoby Creek	Big River
1\1	400	403	363	626	-------	459
2\1	466	523	478	638.	514	429
Reference:	Shapovalov and Taft, 1954	Gidley, 1982	Gidley, 1982	Forsgren, 1979	Harper, 1980	

population mean is made here and the mean sample values were used as population means. There was no significant difference in age specific length between 1/1 and 2/1 fish in Big Sur compared to Waddell Creek in Santa Cruz County and the Garcia River in Mendocino county. There was no significant difference between age specific length of 1/1 aged fish in the Big Sur River and the Gualala River, Mendocino county. There were no 1\1 fish in Jacoby creek which is why no comparison was made for that age group in that location. There was a significant difference in age specific length between the Big Sur River sample and the Mad River sample located in Humboldt county, northern California, in the 1\1 and 2\1 age groups, the Gualala 2/1 age group and the Jacoby Creek 2/1 age group (Table 12).

Comparison of the proportion of age groups that make up the spawning runs in Big Sur River and Waddell Creek

The chi square analysis shown in Table 13 gives the observed and expected counts of fish in each total age category for the Big Sur River and Waddell Creek. Each age category that occurred in the Big Sur River was used in the analysis. There were many age groups found in Waddell Creek that were not found in Big Sur River and these age compositions were not used in the comparison. There is a significant difference between two drainages and the proportion of age groups comprising the spawning run. High chi square totals give low p-values. In this test the one chi-square value that stands out as being high is the 11.707 which reflects the comparison of proportions between the 1\1 fish. In the Big Sur River there were more 1\1 fish observed than were expected based on the observations in Waddell Creek. Therefore, there is a difference in the number of 1\1

Table 12

P-values derived from t-tests for comparisons of length at age information.

	P-values for comparisons at the following locations				
	Big Sur vs. Waddell Creek	Big Sur vs. Gualala River	Big Sur vs. Garcia River	Big Sur vs. Mad River	Big Sur vs. Jacoby Creek
Total Age					
1\1	.42	.44	.21	**.05**	------
2\1	.36	**.04**	.24	**.00**	**.06**

Table 13

Chi Square Analysis for the proportion of fish that make up each total age group in Waddell Creek and Big Sur River.

Age Group		Waddell Creek (Shapovalov and Taft, 1954)	Big Sur River	Total Count
1\1	Observed	183.00	7.00	
	Expected	187.93	2.07	190
	Chi Square value	.129	11.707	
1\2	Observed	165.00	1.00	
	Expected	164.19	1.81	166
	Chi Square value	.004	.363	
2\1	Observed	1168.00	13.00	
	Expected	1168.11	12.89	1181
	Chi Square value	.000	.001	
2\2	Observed	1022.00	7.00	
	Expected	1017.77	11.23	1029
	Chi Square value	.018	1.592	
	Observed Total	2538.00	28.00	2566

Chi Square = .129 + 11.707 +
.004 + .363 +
.000 + .001 + d.f. = 3
.018 + 1.592 = 13.815 p-value = .003

fish that contribute to the spawning runs in Waddell Creek and Big Sur River. The age categories 1/2, 2/1, and 2/2 occur in similar ratios in Big Sur River and Waddell Creek.

Comparison of Big Sur River steelhead with other populations on the western coast of North America

Table 14 (after Busby et. al., 1996) gives information on the Big Sur River population. The chart notes populations along the entire western coast of North America and their primaryand secondary contributions of age groups that compose the first spawners of the spawning runs.

Twenty nine percent of the first spawners in the Big Sur River spawning run are in the 2/1 age group, and 25% of the first spawners in the Big Sur River spawning run are in the 1/1 age group. Big Sur River represents the southern most extension of this compiled data. The general trend shows that there is a cline of smolt ages with younger smolts occurring in southerly drainages.

Discussion

Smolts

The frequency distribution histogram (Figure 7) of the back-calculated smolt length had a relatively normal distribution with a mean of 188.4 millimeters. There were clearly more 2/ migrants than 1/ migrants in the Big Sur River compared to other areas (Table 5) with the 2/ migrants being 42.6 millimeters larger than 1/ migrants on average due to the extra year of fresh water growth (Table 7).

A sample of smolts taken by California Department of Fish and Game (1993) had an average length of 145.7 millimeters (Table 9). A two-sample t-test shows (Table 4) back calculated smolt lengths to be significantly different from observed smolt lengths at the alpha = .05 level of significance. There are two possible reasons for this discrepancy. (1) there could have been a difference of length between brood years caused by a difference in environmental rearing conditions of juvenile fish, or (2) there may be a size selective ocean mortality for smaller smolts (Ward and Slaney, 1989). Ward and Slaney (1988) demonstrate that smolt-to-adult survival for steelhead was positively correlated with smolt size using smolt data covering 1977-1982. Ward and Slaney (1989) found that the mean back-calculated smolt length (BSL) was 192.5 millimeters whereas the mean observed smolt length (OSL) was 176.2 millimeters. This is similar to my findings in the Big Sur River where the OSL was 145.7 millimeters and the BSL was 188.4 millimeters. The annual mean differences in Ward and Slaney's study between BSL and OSL ranged from a low of 9 millimeters to a high of 24.5 millimeters. Variations in OSL and BSL from year to year suggested that conditions for survival in the ocean can change (Ward

Table 14

Most common life history patterns reported for selected steelhead populations; frequency of occurrence in sample is shown in parenthesis. Format used is freshwater age/ocean age at first spawning migration. Populations are generally arranged from north to south. This table is found in the Status Review of West Coast Steelhead from Washington, Idaho, Oregon, and California, (After Busby et al., 1996).

Population	Run type	Life history (frequency)				Sample	Reference
		Primary		Secondary		Size	
Alaska							
Karluk River	S	3/2	(.42)	2/2	(.36)	62	Sanders 1985
Anchor River	S	3/2	(.61)	3/1	(.23)	80	Sanders 1985
Copper River	S	3/2	(.73)	3/1	(.10)	30	Sanders 1985
Situk River	S/O	3/2	(.43)	3/3	(.32)	211	Sanders 1985
Sitkoh Creek	O	3/2	(.38)	3/3	(.27)	497	Sanders 1985
Karta River	O	3/2	(.46)	3/3	(.20)	542	Sanders 1985
British Columbia (mainland)							
Babine River	S	3/2	(.62)	3/3	(.17)	100	Narver 1969
Cheakamus R.	O	3/2	(.34)	2/3	(.25)	64	Withler 1966
Capilano River	O	3/2	(.40)	2/2	(.26)	70	Withler 1966
Capilano River	S	3/2	(.49)	3/3	(.31)	86	Withler 1966
Seymour River	O	3/2	(.38)	3/3	(.22)	58	Withler 1966
Seymour River	S	3/2	(.48)	2/3	(.24)	25	Withler 1966
British Columbia (Fraser River Basin)							
Coquitlam River	O	3/2	(.49)	2/2	(.23)	146	Withler 1966
Alouette River	O	2/2	(.32)	2/3	(.32)	131	Withler 1966
Chilliwack River	O	2/2	(.31)	2/3	(.31)	770	Maher and Larkin 1955
Chehalis River	O	3/3	(.34)	3/2	(.33)	111	Withler 1966
Coquihalla River	O	3/2	(.49)	3/3	(.18)	39	Withler 1966
Coquihalla River	S	3/2	(.63)	2/2	(.15)	150	Withler 1966
British Columbia (Vancouver Island)							
Keogh River	O?	3/2	(.40)	3/3	(.19)	1391	Ward and Slaney 1988
Nanaimo River	?	2/1	(.41)	3/1	(.26)	228	Narver and Withler 1974
Nahmint River	S	3/2	(.71)	2/2	(.19)	58	Narver 1974
Washington							
Skagit River	O	2/2	(.48)	2/3	(.33)	n/a	WDFW 1994
Deer Creek	S	2/1	(.95)	3/1	(.05)	n/a	WDFW 1994
Snohomish River	O	2/2	(.47)	2/3	(.36)	n/a	WDFW 1994
Green River	O	2/2	(.52)	2/3	(.17)	100	Larson and Ward 1954
Puyallup River	O	2/2	(.61)	2/3	(.28)	n/a	WDFW 1994
Nisqually River	O	2/2	(.51)	2/3	(.28)	n/a	WDFW 1994
Hoh River	O	2/2	(.74)	2/3	(.14)	n/a	WDFW 1994
Quillayute River	O	2/2	(.46)	2/3	(.40)	n/a	WDFW 1994
Chehalis River	O	2/2	(.66)	2/3	(.15)	100	Larson and Ward 1954

Columbia River Basin							
Toutle River	O	2/2	(.73)	2/3	(.11)	37	Howell et al. 1985
Cowlitz River	O	2/2	(.55)	2/3	(.34)	56	Howell et al. 1985
Kalama River	O	2/2	(.65)	2/3	(.18)	1363	Howell et al. 1985
Kalama River	S	2/2	(.67)	2/1	(.17)	909	Howell et al. 1985
Willamette River	O	2/2	(.92)	3/2	(.08)	141	Howell et al. 1985
Washougal River	S	2/2	(.71)	2/1 & 2/3	(.14)	07	Howell et al. 1985
Wind River	S	2/2	(.58)	2/3	(.26)	19	Howell et al. 1985
Klickitat River	S	2/2	(.75)	2/1	(.14)	148	Howell et al. 1985
Deschutes River	S	2/1	(.35)	1/2	(.22)	100	Howell et al. 1985
Yakima River	S	2/1	(.47)	2/1	(.42)	64	BPA 1992
Wenatchee River	S	2/1	(.65)	3/1 & 3/2	(.12)	17	Howell et al. 1985
Entiat River	S	2/1	(.88)	2/2	(.12)	08	Howell et al. 1985
above Wells Dam	S	2/2	(.41)	3/2	(.24)	349	Howell et al. 1985
Snake River Basin							
Clearwater River	S	2/1	(.34)	2/2	(.25)	510	Whitt 1954
S.F. Salmon River	S	3/3	(.49)	2/3	(.31)	65	BPA 1992
Lemhi River	S	2/2	(.86)	2/1	(.09)	353	BPA 1992
Oregon							
Nehalem River	O	2/2	(.73)	2/3	(.08)	310	Weber and Knispel 1977
Alsea River	O	2/2	(.52)	2/3	(.22)	978	Chapman 1958
Siuslaw River	O	2/2	(.67)	2/3	(.16)	125	Lindsay et al. 1991
Rogue River	O	2/2	(.60)	3/2	(.17)	547	ODFW 1990
California							
Klamath River	S	2/1	(.52)	1/1	(.19)	391	Kesner and Barnhart 1972
Mad River	O	2/2	(.69)	2/1	(.26)	35	Forsgren 1979
Jacoby Creek	O	2/2	(.50)	2/1	(.26)	109	Harper 1980
Van Duzen River	S	1/2	(.62)	1/3	(.29)	58	Puckett 1975
M.F. Eel River	S	2/1	(.45)	2/2	(.33)	82	Puckett 1975
Sacramento River	O?	2/1	(.36)	2/2	(.31)	83	Hallock 1989
Waddell Creek	O	2/1	(.39)	2/2	(.30)	3888	Shapovalov and Taft 1954
Big Sur River	O	2/1	(.29)	1/1	(.25)	28	

O = Ocean maturing; S = Stream maturing.
n/a sample sizes were not indicated in reference

and Slaney, 1989). Ward and Slaney's BSL data was normally distributed with a slight skew to the right and the OSL data was truncated at 130 millimeters. Differences between the shape of the distributions appeared mainly in the lower length intervals which would be consistent with a size selective mortality directed toward smaller fish. However, Ward and Slaney state that they have not identified the mechanisms that result in poorer survival of smaller smolts. The length data found for OSL and BSL in the Big Sur River follow a similar trend (Figures 5 and 6).

Both 1/ and 2/ Big Sur River smolts were significantly larger than Waddell Creek smolts. Sample sizes at Waddell Creek are quite large which suggests that the differences found are most likely real differences. One reason for the significantly larger smolt size of fish in the Big Sur River could be due to climatic effects.

Climatic differences in the range of steelhead

Waddell Creek exists in Santa Cruz county in the coastal redwood forest vegetative zone. These forests are dominated by *Sequoia sempervirens* which forms a dense canopy that blocks most of the sunlight (Holland and Keil, 1995) which in turn creates cooler water temperatures where productivity is lower than it is in areas with warmer water temperatures.

Climate can also determine the length of the winter season which in turn affects fish growth rates and maturation. It is generally accepted that in temperate climates the growth rate of salmonids diminishes (sometimes even to zero) in winter. This is the basis of the scale-reading method of age determination. Diminished growth rate is often associated with a reduced rate of feeding and presumably also with the tendency to seek shelter on the bottom (Allen, 1969). The length of the period during which temperatures are low enough to reduce or suppress growth will, of course, impose a seasonal limitation on the total amount of growth which can be made in the freshwater growth years (Allen, 1969). The length of the cold period in more northerly latitudes is longer which gives fish in these areas a smaller window in which to grow.

One other temperature related environmental factor which effects differences in fish growth as related to water temperature is the amount of invertebrate drift. Many species of invertebrates, though not all, exhibit high rates of downstream drift in a diel periodicity. Some species are day-active, for whom water temperature may be the phase-setter where water temperature is one of the factors that sets the magnitude of the drift (Waters, 1969). Therefore, fish in warmer, more southerly creeks and rivers mature at a faster rate because of an increase of the availability of food. This is another seasonal factor affecting fish growth.

Waddell Creek exists north of Big Sur River and in a region of well developed coastal redwood forest. This creates cooler water temperatures in the Waddell Creek drainage and possibly decreases the magnitude of the invertebrate drift, although the winter season is generally the same length in Waddell Creek as it is in the Big Sur River. Decreased water temperature results in smaller fish at a given age. If there is a size-selective mortality occurring in the ocean then smolts would evolve through selection to migrate at an older age and, therefore, at a larger size. This would give them sufficient time to develop, and enter the ocean. Table 14 demonstrates that fish in British Columbia, where the length of the winter season would play a role, spend three years in fresh water before becoming mature enough to smolt.

The Big Sur River exists at the southern border of the coastal redwood forest. Because this area is farther south it starts to pick up coastal scrub and chaparral vegetation types on dry exposed hill slopes signifying a drier environment. There are sections of the river where redwoods occur and the canopy blocks out most of the sunlight, however, there are also reaches of the river too dry for redwoods where water temperatures can increase. This increases water temperature, invertebrate drift, and decreases the time it takes for juveniles to reach smolting size because growth occurs at a faster rate. It follows that there is a higher proportion of 1/ smolts in Big Sur River than in other more northerly rivers where temperatures are colder and primary productivity is lower in comparison (Table 14).

Comparison of average smolt length

Comparisons of average smolt length regardless of age were made with Jacoby Creek in northern California and the Alsea River in northern Oregon. Big Sur River smolts were significantly larger compared to both locations. Jacoby Creek and the Alsea River also exist in the heart of the coastal redwood forest, however, they have the added effect of colder temperatures and increased precipitation moving north. Primary productivity as a general rule will decrease moving from the Big Sur River north. Therefore, the southern extension of the range of steelhead will have the greatest primary productivity and migrants will be either larger or younger at smolting.

Comparison of smolt age

The chi square analysis performed to determine whether there was a relationship between the proportion of 1/ and 2/ smolts and location (Big Sur River vs. Waddell Creek) indicated a higher proportion of 2/ smolts in the Big Sur River and a lower proportion of 1/ smolts in the Big Sur River. Even though the 2/ smolts were the dominant migrants in terms of numbers in the Big Sur River drainage, the 1/ migrants made up 25% of the smolts which is greater any other drainage shown in Table 14 except for the Van Duzen River which is also in California. The Van Duzen River represents an anomaly n the data where at least 91% of the population smolted at 1/. This is unusual because of the size selective mortality of smaller smolts in the ocean. The Van Duzen River must have strong pressures on smolts to migrate at an earlier age. Fish are maturing earlier at the southern ends of the range which explains why a greater portion of the run is made up of 1/ smolts. However, size-selective mortality in the ocean may be selecting for fish at this southern extent of their range to smolt as a larger 2/ migrant rather than a relatively smaller 1/. This may be an example of stabilizing selection where there is pressure on fish to migrate early because the increased primary productivity in the system causes the fish to mature faster. Fish in this case should be ready to smolt as a 1/. Selective pressure on the other end may exist because of the size selective ocean mortality causing the fish to evolve to smolt as a larger 2/. This could be a possible reason why there is a greater proportion of 1/ fish in the Big Sur River than more northerly populations, but 2/ smolts dominate the run.

These differences found in smolt length and age could also be attributed to genetic differences between populations (Nielsen, 1994). However, the cline that these differences in age and size reflect show that the genetic differences may have occurred in response the environmental differences and pressures.

Adults

The adult length frequency distribution is skewed to the left with larger sizes being more common (Figure 8). A possible explanation of this could be that larger steelhead survive ocean years better than small steelhead. Larger fish may have an increased ability as a predator and are possibly more effective at avoiding predation. For example, anglers think that sea lions are putting pressure on the steelhead population. If that is true then smaller steelhead would have a greater chance of being taken by sea lions as compared to larger fish due to decreased swimming speed compared to larger steelhead. The histogram suggests size selective mortality of smaller adults.

The age specific length comparison of 1/1 and 2/1 fish between Waddell Creek and the Big Sur River showed that there was no difference in length at first spawning among age groups. As the comparison of length of each age class at first spawning is extended up the coast some differences begin to appear.

It has been documented (Nielsen et al., 1994) that the population of *O. mykiss* in each specific drainage can be genetically distinct. These age specific length comparisons are phenotypic characteristics of genetic differences in populations. Of the 1/1 fish compared the only difference found was between the Mad River and the Big Sur River where fish in the Big Sur were significantly smaller at first spawning. The Big Sur River first spawners in the 2/1 age group were smaller than fish in the Gualala and Mad Rivers and Jacoby Creek. Of all the differences found, fish in the Big Sur River were consistently significantly smaller than the group in comparison. Gidley (1982) states that there might be genetic selection for faster maturing fish in small streams. He also states that because of some favorable environmental condition, southern fish mature faster than northern fish. This could be due to the climate and primary productivity of the system as discussed above. Briggs (1953) suggests that these differences may be due to different steelhead races. Nielsen (1997) has proven through microsatelite and mtDNA analysis that there are different races (populations) of steelhead that exist on a latitudinal cline. The haplotypes derived from mtDNA analysis indicate differences between southern and northern latitudes (i.e. the haplotypes in the southern portion of the range are absent in the northern portion of the range). Southern steelhead have different genetics and environmental conditions which could both lead to earlier maturation at a smaller size. Because conditions in the southern extent of the range tend to be more tenuous, with drought years occurring periodically, these southern steelhead may have evolved to spawn at every opportunity which could be another reason causing the younger spawners in the southern extent of the range.

A second comparison I made between adult steelhead in Waddell Creek and the Big Sur River comparing the proportion of total age groups that make up the spawning runs. There was a significantly higher number of 1/1 aged fish in the Big Sur River compared to Waddell Creek. This is further evidence of a latitudinal trend where southern steelhead are of a different genetic stock that mature earlier in south coastal habitats that tend to be highly variable.

In conclusion, there are different selective pressures acting on smolt age and age at first spawning. Smolts have evolved with two different types of pressure. First, they are pressured to smolt at an earlier age because the environment is conducive to faster growth at the southern extent of the range. Second, there is pressure on smolts to migrate at a later age and, therefore, larger size because of the size selective mortality of smaller smolts in the ocean. Therefore, the majority of smolts are 2/, however, they are larger than populations to the north because of increased growth rates at the southern extent of the range.

The adults have a different set of pressures that are affecting age at first spawning. There are different genetics at the southern portion of the range. First, there are different genetic stocks from drainage to drainage. Second, there are different evolutionary significant units. Also, the environment is considerably more tenuous in the southern extent of the range due to increased water temperatures, consecutive drought years, and freshwater habitat manipulation. Fish may have evolved to spawn at every opportunity because of the unknown, tenuous environmental conditions from year to year. The different environment and different genetics in the southern portion of the range could be why we see a greater proportion of /1 fish spawning for the first time.

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