AN ABSTRACT OF THE THESIS OF

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Title: Influence of Landscape-Scale Variables on the Age and Growth of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in Headwater Streams

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This thesis provides the first general description of the natural variation in age structure, growth rates, and survival in headwater populations of coastal cutthroat trout *Oncorhynchus clarkii clarkii* from western Oregon, and a subsequent synthesis of these life-history characteristics across the range of the subspecies. Age, growth, and survival were estimated by analyzing scales from 4,250 fish collected from 37 headwater watersheds in western Oregon from 1999 to 2001. Age was validated for 234 marked and recaptured coastal cutthroat trout from two watersheds, and >94% of the scales exhibited the expected number of annuli between capture dates. Variation among readings was low (< 9%), and there was only a slight bias between readings for older fish (primarily age-5 fish). Missing first-year annuli, often observed in cutthroat trout subspecies, were not observed for these populations. Mean relative growth rates decreased with age and size. In three populations maximum age was 3 years, but in the majority, maximum age was 4 (24 populations) or 5 years (8 populations). Annual survival rates of age-3

coastal cutthroat trout (i.e., between age-2 and age-3) ranged from 23% to 65%. Akaike's Information Criterion (AIC) was used to select multiple regression models that "best" described biological response (i.e., length at age-1, mean length, and survival) to physical habitat variables. The model with January water temperature and calcium ions as predictor variables was the "best approximating model" for predicting mean length at age 1. The model with maximum pool depth and stream channel connectivity was most useful for predicting mean fish length in a watershed, and mean survival was best predicted by a model with mean July water temperature and maximum pool depth as predictor variables. Summary of range-wide life-history data for coastal cutthroat trout suggests that patterns in growth, age, and length do not follow a generalized geographic trend from north to south, and at least some differences appear to be related to life-history type.

Influence of Landscape-Scale Variables on the Age and Growth of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in Headwater Streams

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I understand that my thesis will become a part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

William G.Rehe, Jr., Author

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Influence of Landscape-Scale Variables on the Age and Growth of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in Headwater Streams

Chapter 1:

Introduction

The study of fish growth has interested scholars since the Classic Age of the Greek Empire. Aristotle was the first person to record comments on the subject in his text "Historia Animalium," where he noted the technique used by Greek fishermen to determine distinct classes of tuna (Bell 1962). Leeuwenhoek, a Dutch microbiologist, was the first person to age fish (carp *Cyprinus carpio*) using scales. Later scientists used other hard parts, such as vertebrae (Hederstrom 1854, cited by Bell 1962) and otoliths (Reibisch 1899, cited by Bell 1962). Estimation of fish age and growth is important to fisheries biology because it provides essential information needed to understand life history characteristics (Chugunova 1963), such as age at maturity, life span, and environmental suitability (Lux 1971; Jearld 1983).

The phenomenon of growth is extremely complex, both in definition and process. The meaning of growth depends on the context of the research (Weatherley 1972). Growth can be either positive or negative, and measured as change in energy content, cell numbers, or biomass (length or mass). Early investigators of growth believed that a strict definition of growth could lead to artificial constraints on growth research (Bertalanffy 1938). Growth, in its simplest form, represents the net production of a biological process that transforms food, through assimilation and metabolic pathways, into waste, activity, and change in gonad and body mass (Bertalanffy 1938).

The pattern of growth of individual organisms can be characterized as determinate or indeterminate. Determinate growth patterns are usually found in higher vertebrates, like mammals or birds, and this pattern is characterized by fixed maximum body size, relatively small variance in size within and among populations, and or a direct positive relationship between body size and age (Weatherley and Gill 1987). Indeterminate growth is found in plants and lower vertebrates like fish. Organisms with indeterminate growth display a weak relationship between size and age (Weatherley 1972), have high intraspecific differences in growth rates among populations (Ericksen 1997), and appear to grow in relation to food supply.

Abiotic environmental factors such as temperature, light, and oxygen, influence fish growth substantially (Fry 1971; Brett 1979). Temperature has a pervasive effect on growth rates because it acts at many levels (e.g., internal and external environments) and interacts with other abiotic factors. Temperature is a controlling factor (Fry 1971) and assists in governing the rate of metabolic processes in the body. External processes, such as incubation and emergence of larvae (Matthews 1998), daily or seasonal migration (Northcote 1997), and distribution (Fausch 1989) are directly related to water temperature regimes.

Temperature also affects developmental stages of fish. For example, coastal cutthroat trout *Oncorhynchus clarkii clarkii* spawning activities typically occur between December and June. Peak spawning in Washington, Oregon, and British Columbia commences in February when water temperatures reach about 5º C (Behnke and Zarn 1976; Pauley et al. 1989; Trotter 1989; Stolz and Schnell 1991, Johnson et al. 1999). Local spawning times for cutthroat trout vary depending on latitude, elevation, water temperature, and stream flow (Stolz and Schnell 1991).

Early life stages in the development of salmonids (i.e., egg and alevin) are the most sensitive (Bell 1973; Hunter 1973; Smith et al. 1983; Hicks 2000). Duration of egg incubation and survival to emergence vary among subspecies and populations, but both stages of development are dependent on temperature (Merriman 1935; Snyder and Tanner 1960). Optimum incubation temperatures for cutthroat trout are approximately 10-11ºC (Merriman 1935; Snyder and Tanner 1960), and anadromous coastal cutthroat trout have been shown to require about 300 degree-days (approximately 6-7 weeks from spawning) for incubation and another 150-200 degree-days before they emerge from the gravel as fry (Stolz and Schnell 1991, Johnson et al. 1999).

Juvenile cutthroat trout are susceptible to developmental problems related to temperature. For example, low ambient water temperatures can retard growth through the slowing of metabolic rates (Brett 1979). Growth of juvenile salmonids is paramount to individual survival and cohort persistence because larger individuals often have a wider variety of feeding strategies, access to more prey sources, and a greater ability to avoid predators (Martin 1983;

Puckett and Dill 1985). The optimal temperature range for the development of juvenile cutthroat between 11 and 21ºC. Equilibrium and swimming ability fail at temperatures between 28 and 30ºC, depending on the cutthroat trout subspecies, strain, and water chemistry (Heath 1963; Dwyer and Kramer 1975).

Light affects fish growth in multiple ways (e.g., quality, quantity, and photoperiod; Warren 1971). Light quality and quantity influence fish behavior by stimulating responses from the pituitary, endocrine, and sympathetic system (Brett 1979). Photoperiod (the ratio of daylight to darkness) is responsible for the production of growth hormones and influences internal rhythms daily and seasonally (Brett 1979).

Oxygen works as both a limiting factor to regulate metabolites (i.e., chemicals necessary for metabolism) and as a direct factor, influencing metabolic rates (Fry 1971). Oxygen content in the water is influenced by both abiotic and biotic factors. For example, oxygen saturation in water is affected by temperature, but biotic factors, such as fish densities and vegetation, can also influence oxygen levels. The effect of fish density on oxygen supply varies depending on the oxygen demand of the fish and the age structure of the population. Older fish have a higher oxygen demand because they require increased amounts of energy to maintain their larger size (Behnke 1992). Vegetation can influence the concentration of oxygen in water, either directly or indirectly. Daily oxygen content can fluctuate because of the influence of light on photosynthesis (Brett 1979); as photosynthesis rates increase, phytoplankton and aquatic vegetation produce more energy and oxygen.

Biotic factors affect growth by influencing metabolic processes that convert food into usable items like proteins, carbohydrates, and enzymes (Warren 1971). In order for an organism to grow, metabolic energy must first be used to satisfy body maintenance and behavior costs. Any energy left over from this process may then be used for growth. The main two biotic factors that influence cutthroat trout growth are ration (i.e., food) and organism size (Weatherley 1990; Boss and Richardson 2002).

Food habits of coastal cutthroat trout vary by location and availability of prey items (Romero et al. 2005). The diet of anadromous coastal cutthroat trout in the Columbia River basin is primarily fish throughout the year, but there is an increasing dependency on insects during the summer months (Pearcy et al. 1990). Sumner (1972) found that sea-run cutthroat trout were opportunistic predators, and their diets were dependent on what prey items were available. In a study of diet preference between sexually mature and immature migratory anadromous cutthroat trout, the majority of stomach items were found to be aquatic insects (Specht 1978). Both immature and mature trout had similar composition of prey items, but immature cutthroat trout contained numerically more insects.

Growth of trout depends not only on the availability of food items, but also on the age and size of the fish (Martin 1983; Rosenfeld and Boss 2001). Fish have a general pattern of growth rates that decreases with an increase in fish size and age (Tomasson 1979; Martin 1983; Rosenfeld and Boss 2001). Smaller fish have lower absolute energy requirement compared to larger, older fish, giving them a selective advantage in streams with low productivity and higher temperatures (Rosenfeld and Boss 2001). Hughes and Reynolds (1994) proposed that differences in energetic requirement of fish influenced the decrease in maximum body size along an upstream gradient.

The seasonal pattern of growth from spring to fall appears to be highly variable. Growth of cutthroat trout in streams of the Olympic Peninsula, Washington, decreased from March through October (Martin 1983), but in the Cascade Mountains of Oregon, growth was greatest for all sizes of cutthroat from April through October (Aho1977). Cutthroat trout growth in the Rogue River (Oregon) began in April and May, stabilized in October, and declined with the onset of gonadal development (Tomasson 1979). These studies underscore the variability of growth with size class, environmental conditions, and location.

Competition is another biotic factor that can influence the expression of growth in fish (Brett 1979). The effects of competition on growth characteristics of fish are influenced by fish abundance, available space, and fish size (Brett 1979, Grant and Kramer 1990; Bohlin et al. 2002; Paukert and Willis 2004; Harvey et al. 2005). Salmonid density (i.e., density dependent growth) has been suggested as a mechanism that can regulate size structure and population numbers (Heath 1992; Elliott 1994). Furthermore, competition between cutthroat trout and other stream dwelling salmonids has been demonstrated in laboratory and experimentally manipulated streams (Glova 1986; Northcote 1995; Sabo and Pauley 1997).

Population structure is directly related to the interaction of growth and mortality. The causes of mortality can be divided into two general components: fishing and natural mortality (Willis and Murphy 1996). Fishing mortality is the result of harvest or hooking deaths, but natural mortality is related to old age, disease, parasites, predation, and abiotic factors, such as temperature or stream flow (Fry 1971). Water temperature can directly influence the survival rates of cutthroat trout, and adult cutthroat trout appear to have less tolerance to increased water temperature than juveniles (Dwyer and Kramer 1975; Vigg and Koch 1980). Upper lethal water temperature varies by subspecies and location, and may be related to water chemistry, length of time at extreme temperatures, and genetics (Behnke and Zarn 1974; Vigg and Kock 1980; Pauley et al. 1989). For example, Lahontan cutthroat trout *Oncorhynchus clarki henshawi* in high alkalinity water from Pyramid Lake (California) exhibited an upper lethal temperature of 18.5-20.2ºC, but upper lethal temperature of individuals in the Truckee River (California) was 21.8-23.0ºC (Vigg and Koch 1980). Cutthroat trout have a preferred water temperature of 9-12ºC (Bell 1973), and coastal cutthroat trout have a lower and upper lethal temperature range of 0.5 and 23ºC, respectively. Metabolic rates are positively correlated to water temperatures

(Bret 1979), and even if ration intake rises, larger fish can lose weight and length because of higher caloric needs related to increased metabolism (Nickelson and Larson 1974).

Cover may also play a role in the survival of isolated populations of coastal cutthroat trout. In an experiment on the effect of food and cover on the survival of resident coastal cutthroat trout in stream enclosures, Boss and Richardson (2002) found that cover increased summer survival by up to 50%. The main mechanisms for increased survival from cover appears to be reduced predation and increased protection from unfavorable environmental condition (Boss and Richardson 2002; Mitro and Zale 2002).

Previous research has demonstrated the effect of riparian canopy modification on the growth of fish (Hawkins et al. 1983; Wilzbach and Hall 1985; Wilzbach et al. 1986). It appears that as stream temperature rises with decreased riparian cover, there is a corresponding increase in the availability of prey items, foraging efficiency, and short-term growth rates (Johnson and Jones 2000; Romero et al. 2005). Maximum stream temperatures were 7ºC higher and occurred earlier in the season in logged than unlogged sections. Daily fluctuations in stream temperatures also increased 2-8ºC, and it was at least15 years before temperature returned to pre-harvest levels.

Other anthropogenic changes, such as weirs, culverts, and dams, can influence population persistence of coastal cutthroat trout by restricting their ability to seasonally migrate within stream networks for feeding, refuge, or spawning habitat. Land-use practices, such as irrigation and municipal water withdrawals, threaten to further change seasonal flow patterns in streams and reduce survival of all age groups of cutthroat trout. Suitable stream flows are important for maintaining the oxygenation of fertilized eggs, flooding lateral habitat for larval fish development, and providing adequate dissolved oxygen for juvenile and adult fish.

In this thesis, I describe the variation in age, growth, and survival of coastal cutthroat trout in headwater streams across western Oregon. I also investigated and environmental variables that influence population characteristics of this subspecies of cutthroat trout. The second chapter provides an overview of the methodology used to determine age and growth of coastal cutthroat trout. It documents the variation of age, growth, size, and survival of coastal cutthroat trout in western Oregon and compares findings to those of previous studies across the range and among multiple life-history forms. The purpose of chapter three is to evaluate the influence of environmental characteristics on the population structure (i.e., growth, age, size, and survival) of coastal cutthroat trout in headwater watersheds of western Oregon. The final chapter provides a summary of the major conclusion of this thesis. The information provided in this thesis increases our understanding of this complex subspecies of cutthroat trout by identifying environmental variables that influence age and growth characteristics in headwater streams at a variety of spatial scales. Ultimately, such information is critical for regulation and restoration activities aimed at preventing further declines in the distribution and abundance of the coastal cutthroat trout.

Chapter 2:

Age and Growth Patterns of Coastal Cutthroat Trout in Headwater Streams of Western Oregon

Abstract- The coastal cutthroat trout *Oncorhynchus clarkii clarkii* is the least studied of the seven species of Pacific salmonids, and although information about the anadromous life-history type of the subspecies has been increasing over the last decade, there is little information about age structure, recruitment, growth rates, and mortality available for potamodromous life histories, especially headwater forms. In the current study, we developed the first general description of the natural variation in age structure, growth rates, and survival in headwater populations of coastal cutthroat trout from western Oregon and a synthesis of these life-history characteristics across the range of the subspecies. Age, growth, and survival of coastal cutthroat trout were estimated by analyzing scales from 4,250 fish collected from 37 headwater watersheds in western Oregon from 1999 to 2001. Missing first-year annuli, often observed in cutthroat trout subspecies, were not observed. Mean relative growth rates decreased with age (0.76 mm/mm/year and 0.24 mm/mm/year for age-1 and age-3 fish, respectively, and size (0.79 and 0.15 mm/mm/year for 40- and165-mm length groups, respectively). In three populations (8%), maximum age was 3 years, but the majority had a maximum age of 4 (70%) or 5 years (22%). Annual survival rates of age-3 coastal cutthroat trout (i.e., between age-2 and age 3) ranged from 23% to 65%. Summary of range-wide life-history data for coastal cutthroat trout suggests that patterns in growth, age, and length do not follow a generalized geographic trend from north to south, and at least some differences appear to be related to life-history type.

Introduction

Cutthroat trout *Oncorhynchus clarkii* have one of the broadest geographic distributions of any trout species in North America (Behnke 1988, Trotter 1989). The species can be found in the near-shore Ocean (Sumner 1972; Pearcy et al. 1990), lakes (Ericksen 1997; Rooper et al. 2000; Gresswell et al.1997), rivers (Hagenbuck 1970; Tomasson 1979; Fuss 1982; Johnson et al. 1994), and small headwater streams (Downs 1995; Kruse et al. 1997; Gresswell et al. 2004). There are 4 major lineages with 14 recognized subspecies, 9 with scientific names, 4 unnamed, and 1 extinct (Behnke 1988, Stolz and Schnell 1991).

Cutthroat trout have declined in numbers and distribution because of invasive species, overharvest, habitat simplification and destruction, and migration barriers (Gresswell 1988; Young 1995; Williams and Nehlsen 1997). A number of cutthroat trout subspecies, including coastal cutthroat trout, have been listed as threatened or as a species of special concern (Nelsen et al. 1991; Trotter et al. 1993; Gerstung 1997). According to the Endangered Species Committee of the American Fisheries Society, all anadromous coastal cutthroat trout in Washington, Oregon, and California have an elevated level of extinction risk (Nehlsen et al. 1991). Declines of coastal cutthroat trout appear to be greatest in the Columbia River basin and southward, and a number of anadromous runs of coastal cutthroat trout above the Bonneville Dam are extinct (Nehlsen et al. 1991; Williams and Nehlsen 1997; Johnson et al. 1999). Populations of coastal cutthroat trout appear to be more secure in parts of Washington, British Columbia, and Alaska, apparently because of pristine freshwater habitat and favorable ocean conditions in northern British Columbia and Alaska (Williams and Nehlsen 1997; Leider 1997; Schmidt 1997; Slaney et al. 1997).

The coastal cutthroat trout is the least studied of the seven species of Pacific salmonids (Hall 1997; Johnson et al. 1999). Much of the information pertaining to this subspecies has extracted from anecdotal reports or incidental encounters during the study of other salmonid species, and currently little is known about the life-history strategies in many basins (Hall 1997; Johnson et al. 1999). This situation is related to the low commercial value of the subspecies, a limited appeal with recreational anglers, and the complex life-history organization (Johnson et al. 1999). Coastal cutthroat trout have five life-history forms (Pauley et al. 1989; Trotter 1989, Northcote 1997). Anadromous populations live in lakes (lacustrine-anadromous) or streams (fluvial-anadromous), and individuals migrate to feed in estuaries and along the coast of the Pacific Ocean. Potamodromous populations live in rivers and migrate to small tributaries (fluvial-adfluvial-fluvial) to spawn and rear, or have restricted migration within the lotic system home range (fluvial). Lacustrine-adfluvial populations live in lakes and migrate to tributaries to spawn and rear.

Early researchers recognized the difficulties in estimating age and growth of coastal cutthroat trout because of variability in life-history forms, coexistence of numerous life-history forms in the same habitat, and the wide range of habitats occupied (Giger 1972; Tomasson 1979). Age and growth analysis by the scale method can be further complicated by the difficulty of identifying annular marks because of high rates of scale regeneration, lack of first-year annuli, and the small scale size (Knudsen 1980; Moring et al. 1981; Johnson et al. 1999). Despite these difficulties, scale analysis is often the preferred method because it is cost effective, relatively quick, and non-lethal. Advances in high-resolution analysis have increased the utility of scales for assessing the age of coastal cutthroat trout in Alaska (Ericksen 1997; Ericksen 1999; Rooper et al. 2000), but the techniques have not been broadly utilized.

Information about the anadromous life-history type of the subspecies has been increasing over the last decade, but there is little information on potamodromous life histories, especially headwater forms (Trotter 1989). An important data gap in knowledge of age structure, recruitment, growth rates, and mortality exists for many populations of coastal cutthroat trout (Johnson et al. 1999). Research on distribution of coastal cutthroat trout in 40 small watersheds (500-1,000 ha) in western Oregon (Gresswell et al. 2004; Gresswell et al. 2006) provided an opportunity to examine age and growth of fluvial cutthroat trout in headwater streams. In the current study, we evaluated age, growth, and size of coastal cutthroat trout in 37 of these headwater streams. The occurrence of missing first year annuli and scale regeneration was assessed to prevent bias in age estimation. Finally, we compared headwater populations in western Oregon to other life-history forms of this subspecies to determine trends in growth, longevity, and size across the range of coastal cutthroat trout.

Methods

Study area.- The historical range of coastal cutthroat trout is associated with the coastal temperate rainforest along the Pacific coast, traversing about 3,000 km from Prince William Sound, Alaska to Humboldt Bay in northern California and inland about 160 km to the crest of the Cascade Mountains (Behnke 1992). In western Oregon, coastal cutthroat trout are found in small coastal streams and lakes (Sumner 1972), large river systems (Tomasson 1979), and isolated headwater streams (Gresswell et al. 2004; Guy 2004). All five life-history forms of coastal cutthroat trout are present in Oregon.

During 1999–2001, coastal cutthroat trout were collected from watersheds three ecoregions (Cascade, Coast Range, and Klamath) across western Oregon (Gresswell et al. 2006; Figure 1). The Coast Range ecoregion is characterized by mild, moist winters and short dry summers. Topographically, study watersheds in this ecoregion occur from 287 to 923 m above mean sea level (ams), and mountains are steep with high gradient canyons prone to frequent disturbance from landslides. This area is heavily forested and undergrowth is thick. Dominate tree species are Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*) (Johnson et al. 1999). Primary land uses are timber harvesting and agriculture.

Like the Coast Range ecoregion, the westslope of the Cascade Mountains is characterized by dense forests. The primary tree species are Douglas fir noble fir (*Abies procera*), Engelmann spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*) (Johnson et al. 1999). Rainfall in the Cascade Mountains is spread throughout the year, but the majority falls between October and March. Elevation of study sites in this region was 758-1,583 m (ams).

The Klamath Mountain ecoregion has a history of mixed land use, including timber harvest, livestock grazing, and mining. This region is more arid, and forests are primarily Douglas fir and mixed oak (*Quercus* spp.) stands. Precipitation is lower because of rain-shadow effects, and much of the precipitation falls in winter. Summers are hot and dry. Topography in this ecoregion varies, and elevation of study watersheds was 648-1,085 m (ams).

Scale collection and age estimation.- Watersheds were randomly selected from 269 watersheds (500–5,800 ha) that occurred upstream from barriers to fish movement and where fluvial coastal cutthroat trout were the only salmonids (Gresswell et al. 2004). Watersheds that were known to contain hatchery fish or were located in non-forested areas were excluded. Because of the potential influence of physiography and geology (Lanka et al. 1987; Kruse et al. 1997) on age and growth characteristics, the above-barrier watersheds were divided by ecoregion and erosion potential (based on bedrock type; Gresswell et al. 2004). Subsequently, 40 sample watersheds were selected in proportion to their occurrence in each stratum (i.e., ecoregion and bedrock type).

Coastal cutthroat trout scales were collected in each watershed during summer low-flow periods between 1999 and 2001. Fish were captured using single-pass electrofishing without blocknets (Bateman et al. 2005). Scale samples were obtained for up to10 fish per 10-mm length group (e.g., 90–99 mm) in each stream segment where fish were present. Segment boundaries were defined by junctions with tributaries that were contributing greater than 15% of the mainstem discharge, or by geologic barriers to fish migration (Gresswell et al. 2006). Captured fish were anesthetized with clove oil, weighed to the nearest g, and measured to the nearest mm (fork length or FL). In each segment, scale samples were collected from up to 10 cutthroat trout in each 10-mm length category for age determination. Scales were removed from the area between the dorsal fin and the lateral line and adhered to gummed scale cards.

A subsample of fish was assembled for aging by randomly selecting individuals from each watershed (all segments combined) without replacement. Scales were initially screened to determine if they were usable (i.e., at least three scales on the card that were not regenerated). Regenerated scales had a relatively larger focus that was clear, pebbly, or irregular in shape (Ericksen 1999). Unusable scales were replaced by selecting another scale from the same sample, when possible, or randomly selecting a scale from another fish in the length group. Ultimately, up to10 fish per 10-mm length group were select in each watershed. Four watersheds (Blowout, N.F. Buckeye, Racks and Straight creeks) were removed from the study because of the low number of usable scales.

Scales were pressed in acetate, and images were digitized using a Leica DMLS stereomicroscope and Image-Pro® Plus version 4.5 software. To aid in identification of annual marks, scale images were converted from color to 8–bit monochrome, then a smoothing and sharpening filter was applied. Computer software was used to draw a reference line along the longest axis from the focus to the anterior edge of the scale. A 45° line was drawn off the reference line to help identify patterns in scale image (Ericksen 1999; Rooper et al.2000). The distance from the scale focus to each circulus, annulus, and scale edge was measured along the reference line and exported to a spreadsheet.

Annuli were identified on the anterior portion of the scale between the areas created by the 45º lines drawn off the reference line. We chose this area to examine scale growth patterns because scales are often resorbed along the dorsal and ventral edges because of stress, and it reduced the misidentification of checks or false annuli as annual marks (Ericksen 1999; Rooper et al. 2000). The criteria for identifying annuli were: (1) the annulus crosses over prior circuli; (2) spacing of circuli is wider during rapid summer growth and closer together during slower fall growth; and (3) circuli are wavy during faster growth and straighter during slower growth (Lux 1971). Age was assigned by counting the number of annuli and adjusting for missing first annulus (when necessary). Aging of the coastal cutthroat scales was performed by a single reader to maintain consistency of results (Rooper 2000).

In order to determine if the first-year annulus was absent (i.e., scale was not formed during the initial year of growth), the number of circuli to the first annulus was recorded. The "number of circuli" criterion has been commonly used for establishing the presence/absence of the first annulus in cutthroat trout (Lentsch and Griffith 1987), but the number often applied to cutthroat trout (< 8 circuli to the first annulus) was originally developed for a population of Yellowstone cutthroat trout *O. clarkii bouvieri* (Laakso and Cope 1956). Lentsch and Griffith (1987) questioned validity of extrapolating this number to other populations, and they found that variability associated with circuli number and first-annulus formation was strongly related water temperature, or the number of degree-days (i.e., one unit is accumulated for each degree Celsius above 0 ^{o}C per day) to which the fish was exposed during the initial growth year. Therefore, the relationship between the number of circuli to the first annulus and the number of degree-days accumulated during the growing season was evaluated in two of the streams in this study. Recording thermographs were placed near the mouth of a low-elevation watershed (Camp Creek; elevation 235 m abs) and a high-elevation watershed (Cavitt Creek; 1,019 m ams), and the number of degree days was calculated for each stream between April 1 and November 30. In western Oregon, this period generally corresponds to the period from spawning until the end of the growing season when water temperatures drop below 5^{o}C.

Validation and verification.- Age estimates were validated by examining scales from individual fish that were marked and recaptured (Jearld 1983; Devries and Frie 1996) in Camp (Hendricks 2003) and Hinkle (Bateman et al. 2004) creeks.. Validation was assessed by counting the number of annual marks on the scales between mark-recapture events (i.e., one annulus was formed on the scale each year; Beamish and McFarlane 1983; Devries and Frie 1996). Paired scales (collected from the same individual after at least 1 year) were independently aged, and the results compared to verify the expected number of annular marks appeared.

Scale-reader precision and bias were evaluated using multiple readings of paired scales from Camp and Hinkle creeks, known-age fish from hatchery brood stocks, and the scale samples from the study watersheds. Age was independently estimated three times for each fish over a 3-week period (Rooper 2000). Coefficient of variation (CV) was used to assess the repeatability of age estimated for the three readings (Chang 1982). Coefficient of variation was used to interpret precision because (1) variance is an unbiased and consistent estimator, and (2) CV can be summed across samples (fish) to yield a mean coefficient of variation. Age frequency tables and age bias plots based on multiple scale readings were used to visually detect systematic differences in age estimation between independent readings (Campana et al. 1995).

Growth.- Length of coastal cutthroat trout at previous age was back-calculated from scales using the direct proportion method (Francis 1990). To reduce the influence of size-selective mortality (i.e., Lee's phenomenon), only the last full year of growth before capture was estimated for each fish (Gutreuter 1987).

Growth increments were converted to relative growth rates (RG) to reduce the effect of fish size on growth (Warren 1971) using the formula:

$$RG_i = (L_{ie} - L_{ib})/L_{ib}$$

where:

RG_i = relative growth rate (mm/mm/year),

L_{ib} = length of fish at beginning of growth year,

and

L_{ie} = length of fish at the end of the growth year.

Survival.- Static (time-specific) life tables were used to estimate survival rates of age-3 (i.e., between age-2 and age 3) coastal cutthroat trout in all 37 watersheds (Hilborn and Walters 1992, Quinn and Deriso 1999). Static life tables use age data collected from a population at one particular time and assume that results are similar to a cohort followed through time. In contrast, dynamic life tables follow a group of individual fish born during the same year (i.e., a cohort) through time, and the assumption of interannual equilibrium in unnecessary. To test the validity of the equilibrium assumption in this study, data from one watershed (Camp Creek) that was sampled in multiple years (1999-2001) were used to estimate survival using both dynamic and static life tables. Analysis of variance (ANOVA) was used to determine if differences in survival estimates based on the two life-table types were statistically significant ($\alpha = 0.05$).

Subsequently, survival rates for all watersheds were compared with ANOVA, and Tukey-Kramer multiple comparison procedures were used to identify differences between among individual watersheds. Both types of life tables calculate survival as:

$$S = C_{a+1}/C_a$$

where:

S = survival from age a to $a + 1$

C_{a+1} = catch-at-age $a + 1$

C_a = catch-at-age a

A summary of age and growth characteristics for coastal cutthroat trout throughout the native range was developed from published literature, and mean length at age (mm), maximum age (years), and maximum length (mm) were compared among life-history types and geographic location with ANOVA. Tukey-Kramer multiple comparison procedure was used to evaluate differences among individual samples. All statistical analyses were performed in Number Cruncher Statistical System (NCSS; Hintze 2001).

Results

Validation and Verification

The mean number of fish with regenerated scales was 56%-74% per watershed. Formation of annuli on scales was validated for 234 coastal cutthroat trout (length range = 80-175 mm). Approximately 97% and 94% of the scales from Camp and Hinkle creeks, respectively, formed the expected number of annuli between capture dates.

Reader precision and bias was estimated for 4,834 scales from a combination of mark-recaptured fish from Camp and Hinkle creeks, known-age brood stock fish from Leaburg and Fall River hatcheries, and the study watersheds. Coefficient of variation among age estimates for individual fish (Chang 1982) ranged from 4.8% to 8.3% for all of the readings. Differences in the calculated lengths at age from the three independent readings were not statistically significant ($P = 0.78$; one-way analysis of variance F-test).

The mean number of circuli to the first annulus was 4-7 (Table 1). Scales with more than eight circuli to the first annulus were common, but there was a strong relationship ($P < 0.01$) between the number of circuli to first annulus and elevation (Figure 2; $R^2 = 0.71$); counts were higher in lower elevation streams with longer growing seasons and a greater number degree-days. The number of degree-days was 2,751 at Camp Creek and 2,159 at Cavitt Creek. Both estimates exceed the minimum number of degree-days (1500) reported to insure that all fish formed an annulus at age 1 (Lentsch and Griffith 1987).

There was a statistically significant relationship ($P < 0.05$) between frequency of regenerated scales and stream gradient (Figure 3; $r^2 = 0.87$), but relationships between stream elevation ($r^2 = 0.27$), width ($r^2 = 0.~06$), or depth ($r^2 =$ 0.09) failed to explain more than 27% of the variation in the number of regenerated scales. Percent scale regeneration was positively related to fish length ($r^2 = 0.90$; $P < 0.01$); frequency of scale regeneration ranged from 39% for 40-69 mm fish to more than 77% for fish larger than 140 mm.

Age and Growth

Age of coastal cutthroat trout in headwater streams in western Oregon ranged from 1-5 years (maximum length = 58-259 mm; FL). Age composition differed among study watersheds, and longevity (maximum age) ranged between 3 and 5 years. Maximum age was 3 years in five streams (14%), but in the majority of streams, maximum age was 4 (65%) or 5 (22%) years. Differences in maximum age and length were not statistically different among ecoregions (P = 0.24 and 0.31, age and length, respectively; analysis of variance F-test).

The mean relative growth rates in populations ranged from 0.37 to 0.64 mm/mm/year. Mean growth rate declined with age (0.76, 0.36, and 0.24 mm/mm/year, for age-1, age-2, and age-3 cutthroat trout, respectively; Figure 4A). Similarly, mean relative growth rates for 25-mm length groups decreased with increasing fish length (0.79-0.15 mm/mm/year for length groups from 40 to 165 mm; Figure 4B).

Mean length at age was statistically different among watersheds. Differences among watersheds were influenced by ecoregion but not latitude and longitude. For example, differences in mean length among ecoregions were statistically significant ($P < 0.01$; analysis of variance F-test). In contrast, relationships with mean length at age as the response variable and latitude (P = 0.08; $r^2 = 0.09$) and longitude ($P = 0.55$; $r^2 = 0.01$) as the predictor variable explained less than 10% of the variation in mean length at age.

Annual survival rates of age-3 (i.e., between age-2 and age 3) coastal cutthroat trout were highly variable among watersheds, ranging from 23% to 65% (Table 2). Survival rates did not differ significantly by year sampled ($P = 0.84$; analysis of variance F-test). Type of life table (static or dynamic) used did not appear to influence survival rates estimated in multiple year data collected from Camp Creek ($P < 0.01$; analysis of variance F-test).

Range-wide Summary

Maximum age, and maximum and mean length at age data were available for 3 lentic and 48 lotic coastal cutthroat trout populations distributed from northern California to southeast Alaska (Table 3). All known life-history forms were included in the summary. Additional populations were excluded because they contained experimentally manipulated fish that might not represent life-history variation found in natural populations.

Maximum age ranged from 1 (Moring and Younker 1979) to 11 years (Rooper et al. 2000), with a mean of 4 years for all populations (Table 3). Mean maximum age was highest for lentic and fluvial populations (both anadromous and potamodromous; 11 years; Armstrong 1971; Rooper et al. 2000), and lowest for headwater stream populations (mean maximum age = 6 years; Moring and Younker 1979; Tomasson 1979; Fuss 1982). Fluvial populations (stream and river combined) exhibited the greatest range of maximum fish age (1-6 years). Mean maximum age differed among states ($P < 0.01$; analysis of variance F-test) and among life-history forms ($P < 0.01$; analysis of variance F-test). The mean maximum age observed for coastal cutthroat trout in Alaska was significantly greater than populations in British Columbia, Washington, Oregon, and California.

Maximum length for coastal cutthroat trout ranged from 117 to 550 mm; the mean maximum length for all studies was 261 mm. The largest fish were captured in the Pacific Ocean or large rivers (mean = 422–550 mm). Mean maximum length did not differ among states ($P = 0.13$; analysis of variance F-test), but there were statistical differences among life-history forms ($P < 0.01$; analysis of variance F-test). Fluvial-adfluvial and lacustrine-adfluvial had the greatest mean maximum length (550 mm and 434 mm, respectively), and adfluvial-fluvial and lacustrine-anadromous coastal cutthroat trout were larger (mean = 340 mm and 381 mm, respectively) than those from headwater streams (mean = 189 mm).

Mean length at ages 1-4 varied throughout the range of coastal cutthroat trout (Table 3). Differences among study locations in mean length at age 1 and age 2 were statistically significant ($P \leq 0.01$ and 0.03, respectively; analysis of variance F-test). Specifically, mean length at age for age-1 coastal cutthroat trout in Alaska was greater than all other populations (Tukey-Kramer multiple comparison procedure). Mean length at age also varied significantly among life-history forms

($P \leq 0.01$; analysis of variance F-test). Fluvial-adfluvial, lacustrine-adfluvial, and fluvial-anadromous had the greatest mean length at ages 1-4, and headwater stream populations had a smaller mean length at given age. Mean lengths at age 5 and 6 were not compared to geographic or life-history patterns because the sample sizes were too small.

Discussion

Our data suggest that age and growth can be reliably determined from scales of coastal cutthroat trout in headwaters watersheds. Age was validated for 234 coastal cutthroat trout, and almost all of the scales (97% and 94% of fish from two streams) formed the expected number of annuli between captures. Ericksen (1997) reported similar results with 88% to 94% of cutthroat trout in southeast Alaska forming the expected number of annual marks between captures.

Scale regeneration is common among trout species, including all five life-history forms of coastal cutthroat trout in Alaska, British Columbia, and Oregon (Wyatt 1959; Cooper 1970, Moring et al.1981; Ericksen 1997). Furthermore, there appears to be a difference in the number of regenerated scales among life-history forms. Scale regeneration was >50% in samples of fluvial–adfluvial and fluvial coastal cutthroat trout from the Willamette River and its tributaries, and in 48 of the samples, regeneration exceeded 90% (Moring et al. 1981). Scale regeneration in populations of lacustrine-adfluvial and lacustrine-anadromous populations in southeast Alaska was less common (33-40%) than stream populations of coastal cutthroat trout (Ericksen 1997).

Differences in the percent of regenerated scales may be related to the environments occupied by the different life-history types. Previous research has suggested that fish density and stream characteristics such as gradient, width, and depth might play a role in scale regeneration. For example, scale regeneration is more common in smaller, high-elevation streams than in larger streams, rivers (Moring et al. 1981), and lakes (Rooper et al. 2000). In our study, stream gradient was the only physical characteristic with a statistically significant relationship with the number of regenerated scales

There also appears to be a relationship between fish length and the number of regenerated scales (Figure 5). For example, Cooper (1971) reported that the percent of regenerated scales ranged from 40% for 40-49 mm (FL) coastal cutthroat trout to >80% for fish >140 mm. Our findings were similar to Cooper (1971), with frequency of scale regeneration ranging from 39% for 40-69 mm fish to >77% for fish>140 mm.

The lack of a first-year annulus has been shown to cause aging bias in cutthroat trout from Alaska, Montana, and Wyoming (Lentsch and Griffith 1987; Downs 1995; Ericksen 1997), but this phenomenon was not observed for populations of headwater coastal cutthroat trout in western Oregon. Because the length of the growing season has been directly linked to the formation a first-year annulus, we examined the number of degree-days accumulated in two watersheds.

The number of degree-days estimated for both Camp and Cavitt creeks were nearly twice the estimate 1,500 degree-days proposed by Lentsch and Griffith (1987) as minimum number necessary for all fish in the population to develop an annulus following the first year of growth.

The occurrence of eight or more circuli to the first annulus has commonly been used as the criterion for adding an additional year to estimated age of cutthroat trout (Laakso and Cope 1956; Downs et al. 1997). We found that nearly 10% of all scales from headwater watersheds in western Oregon had more than seven circuli to the first annulus; however, it does not appear that any of the fish in this study lacked a first-year annulus. Scales samples collected in lower elevation watersheds had higher than expected circuli counts, but all had distinct annular marks meeting the criteria for annuli (Lux 1971). We found an inverse relationship between the number of circuli to the first annulus and elevation, and assume that this observation is related to mean January temperature and number of degree-days accrued during the growing season.

Coastal cutthroat trout appear to be a short-lived species throughout the range, regardless of life-history strategy. In the 37 barrier-isolated populations of stream resident (nonmigratory) coastal cutthroat trout in western Oregon, we found that maximum age ranged from 3 to 5 years. Moring et al. (1981) found that maximum age of fluvial-adfluvial and fluvial coastal cutthroat trout from 110 streams in the Willamette Valley ranged was 6 years. Fluvial-adfluvial and fluvial populations in streams of the Cascade Mountain streams exhibited a similar pattern, and few coastal cutthroat trout lived more than 4 years (Wyatt 1959). Anadromous, potamodromous, and stream resident coastal cutthroat trout had a maximum age of 4 years in the Rogue River of southern Oregon (Tomasson 1979). A maximum age of 4 years was also observed for anadromous and stream resident populations of cutthroat trout in large coastal rivers on the Olympic Peninsula of Washington (Fuss 1982). Lacustrine populations of coastal cutthroat trout appear to reach a greater maximum age than lotic populations, reaching up to 11 years (Ericksen 1997; Rooper et al. 2000).

Growth of trout depends not only on the availability of food items, but also on the age and size of the individual (Martin 1983; Boss and Richardson 2002). Relative growth rates observed in the current study decreased as size and age increased, a result previously observed in other populations of coastal cutthroat trout (Fuss 1982; Martin 1983; Rosenfeld and Boss 2001). Smaller fish have lower absolute energy requirements compared to larger, older fish, and therefore, smaller fish may have a selective advantage in streams with low productivity and higher temperatures (Rosenfeld and Boss 2001). Hughes and Reynolds (1994) proposed that differences in energetic requirements of fish influenced a decrease in maximum body size along an upstream gradient.

Mean survival rate for 3-year-old-fish in this study ranged from 23% to 65%. Because of the short lifespan (3-5 years), the only way to compare survival rates was to examine annual survival of fish from age-2 to age-3. We used life tables to estimate annual survival because we did not have enough data to use regression techniques (Ricker 1975). Life tables have similar assumptions as catch-curve regressions: (1) constant recruitment; (2) constant survival; and (3) equal survival among year classes. Because most of our data was collected during a single sampling event, static life tables were employed. In one watershed, Camp Creek, data were collected over multiple years, and it was possible to follow a cohort through time using a dynamic life table. We found no statistical difference between the results of the two techniques for Camp Creek.

Annual survival rates were directly related to the lifespan (3-5 years) of these headwater populations of coastal cutthroat trout, and survival rates were significantly different among populations with different maximum ages. Estimates of survival and maximum age were similar to a previous study in the Cascade Mountains of western Oregon (survival rates range = 32-45%; Aho 1977).

Range-wide characteristics

Variation in growth characteristics (e.g., relative growth rate, maximum age, and maximum length) among coastal cutthroat trout life-history forms has been previously reported in studies conducted in Washington, Oregon, and British Columbia (Cooper 1971; Thomasson 1978; Nicholas 1979; Fuss 1982). When these characteristics were compared across the entire range of the subspecies (Table 3), coastal cutthroat trout with migratory life-history forms (fluvial-adfluvial, lacustrine-adfluvial, and fluvial-anadromous) attained greater length at ages 1-4, lived to a greater maximum age, and had greater maximum lengths than nonmigratory forms. These differences among life-history forms appear to be related to variation in habitat productivity and food availability (Fuss 1982; Martin 1983). For example, areas used by anadromous life-forms, such as ocean and estuary habitats, have a greater abundance and diversity of food sources.

Although Johnston and Mercer (1976) suggested that growth of coastal cutthroat trout increased along a latitudinal gradient from north to south, summarization of data collected throughout the range of the subspecies does not support this generalization (Table 3). Age structure, growth, and survival does vary throughout the region, but there was not a strong geographical trend. In fact, it appears that life-history form has more of an effect on size at age than latitude. Coastal cutthroat trout in Alaska (at the northern extent range of this subspecies) actually the greatest length at age 1, the oldest individual fish, and mean maximum lengths that exceeded the mean maximum length throughout the range. Apparently, in the more productive and less disturbed habitats at the northern extent of the range, coastal cutthroat trout are larger and older, despite shorter growing seasons. Furthermore, habitat degradation and simplification appear to be greater south of British Columbia, and human populations are denser in the south (Williams and Nehlsen 1997).

Range-wide synthesis of life-history information on coastal cutthroat trout emphasizes the difficulties of comparing disparate studies. For example, fish in the 16 studies were apparently measured by fork length (as opposed to total length or standard length), and in many cases, the method used was not identified explicitly.

Only three studies identified the method used to back-calculate length-at-age. In order to effectively assess differences in life-history traits throughout the range of any animal or plant species, it is critical to document the methods. Furthermore, tabulating past and present research data into accessible metadata files would greatly assist future attempts at identifying ecological patterns in biological research.

This study provides the first general description of the natural range of variation in age structure, growth rates, and survival of coastal cutthroat trout in headwater populations of western Oregon, and a preliminary synthesis of these life-history characteristics across the range of the subspecies. Age estimation by the scale method proved a useful, non-lethal procedure for coastal cutthroat trout in this study, but validation and verification of age and growth estimates is critical. Estimating the number of degree-days accumulated in streams of western Oregon provided a useful metric for predicting the presence of first-year annuli in headwater fluvial populations of coastal cutthroat trout. We observed a strong relationship between the number of circuli to the first annulus and mean stream elevation. In contrast, scale regeneration appears to be influenced by the stream gradient, habitat type (lotic or lentic), and the age of the fish. Apparently, abrasion associated with stressful conditions associated with lotic habitats or reproductive activities of mature individuals tends to increase scale loss and regeneration, and thereby reduce the utility of scale analysis.

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Table 1. Scale characteristics for age-1 and older coastal cutthroat trout in western Oregon. Standard error (SE) given in parentheses

Stream name	Mean focus radius distance (mm)	Mean scale radius distance (mm)	Mean number of circuli to 1st annulus	Percent of fish with 8 or more circuli to 1st annulus
Augusta Creek	0.06 (0.01)	0.39 (0.09)	6.4 (0.8)	9
Barney Creek	0.07 (0.01)	0.41 (0.14)	5.5 (1.0)	2
Brice Creek	0.06 (0.01)	0.32 (0.07)	6.2 (0.9)	6
Bridge Forty Creek	0.06 (0.01)	0.39 (0.09)	6.2 (0.8)	6
Camp Creek	0.06 (0.01)	0.37 (0.09)	6.4 (0.8)	2
Canyon Creek	0.06 (0.01)	0.44 (0.10)	5.3 (0.8)	7
Cavitt Creek	0.06 (0.01)	0.39 (0.09)	6.4 (0.8)	7
Coffee Creek	0.06 (0.01)	0.37 (0.10)	6.1 (0.8)	3
Dead Horse Creek	0.06 (0.01)	0.45 (0.07	6.3 (0.9)	2
Drowned Out Creek	0.06 (0.01)	0.44 (0.12)	5.1 (0.9)	3
E.F. Laying Creek	0.06 (0.01)	0.39 (0.09)	6.3 (0.9)	10
E.F. Millicoma Creek	0.06 (0.01)	0.36 (0.09)	6.3 (1.0)	3
Glenn Creek	0.06 (0.01)	0.40 (0.11)	6.3 (1.2)	1
Hardy Creek	0.06 (0.01)	0.35 (0.08)	5.5 (0.9)	8
Hunt Creek	0.07 (0.01)	0.43 (0.11)	6.4 (0.8)	2
Little Stratton Creek	0.06 (0.01)	0.40 (0.09)	6.5 (0.8)	4
Lukens Creek	0.05 (0.02)	0.35 (0.16)	6.1 (0.8)	7
Miller Creek	0.06 (0.01)	0.40 (0.11)	5.4 (0.9)	3
Moose Creek	0.07 (0.01)	0.41 (0.10)	6.0 (1.0)	4
Muletail Creek	0.06 (0.01)	0.41 (0.11)	6.3 (1.1)	2
Nevergo Creek	0.07 (0.01)	0.39 (0.08)	5.3 (0.9)	6
N.F. Ecola Creek	0.06 (0.01)	0.42 (0.11)	6.3 (1.3)	3
N.F.E.F. Rock Creek	0.07 (0.02)	0.39 (0.12)	4.5 (0.8)	5
R.F. Salt Creek	0.06 (0.01)	0.43 (0.09)	7.1 (0.8)	4
Rock Creek (Coquille)	0.06 (0.01)	0.50 (0.12)	5.9 (0.9)	5
Rock Creek (Rouge)	0.06 (0.01)	0.43 (0.11)	6.8 (1.1)	5
Rock Creek (Youngs)	0.07 (0.01)	0.42 (0.14)	5.3 (1.0)	2
Salt Creek	0.06 (0.01)	0.43 (0.08)	7.2 (0.7)	7
S.F. Buckeye	0.06 (0.01)	0.41 (0.09)	6.0 (0.9)	8
Slater Creek	0.06 (0.01)	0.42 (0.09)	6.2 (1.0)	2
Slide Creek	0.06 (0.01)	0.42 (0.07)	6.2 (1.2)	1
Sweet Creek	0.07 (0.01)	0.48 (0.14)	6.3 (1.0)	2
Tucca Creek	0.07 (0.02)	0.37 (0.09)	5.4 (0.8)	2
Tumblebug Creek	0.06 (0.01)	0.38 (0.09)	5.7 (0.9)	11
W.F. Brummit Creek	0.06 (0.01)	0.43 (0.13)	6.0 (0.8)	3
W.F. Deer Creek	0.06 (0.01)	0.42 (0.10)	6.2 (0.8)	3
Wolf Creek	0.06 (0.02)	0.40 (0.09)	6.1 (0.9)	2

Table 2. Maximum age and annual survival rates of 3-year-old coastal cutthroat trout based of static life tables.

Stream name	Maximum age	Survival
Augusta Creek	4	0.48
Barney Creek	5	0.58
Brice Creek	4	0.41
Bridge Forty Creek	4	0.45
Camp Creek	4	0.47
Canyon Creek	4	0.37
Cavitt Creek	5	0.65
Coffee Creek	4	0.50
Dead Horse Creek	3	0.23
Drowned Out Creek	4	0.43
E.F. Laying Creek	4	0.42
E.F. Millicoma Creek	3	0.29
Glenn Creek	4	0.41
Hardy Creek	4	0.45
Hunt Creek	5	0.61
Little Stratton Creek	3	0.27
Lukens Creek	4	0.42
Miller Creek	5	0.45
Moose Creek	4	0.48
Muletail Creek	4	0.41
Nevergo Creek	3	0.28
N.F. Ecola Creek	4	0.46
N.F.E.F. Rock Creek	4	0.47
R.F. Salt Creek	4	0.38
Rock Creek (Coquille)	4	0.46
Rock Creek (Rouge)	4	0.51
Rock Creek (Youngs)	5	0.65
Salt Creek	4	0.45
S.F. Buckeye	4	0.43
Slater Creek	3	0.39
Slide Creek	4	0.42
Sweet Creek	5	0.59
Tucca Creek	4	0.45
Tumblebug Creek	4	0.38
W.F. Brummit Creek	5	0.65
W.F. Deer Creek	5	0.62
Wolf Creek	4	0.35

Table 3. Mean fork length at age, maximum age, and maximum length of coastal cutthroat trout from northern California to southeast Alaska. Numbers in parenthesis represent sample size when given.

Location	State or province	Life-history form[a]	Mean length at age						Maximum age (years)	Maximum length (mm)	Reference
			1	2	3	4	5	6			
Eva Lake	AK	L-AN	-	-	185(4)	216(24)	247(36)	306(59)	10	381	Armstrong 1971
Margeret Lake	AK	L-AD	145(3)	158(23)	178(71)	207(71)	231(57)	251(45)	11	314	Rooper et al. 2000
Lymn Creek	BC	F-A	92	137	172	-	-	-	3	187	Mason 1974
Chef Creek	BC	F-A/A-F	50(510)	84(196)	119(32)	134(4)	-	-	4	183	Cooper 1970
Loon Lake	BC	L-AD	134(54)	161(148)	1736(90)	180(93)	197(55)	-	5	200	Jonsson et al. 1984
Prairie Creek	CA	F-A	59	108	169	225	282	340	6	340	Dewitt 1954
Tributary 8 (Lookout Creek)	OR	A-F/F	72(35)	104(18)	123(8)	136(4)	-	-	4	138	Wyatt 1959
Mack Creek	OR	A-F/F	91(24)	120(20)	142(22)	151(4)	-	-	4	161	Wyatt 1959
Lookout Creek	OR	A-F/F	94(10)	127(16)	156(28)	196(6)	239(1)	-	5	239	Wyatt 1959
Willamette River	OR	L-AD	148	205	245	267	338	420	6	434	Moring and Youke
McKenzie River	OR	L-AD/F	119	178	231	276	287	318	6	354	Moring & Youker
Santiam River	OR	L-AD	150	184	227	277	290	-	5	290	Moring and Youke
N. Santiam River	OR	L-AD/F	122	190	256	341	-	450	6	450	Moring and Youke
S. Santiam River	OR	L-AD/F	135	167	218	289	303	-	5	303	Moring and Youke
Long Tom River	OR	L-AD/F	-	214	231	-	-	-	3	304	Moring and Youke
Luckiamute River	OR	L-AD/F	121	164	260	308	-	-	4	308	Moring and Youke
Mary's River	OR	L-AD/F	100	151	184	239	404	-	5	404	Moring and Youke
Muddy Creek	OR	L-AD/F	132	143	213	-	-	-	3	233	Moring and Youke
N. Yamhill River	OR	L-AD/F	108	181	230	-	-	-	3	230	Moring and Youke
S. Yamhill River	OR	L-AD/F	100	186	221	265	-	-	4	278	Moring and Youke
Tualatin River	OR	L-AD/F	120	158	-	-	-	-	2	201	Moring and Youke
Calapooia River	OR	L-AD/F	99	150	164	-	-	-	3	185	Moring and Youke
Fall Creek	OR	L-AD/F	120	140	223	205	-	-	4	238	Moring and Youke
Molalla River	OR	L-AD/F	117	165	207	220	-	-	4	247	Moring and Youke
Pudding River	OR	L-AD/F	110	99	-	-	-	-	2	145	Moring and Youke
Row River	OR	L-AD/F	111	-	-	-	-	-	1	117	Moring and Youke
Thomas Creek	OR	L-AD/F	107	146	173	-	-	-	3	179	Moring and Youke
M.F.Willamette River	OR	L-AD/F	105	141	-	-	-	-	2	161	Moring and Youke
Clatskanie River	OR	A-F	129(1)	165(22)	220(4)	550(1)	-	-	4	550	Hess 1982
Gnat-Big Creek	OR	A-F	110(7)	156(30)	210(5)	340(1)	-	-	4	340	Hess 1982
Scappoose Creek	OR	A-F	104(6)	157(33)	237(7)	-	-	-	3	283	Hess 1982
Tide-Goble Creek	OR	A-F	113(2)	161(17)	204(2)	-	-	-	3	207	Hess 1982
Lookout Creek	OR	A-F/F	-	-	-	-	-	-	-	-	Aho, 1977
Rogue River (estuary)	OR	F-A	91(70)	202(263)	219(34)	341(5)	-	-	4	353	Tomasson 1979
Rogue River (lower river)	OR	F-A	92(18)	176(22)	249(31)	303(10)	322(2)	-	5	382	Tomasson 1979
Rogue River (upper river)	OR	A-F/F	72(16)	160(35)	244(18)	317(4)	390(1)	400(4)	6	425	Tomasson 1979
Rogue River (tributaries)	OR	F	65(59)	103(23)	133(10)	179(4)	189(1)	-	5	189	Tomasson 1979
Sand Creek (Ocean)	OR	F-A	-	404(1)	325(11)	333(123)	345(158)	366(72)	10	514	Sumner 1962
	OR	F-A	107(13)	132(71)	175(107)	210(52)	239(10)	-	5	239	Sumner 1962

Table 3 Continued

Sand Creek (Stream)											
Kelsey Creek	WA	A-F/L-AD	134	175	229	-	-	-	3	232	Scott 1986
Bear Creek	WA	A-F	78	95	128				3	128	Scott 1986
Gold Bar Creek	WA	A-F/F	118	144	174	-	-	-	3	199	Chilcote et al.1980
Hurst Creek	WA	F-A/A-F/F	73(28)	108(28)	139(17)	170(4)	-	-	4	203	Fuss 1982
Miller Creek	WA	F-A/A-F/F	74(35)	109(35)	141(14)	-	-	-	3	188	Fuss 1982
Octopus Creek	WA	F-A/A-F/F	78(50)	113(25)	155(3)	-	-	-	3	187	Fuss 1982
Snahapish River	WA	F-A/A-F/F	73(24)	112(24)	140(15)	174(3)	-	-	4	191	Fuss 1982
Hoh River	WA	F-A/A-F/F	73(19)	106(19)	140(11)	-	-	-	3	202	Fuss 1982
Braden Creek	WA	F-A/A-F/F	74(121)	113(119)	147(55)	186(9)	-	-	4	226	Fuss 1982
Elk Creek	WA	F-A/A-F/F	71(28)	112(28)	150(17)	-	-	-	3	195	Fuss 1982
Winfield Creek	WA	F-A/A-F/F	70(75)	109(75)	142(30)	-	-	-	3	174	Fuss 1982
Goodman Creek	WA	F-A/A-F/F	72(59)	109(59)	147(43)	179(8)	-	-	4	204	Fuss 1982
Pacific Ocean	WA	F-A	-	-	176(19)	199(42)	248(19)	-	5	289	Fuss 1982
	Mean		101	151	191	246	284	356	4	261	
	SE		3.8	7.2	6.6	15.3	15.8	23.2	0.3	13.8	
	Range		50-150	84-404	119-325	134-550	189-404	251-450	1-11	117-550	

Location	State or province	Life-history form	Mean length at age (mm) 1	2	3	4	5	6	Maximum age (years)	Maximum length (mm)	Reference
Augusta	OR	F	56	100	139	179	-	-	4	218	Current study
B40	OR	F	59	107	154	202	-	-	4	213	Current study
Barney	OR	F	59	107	148	177	172	-	5	241	Current study
Brice	OR	F	60	103	132	-	-	-	4	160	Current study
Camp Avg	OR	F	67	96	130	165	-	-	4	237	Current study
Canyon	OR	F	56	102	149	192	-	-	4	212	Current study
Cavitt	OR	F	54	96	134	164	165	-	5	201	Current study
Coffee	OR	F	48	90	132	174	-	-	4	190	Current study
Deadhorse	OR	F	50	90	133	-	-	-	3	173	Current study
Drownedout	OR	F	55	96	131	166	-	-	4	200	Current study
EF Laying	OR	F	56	98	132	157	-	-	4	181	Current study
EF Millicoma	OR	F	55	95	135	-	-	-	4	177	Current study
Glen	OR	F	56	98	139	166	-	-	4	202	Current study
Hardy	OR	F	56	99	140	167	-	-	4	178	Current study
Hunt	OR	F	56	99	141	179	242	-	5	253	Current study
L Stratton	OR	F	48	89	136	-	-	-	3	171	Current study
Lukens	OR	F	62	103	138	172	-	-	4	199	Current study
Miller	OR	F	50	90	129	165	184	-	5	197	Current study
Moose	OR	F	60	107	145	173	-	-	4	211	Current study
Muletail	OR	F	50	89	125	147	-	-	4	173	Current study
Nevergo	OR	F	56	103	147	155	-	-	4	203	Current study
NF Ecola	OR	F	55	97	141	171	-	-	4	188	Current study
NFEF Rock	OR	F	55	97	131	180	-	-	4	206	Current study
RF Salt	OR	F	55	99	137	146	-	-	4	184	Current study
RockC	OR	F	52	93	123	136	-	-	4	179	Current study
	OR	F	55	99	139	167	-	-	4	189	Current study

Table 3 Continued

RockR											
RockY	OR	F	55	98	137	163	199	-	5	220	Current study
Salt	OR	F	53	99	141	174	-	-	4	183	Current study
SF Buckeye	OR	F	54	98	135	151	-	-	4	167	Current study
Slater	OR	F	53	96	136	-	-	-	3	172	Current study
Slide	OR	F	57	101	134	156	-	-	4	167	Current study
Sweet	OR	F	57	102	135	164	186	-	5	214	Current study
Tucca	OR	F	55	93	123	162	-	-	4	174	Current study
Tumblebug	OR	F	57	98	127	160	-	-	4	177	Current study
WF Brummit	OR	F	49	89	129	166	194	-	5	222	Current study
WF Deer	OR	F	51	91	127	152	180	-	5	196	Current study
Wolf	OR	F	53	92	127	164	-	-	4	193	Current study
	Mean		55	97	137	166	190		4	195	
	SE		0.64	0.84	1.20	2.32	8.35		0.1	3.7	
	Range		48-67	89-107	123-154	136-202	165-242				

[a]Life-history form: L-AN = lacustrine-anadromous, F-A = fluvial-anadromous, A-F = adfluvial-fluvial, F = fluvial, L-AD = lacustrine-adfluvial

Figure Legends

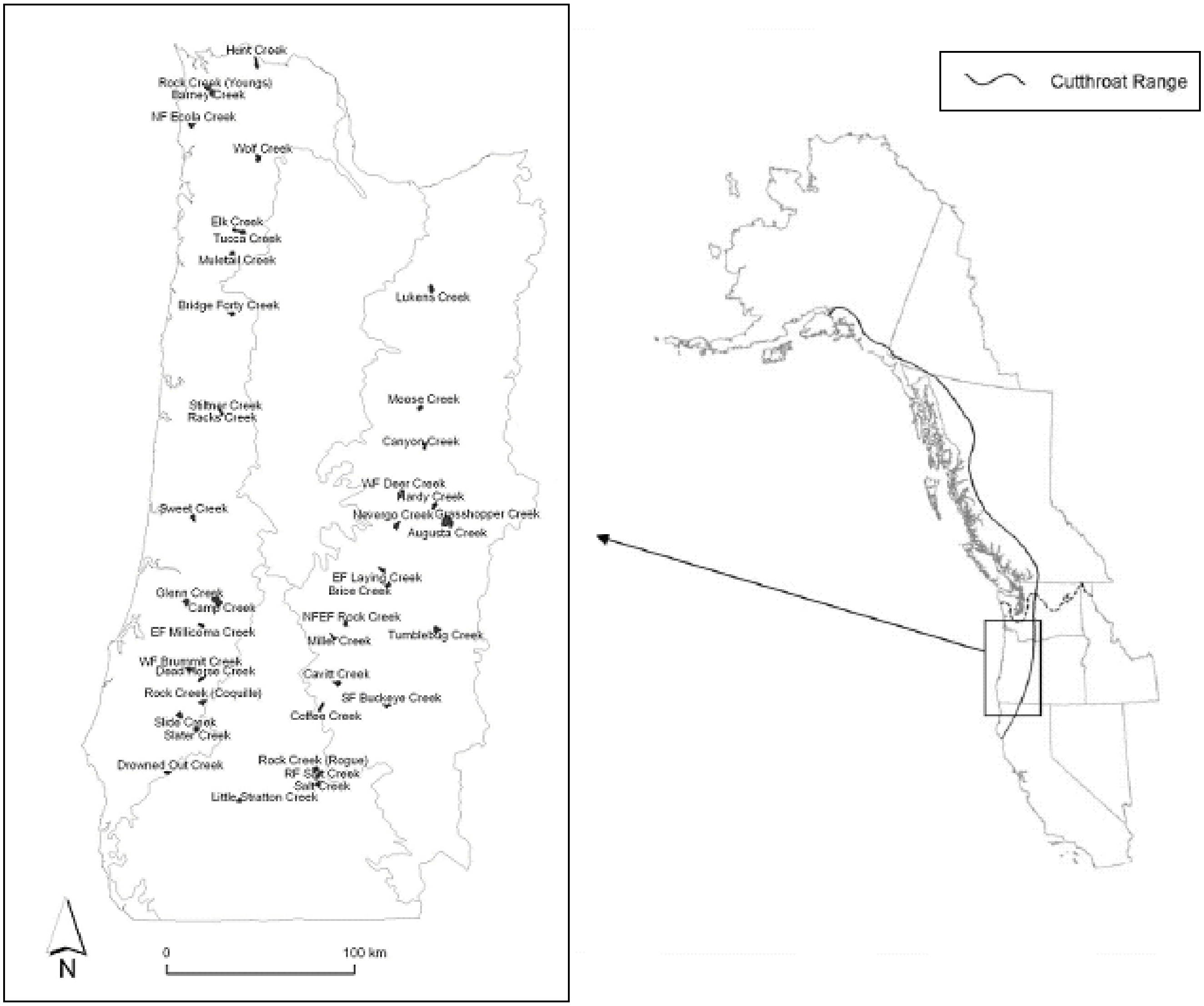
Figure 1. Locations of 37 sample watersheds in western Oregon that occur above natural barriers to upstream movement and containing populations of coastal cutthroat trout.

Figure 2. Relationship between elevation (predictor variable) and mean number of circuli to the first annulus (response variable) for 37 headwater populations of coastal cutthroat trout in western Oregon.

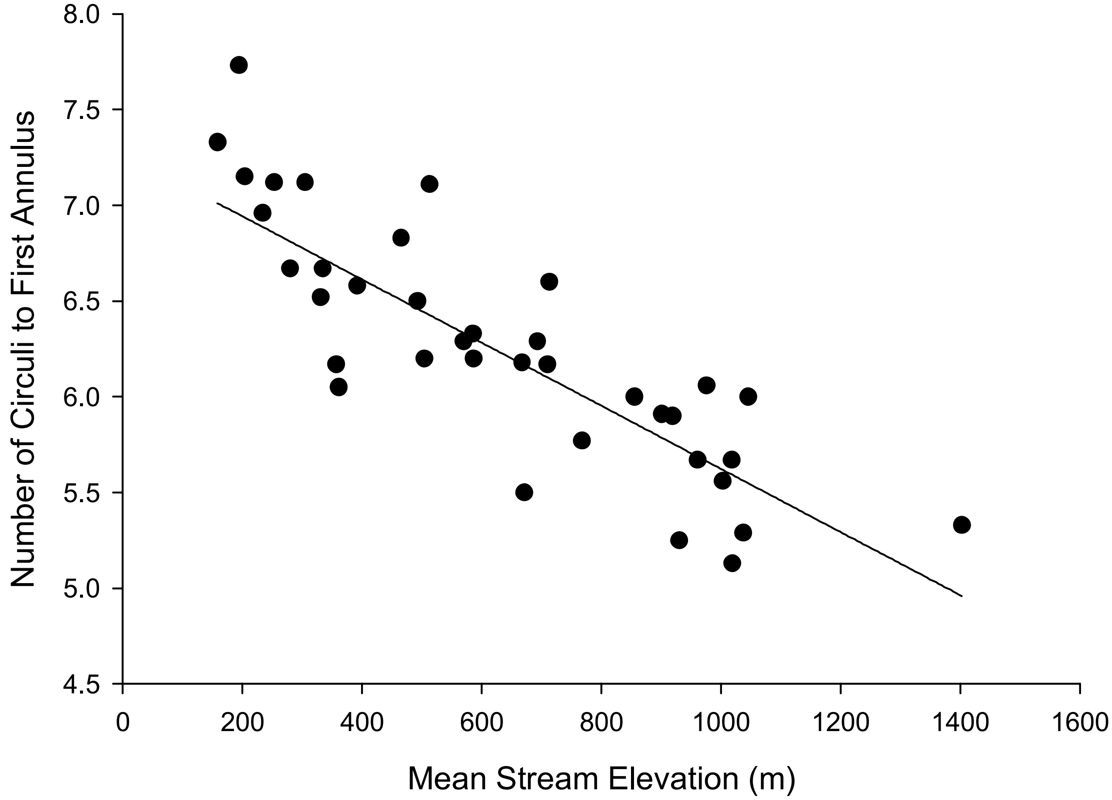
Figure 3. Relationship between stream gradient (predictor variable) and the frequency of scale regeneration (response variable) of 37 headwater populations of coastal cutthroat trout from western Oregon.

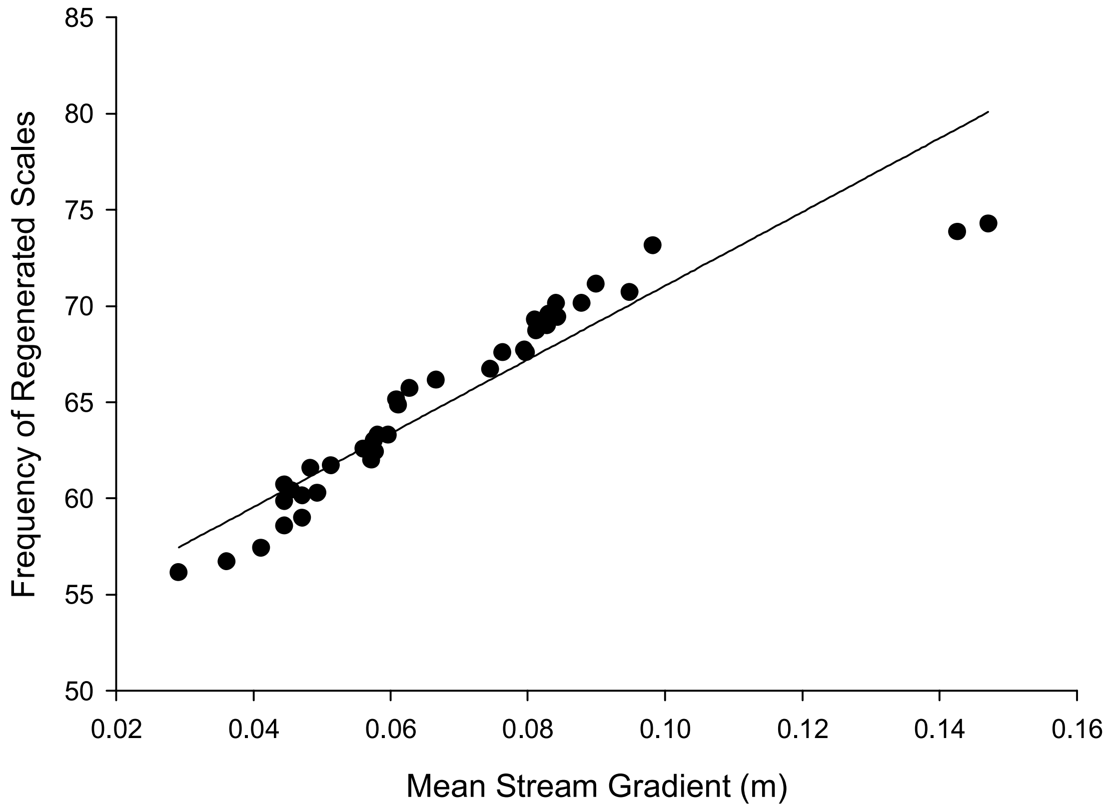
Figure 4. Mean annual relative growth rates by (a) 25-mm length groups and (b) age groups for 37 headwater populations of coastal cutthroat trout in western Oregon.

Figure 5. Relationship between mean length of coastal cutthroat trout (predictor variable) and the percentage of regenerated scales (response variable) in 37 headwater populations from western Oregon.

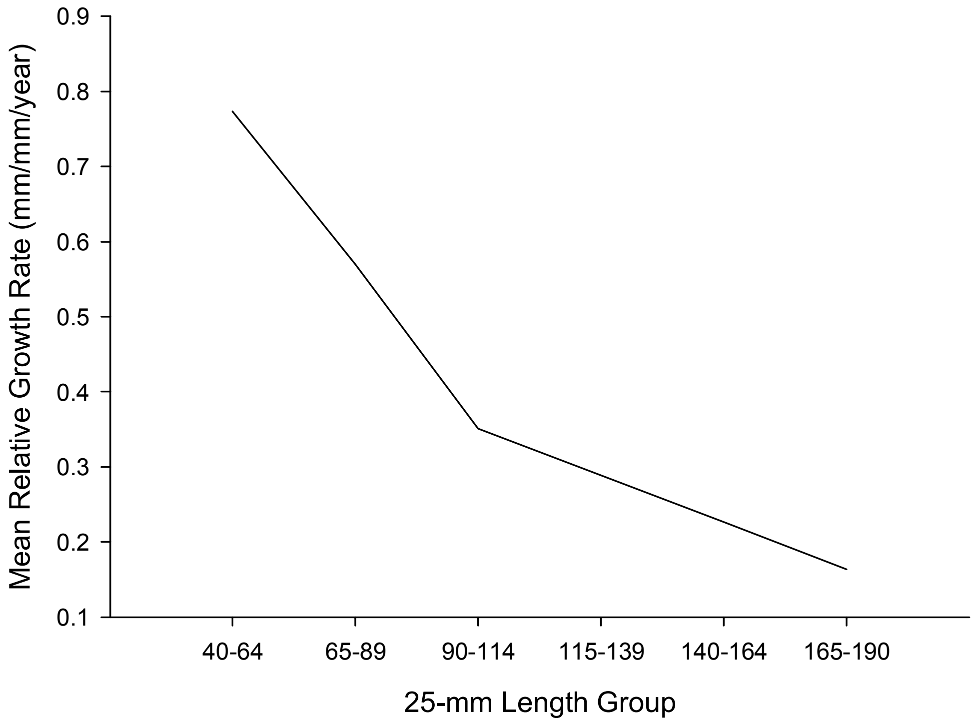


Cutthroat Range
Hent Creek
Rock Creek (Youngs)
Barney Creek
NF Ecola Creek
Wolf Creek
Elk Creek
Tucca Creek
Muletail Creek
Bridge Forty Creek
Lukens Creek
Stilmer Creek
Racks Creek
Moose Creek
Canyon Creek
WF Deer Creek
Hardy Creek
Sweet Creek
Nevergo Creek
Grasshopper Creek
Augusta Creek
EF Laying Creek
Brice Creek
Glenn Creek
Camp Creek
NFEF Rock Creek
EF Millicoma Creek
Tumblebug Creek
Miller Creek
WF Brummit Creek
Dead Horse Creek
Cavitt Creek
Rock Creek (Coquille)
SF Buckeye Creek
Slide Creek
Coffee Creek
Slater Creek
Rock Creek (Rogue)
Drowned Out Creek
RF Salt Creek
Salt Creek
Little Stratton Creek
N
0
100 km

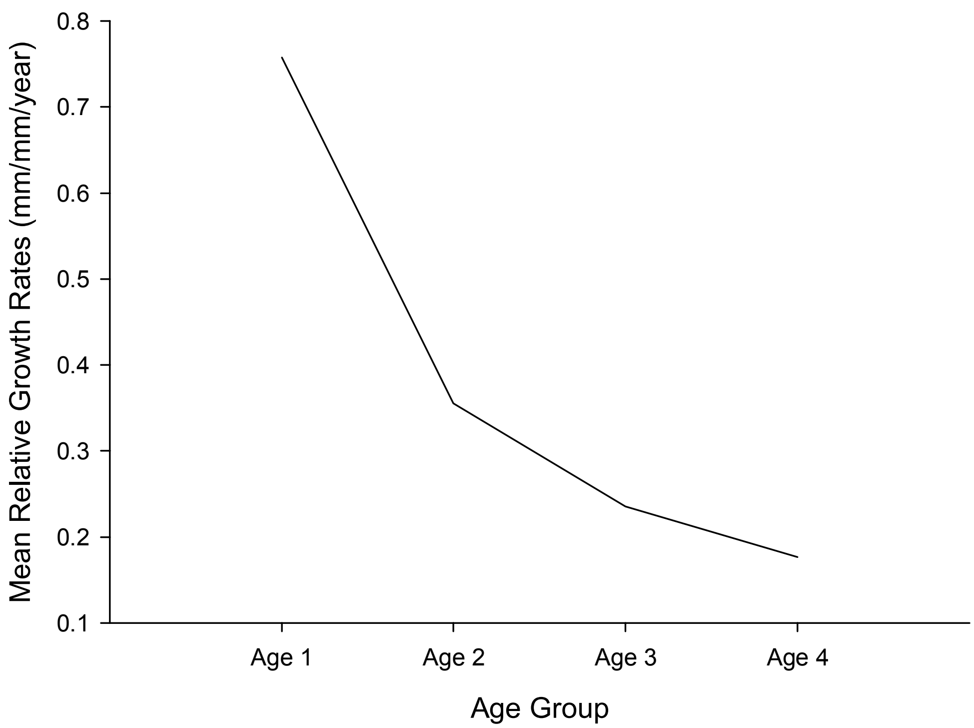

Number of Circuli to First Annulus
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
0
200
400
600
800
1000
1200
1400
1600
Mean Stream Elevation (m)

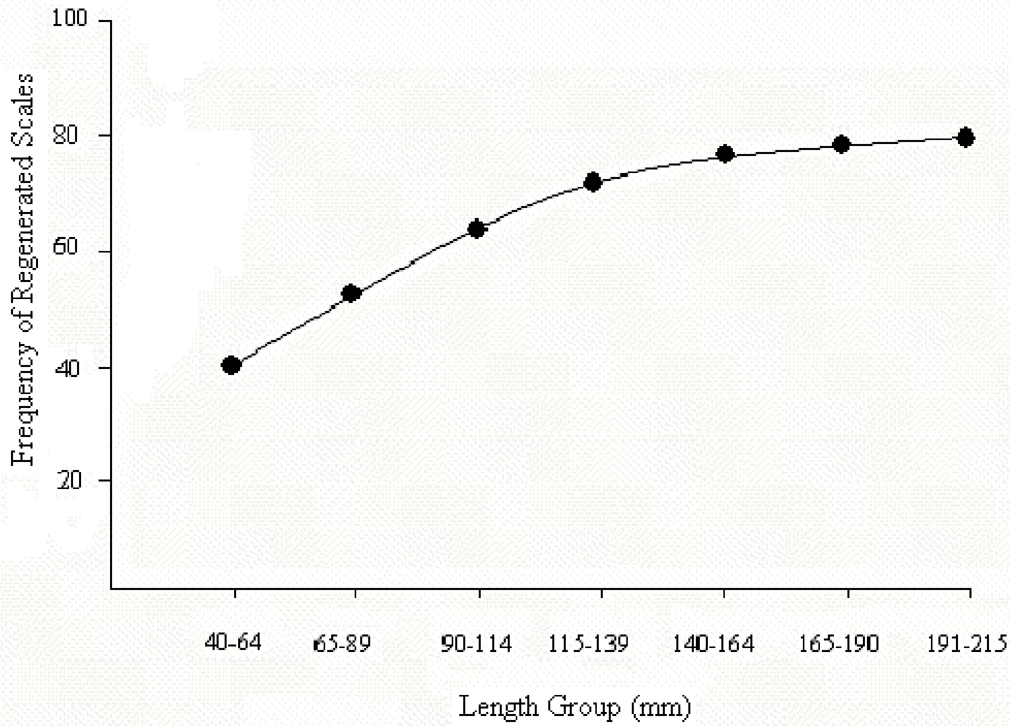

Frequency of Regenerated Scales
85
80
75
70
65
60
55
50
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Mean Stream Gradient (m)

(A)


0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Mean Relative Growth Rate (mm/mm/year)
40-64
65-89
90-114
115-139
140-164
165-190
25-mm Length Group

(B)


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Mean Relative Growth Rates (mm/mm/year)
Age 1
Age 2
Age 3
Age 4
Age Group


100
80
60
40
20
Frequency of Regenerated Scales
40-64
65-89
90-114
115-139
140-164
165-190
191-215
Length Group (mm)

Chapter 3

Influence of Basin-Scale Environmental Variables on the Population Structure of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in Western Oregon

Abstract- We examined the influence of environmental characteristics of headwater streams on the biological variables describing age and growth structure in populations of coastal cutthroat trout *Oncorhynchus clarkii clarkii* in western Oregon. Scales were collected from trout in 37 watersheds between 1999 and 2001. Age was estimated by the scale method for 4,250 individuals and validated for 234 fish that were marked and recaptured. Length of coastal cutthroat trout at previous age was back-calculated from scales using the direct proportion method, and resulting estimates were used to estimate relative growth rates for the last full year of growth. Three biological variables (length at age 1, mean length of trout captured, and survival) were selected as response variables that described differences in age and growth structure of coastal cutthroat trout across headwater watersheds in western Oregon. Akaike's Information Criterion (AIC) was used to select multiple regression models that "best" described biological response of headwater populations of coastal cutthroat trout to physical variables representing watershed geomorphology and water temperature. A model with January water temperature and calcium ions as predictor variables was the "best approximating model" for predicting mean length at age 1. The model with maximum pool depth and number of vertical steps (>1 m) in the stream channel was most appropriate for predicting mean fish length in a watershed; and mean survival was best predicted by a model with mean July water temperature and maximum pool depth as predictor variables.

Introduction

Hydrological and biological factors interact at multiple spatial and temporal scales to influence fish occurrence, abundance, and distribution (Herger et al. 1996, Torgersen and Close 2004, Gresswell et al. 2006). Broad- to local-scale environmental factors (e.g., geology, climate, temperature, and photoperiod) often cause extensive variation in life-history traits and population dynamics (Yamamoto et al. 1999; Cattaneo et al. 2002). Local differences in fish population characteristics are not only the direct result of aquatic habitat, but also the adjacent terrestrial ecosystem occurring next to, underneath, and above a stream channel (Gomi et al. 2002). Influences from neighboring systems, originating from either natural or human-induced disturbance, can have a cascading effect on population parameters, such as growth patterns, age structure, and survival rates.

Growth is the result of metabolic processes associated with assimilation of food into waste, gonadal development, and production of energy used to satisfy body maintenance and behavior (Bertalanffy 1938; Warren 1971). Additional energy resulting from this process can be used to grow in length or weight. Metabolic demands are affected by food availability (quality and quantity), fish size, and external environment (Weatherley 1990; Boss and Richardson 2002). Environmental factors, through their control over metabolic processes, food availability, and temperature, determine differences in fish growth among years and locations.

Numerous laboratory studies and experimental manipulation of streams have demonstrated that environmental factors can affect on age, size, growth, and survival (Fry 1971; Brett 1979; Wilzbach and Hall 1985). These studies provide insight concerning the environmental features that influence age-class structure and growth characteristics, but interactions between abiotic and biotic habitat factors and anthropomorphic changes in natural environments are less well-understood. Furthermore, most studies are usually focused on one or two sites in a single watershed, and seldom has a single study examined factors influencing growth in multiple watersheds across the landscape.

Recent research that focused on distribution of coastal cutthroat trout in 40 small isolated (above barriers to anadromous fishes) stream networks (500-1,000 ha) in western Oregon (Gresswell et al. 2004) provided an excellent opportunity to expand current knowledge of age and growth characteristics of fluvial forms of cutthroat. The purpose of this paper is to evaluate the influence of environmental characteristics on the growth, age, size, and survival of coastal cutthroat trout in headwater watersheds of western Oregon. Using environmental data collected at multiple spatial scales, we sought to answer the following questions: How do age, growth, size, and survival differ among headwater populations of coastal cutthroat trout in western Oregon? What environmental characteristics of headwater watersheds influence age and growth? Lastly, how do interactions between biological and environmental parameters influence the ecological patterns of age and growth in populations of coastal cutthroat trout in isolated watersheds across western Oregon?

Methods

Study area.- From 1999-2001 coastal cutthroat trout were sampled from three ecoregions (Cascade, Coast Range, and Klamath) across western Oregon during the summer low-flow period (Figure 1). The study watersheds were all located above barriers to migration of anadromous fish. Aquatic species occurring in these watersheds included coastal cutthroat trout, sculpin (*Cottus* sp.), Pacific giant salamander (*Dicamptodon tenebrosus*), tailed frogs (*Ascaphus truel*), and crayfish (Family Astacidae). Elevation of sample watersheds ranged from 287 to 1,583 m (ams), and total watershed area ranged from 500 to 5,800 hectares (Gresswell et al 2004).. Water temperature in the ecoregions varied seasonally (January range: -1-6 ºC; July range: 13-18ºC); mean annual precipitation ranges from 104 to 302 cm (Johnson et al. 1999).

Land-use practices in the study watersheds include timber harvest, mining, agriculture, and livestock grazing. The coast range is densely forested, composed of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Psuedotsuga menziesii*), and red-cedar (*Thuja plicata*), and numerous shrubs and herbaceous plants are found in the undergrowth (Johnson et al. 1999). The westslope of the Cascade Mountains is densely covered by Douglas fir

(*Psuedotsuga menziesii*), noble fir (*Abies procera*), and Pacific silver fir (*Abies amabilis*) at lower elevations and Engelmann spruce (*Picea engelmannii*), grand fir (*Abies grandis*), and mountain hemlock (*Tsuga mertensiana*) at upper elevations. The dominant tree species in the Klamath region are Douglas fir and mixed oak stands (*Quercus* spp.; Johnson et al. 1999).

Scale collection and preparation.- Sample watersheds were located upstream from barriers to upstream fish migration of anadromous fishes, and fluvial coastal cutthroat trout were the only salmonids inhabiting these streams (Gresswell et al. 2004). Because geology and physiographic province were expected to influence habitat and population relationships across western Oregon, the population of watersheds was categorized by ecoregion (Coast Range, Cascade Mountain, and Klamath Mountains; Oregon Natural Heritage Program, 1:250,000) and erosion potential (sedimentary and igneous rock types; reclassified USGS, 1:500,000 geology coverage). A random sample of 40 watersheds was selected from this population by stratified random sampling (Gresswell et al. 2004). Four watersheds (Blowout, North Fork Buckeye, Racks, and Straight Creek) were removed from the sample because of an insufficient number of scale samples, but the remaining 36 watersheds were replicable and representative of the variation in geology, topography, vegetation, and climate across western Oregon. Camp Creek, a stream network that had been sampled annually from 1998 to 2001, was added to the sample (n = 37) for insight into annual variation in age and growth.

In each watershed, coastal cutthroat trout were collected using single-pass electrofishing without blocknets (Bateman et al. 2005). Captured fish were anesthetized, weighed to the nearest g, and measured to the nearest mm (fork length or FL). Scales were removed from the area between the dorsal fin and the lateral line and adhered to gummed cards. Scales were pressed in acetate, and impressions were subsequently digitized in the laboratory using a stereomicroscope and Image-Pro® Plus (version 4.5) software. Fish were aged by counting the number of annuli present on the scale. Coastal cutthroat trout age estimates were validated by examining fish with multiple recaptures, and scale-reader precision and bias were evaluated using repeated estimates of fish that were captured on multiple occasions, known-age hatchery fish, and individuals from the study watersheds (Rehe and Gresswell *in preparation*).

Growth.- Length-at-age was estimated for the last full year of growth by back-calculating with the direct proportion method (Gutreuter 1987; Francis 1990; Ricker 1991). In order to reduce the effect of fish size on growth, growth increments were converted to mean relative growth rates (RG; Warren 1971). The mean length for each age group was fit to a specialized form of the Von Bertalanffy growth formula (Bertalanffy 1938; Ricker 1975) with a surface factor $D = 1$ (Pauly 1984; Gresswell et al. 1997) to estimate the Brody growth coefficient (K) and the theoretical asymptotic length ($L\infty$). In order to compare among watersheds, $L\infty$ was converted to asymptotic weight ($W\infty$) using a length-weight relationship

(Ricker 1975) for all of the fish captured in each of the watersheds. The index of growth performance (P; Pauly 1979) was estimated by combining $W\infty$ and K.

Condition and size.- Least-squares weight-length regressions were calculated for each population, and the slope of the regression was used to compare mean condition among populations (Le Cren 1951). Variables describing size included mean weight and length, and Proportional Stock Density (PSD; Anderson and Neumann 1996).. Quality length (Anderson and Weithman 1978) for the PSD equation was derived from the record length determined from the study populations, not the all-tackle, world record length suggested by Anderson and Weithman (1978). We used the maximum recorded length from our sample watersheds because the all-tackle, world-record length for cutthroat trout (990 mm) was obtained from a Lahontan cutthroat trout *Oncorhynchus clarkii henshawii* (Pyramid Lake), and therefore, it does not represent coastal cutthroat trout found in headwater watersheds.

Survival.- Mean annual survival was estimated for each sample population using static (time specific) life tables (Hilborn and Walters 1992; Quinn and Deriso 1999). Static life tables use age data collected from a population at one particular time and assume that results are similar to a cohort followed through time. To increase comparability among populations, life tables were only constructed using data for 3-year-old fish (Rehe and Gresswell in preparation).

Environmental variables.- Physical variables were assessed using habitat sampling techniques described by Gresswell et al. (2006), and additional watershed-scale variables were derived from remote sensing imagery and geographical information system (GIS) data layers. Stream networks were divided into stream segments (Frissell et al. 1986), geomorphic reach types (Montgomery and Buffington 1997), and channel-unit types (Bisson et al. 1982) using a combination of topographical maps, aerial photographs, and field surveys (Gresswell et al. 2006). Subsequently, environmental variables that might influence age, growth, and survival of coastal cutthroat trout in headwater streams were recorded for all channel units. Variables included: channel-unit size (e.g., length, maximum depth, and width), valley segment type (broad and narrow; Moore et al. 1997), channel type (constrained and unconstrained; Moore et al. 1997), substrate size class (bedrock, boulder, cobble, gravel, sand, and silt; Moore et al. 1997), and woody debris accumulations (i.e., ≥5 pieces, ≥15 cm in diameter and 3 m in length; classified in 10-piece aggregations; Moore et al. 1997)

Chemical data were collected for each study watershed during the habitat survey. Alkalinity, conductivity, and pH were estimated in the field immediately upstream of the isolating barrier (Gresswell et al. 2006). Water samples for assessment of major ions were collected at the same time and transported back to Oregon State University for analysis. January and July water temperatures for each watershed were estimated by averaging the daily mean air temperatures (n = 18 years) using zonal statistics function (www.daymet.org).

Data analysis.- Statistical analysis was performed using Number Cruncher Statistical Systems software (NCSS; Hintze 2001). Environmental and biological data were transformed, when necessary, to conform to normal distribution assumptions (Ramsey and Schafer 2002). Highly correlated data were identified using a Pearson correlation matrix of all derived and measured variables, and subsequently redundant variables were removed. Principal component analysis (PCA) was used to determine which of 11 biological (Table 1) and 24 environmental variables (Table 2) could be used to describe the gradients among study watersheds. Variables with a low component loading (≤ 0.40) during the initial analysis were removed, and the remaining variables were reanalyzed. Parameters with the highest factor loading for each of the principal components (i.e., displayed the strongest correlation between variable and individual component) were selected as either response or predictor variables (Gresswell et al. 1997; McCune and Grace 2001).

Subsequently, two sets of statistical models were evaluated for each response (biological) variable: one set containing models with a single predictor variable (number of models (R) = 7), and a second set composed of the 'best' models (R = 17) from the multiple predictor variables model (Harig and Fausch 2002; Torgersen and Close 2004). Model selection was conducted using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). In order to reduce the influence of correlated variables, no more than one variable from each PCA axis was included in any single model. The models were ordered by AIC values (lower number specifies a better fit) and assessed by delta AIC (a measure of each model as it relates to the best model) and Akaike weights (a measure of strength of the evidence for each model). The ‘best’ model was determined from the set of candidate models as the model with the lowest delta AIC and the largest Akaike weight. To determine which model was ‘best’ among competing models, the evidence ratio (‘best’ model divided by the competing model) was evaluated among top models (Burnham and Anderson 2002). Because of the small sample size, the second-order Akaike Information Criterion (AIC_C) was used.

In order to determine if important predictor variables were discarded during the PCA analysis, two additional sets of regressions were preformed using the environmental variable component scores as predictor variables. One set of regressions used component scores from the PCA with all available environmental variables (full model). A second set used component scores following the removal of variables with low component loadings (reduced model).

Results

Mean relative growth rates for the last full year of growth in populations of coastal cutthroat trout varied by age and size class across all watersheds, but differences among study watersheds were not statistically significant. Index of growth performance (P) for the study watersheds ranged from 1.48 to 3.04, and length at age 1 ranged from 48 to 67 mm (mean = 55 mm). Mean length at age 2 and age 3 also varied among study watersheds (mean length at age 2 = 97 mm; range: 89-107 mm, and mean length at age 3 = 137 mm; range; 123-154 mm).

Differences in mean length of coastal cutthroat trout among watersheds were statistically significant ($F = 6.80$; $P < 0.01$), but differences in mean weight were not ($F = 0.88$: $P = 0.42$). Mean length ranged from 99 (Barney Creek) to 134 mm (North Fork Rock Creek); mean length of coastal cutthroat trout for all watersheds was 119 mm. Mean weight for all watersheds was 18 g, and weight ranged from 6 g (Sweet Creek) to 27 g (North Fork Rock Creek). Biomass ranged from 2.4 to 10.4 g/m^2. The condition of coastal cutthroat trout (as indicated by the slope of the weight-length regression) did not differ significantly among watersheds ($F = 1.69$; $P = 0.20$).

There was little variation among watersheds in mean age of coastal cutthroat trout (range: 1-3 years). Maximum age (longevity) in the watersheds ranged between 3 and 5 years. Maximum age of fish in the majority (65%) of watersheds was 4 years of age. Coastal cutthroat trout in 3 watersheds (14%) only reached 3 years, and in 8 watersheds (22%), trout reached a maximum of 5 years. Mean annual survival for coastal cutthroat trout from age 2 to age 3 was 45%. The lowest annual survival was for Deadhorse Creek (23%) and highest was for West Fork Brummit Creek (65%).

The first three principal components derived from the biological variables explained about 76% of the variation among watersheds (Table 3). The index of growth performance (P), length at age 1, and the Brody growth coefficient (K) were the highest loading variables on the first axis, explaining approximately 30% of the variation. The second and third axes appeared to be related to size structure (mean length of coastal cutthroat trout in the watershed and PSD) and survival (maximum age and survival), explaining an additional 25% and 20% of the variation, respectively.

The first three axes of the environmental variables PCA explained approximately 73% of variation among watersheds (Table 3). Variables related to water chemistry (alkalinity, calcium ions, and conductivity) were closely associated with the first axis. Watershed geomorphology (maximum pool depth and stream width) and watershed-scale habitat (e.g., number of vertical steps, stream connectivity, and percent stream canopy open) described the second and third axes.

Mean length at age 1, mean length, and mean survival were selected as response variables from the first three components of the biological PCA. January water temperature, number of vertical steps, mean maximum pool depth, July water temperature, and calcium ions were the highest ranked variables in the first set of AIC single-variable models used to predict the biological responses (Table 4). For example, the 'best' single-variable model for predicting mean length at age 1 used January water temperature as the predictor variable; evidence ratio was10:1. Similarly, there was strong evidence (10:1) that the 'best' model for predicting mean fish length used number of vertical steps as the predictor variable. The highest ranked single-variable models for predicting mean annual survival had mean maximum pool depth or July water temperature for predictors. The weight of the evidence supporting mean maximum pool depth as the single 'best' predictor was four times as likely (4:1) as the next best model (using July water temperature) to predict mean annual survival.

Models containing January water temperature and mean maximum pool depth occurred most frequently in the multiple regression models representing combination sets of ‘best’ single-variable models used to predict growth, length, and survival of coastal cutthroat trout (Table 5). The model with January water temperature and calcium ion concentration (Figure 2) was three times more likely (3:1) to be the ‘best’ model to predict length at age 1 than the next best model (Table 5). The model with mean maximum pool depth and number of vertical steps was three times more likely (3:1) to predict mean fish length than the next highest ranked AIC model (Table 5). This result suggests that larger fish are associated with an increase in the number of vertical steps and greater maximum pool depths (Figure 3). For models predicting mean survival of coastal cutthroat trout in headwater watersheds, the ‘best’ model included July water temperature and maximum pool depth and was three times more likely (3:1) than the next model.

The ‘best approximating’ models from the combination of single variables suggests that growth, length, and survival of coastal cutthroat trout in headwater watersheds are generally best described by models that included water temperature and mean maximum pool depth (Table 6). Mean length at age 1 for headwater populations in western Oregon was positively associated with higher January water temperatures and higher concentrations of calcium ions. Watersheds with larger fish had greater mean maximum pool depth and number of vertical steps. Mean survival of headwater coastal cutthroat trout in western Oregon was positively associated with mean maximum pool depth and negatively associated with July water temperature (Figure 4).

Discussion

Growth of coastal cutthroat trout during the first growing season varied substantially in headwater streams of western Oregon, and mean length at age 1 ranged from 71 to 103 mm. This finding is consistent with estimates of length at age 1 of other fluvial populations of coastal cutthroat trout in Washington and Oregon (Wyatt 1959; Fuss 1982). Water temperature was the environmental variable with the strongest association to growth of coastal cutthroat trout in the headwater streams in this study. More specifically, comparison of simple- and multiple-variable regression models suggested that January water temperature was the common environmental factor in models predicting mean length at age 1. This finding is not surprising, however, and the relationship between water temperature and trout growth has been demonstrated previously in numerous lentic (Donald et al. 1980; Hubert and Chamberlain 1996) and lotic systems (Platts 1979; Kruse et al. 1997; Deegan et al. 1999). Temperature has a pervasive effect on growth rates because it acts at many levels (e.g., internal and external environments) and interacts with other abiotic factors. For example, in addition to direct effects on the rate of growth, decreased water temperature has been reported to cause delays in spawning timing, increase duration of incubation, and delay emergence (Matthews 1998).

The size structure of coastal cutthroat trout varied greatly among headwater populations in western Oregon. The principal environmental variables related to mean fish length were number of vertical steps and mean maximum pool depth, both of which were positively associated with mean length. The number of vertical steps and maximum pool depth as predictor variables explained over three-quarters of the variation in mean fish length among study basins ($R^2 = 0.79$, $P \leq 0.01$).

Instream obstacles such as vertical steps, culverts, and dams, can affect adult and juvenile fish differently depending on the dimension of the obstacle, when and for how long the obstacle functions as a barrier, and the size and condition of the fish. In our study, the number of vertical steps may act as a mechanism to separate fish by length. Larger fish that can negotiate vertical steps may have access to a greater portion of the watershed than smaller fish, giving them an advantage when selecting feeding habitat.

It has been reported that fish size and the physical height and width of barriers, in conjunction with the corresponding pool depth, influence the success rate of negotiating instream obstacles (Brandt et al. 2005; Lauritzen et al. 2005). For example, the success rate of sockeye salmon *Oncorhynchus nerka* attempting to pass over waterfalls in Alaska was related not only to the size of the fish, but also to pool depth below the falls and the height of the falls (Lauritzen et al. 2005). In a laboratory study on the jumping performance of brook trout, Brandt et al. (2005) reported that fish length interacted with the physical variables to affect success in surmounting waterfalls.

Mean length of coastal cutthroat trout can be positively influenced by pool depth through increases in growth potential (Rosenfeld and Boss 2001), providing refuge for larger fish during periods of desiccation (Northcote 1992; Thorpe 1994; Connolly 1996), and reductions in predation risk (Harvey et al. 1999). Larger coastal cutthroat trout have been shown to occupy pool habitat more frequently than riffles or cascades (Glova 1987; Bisson et al. 1988; Heggenes et al. 1991; Gresswell and Hendricks 2007). Metabolic processes convert food into usable items like proteins, carbohydrates, and enzymes in order to satisfy body maintenance and behavior costs (Warren 1971; Weatherley 1990), and any energy left over from this process may then be used for organic grow in length or weight. Energy for maintenance and behavior may be reduced in pool habitats where it is easier to maintain position.

Growth of trout depends not only on the availability of food items, but also on the age and size of the fish (Martin 1983; Rosenfeld and Boss 2001). Fish growth rates decrease with fish size and age (Tomasson 1979; Martin 1983; Rosenfeld and Boss 2001). Smaller fish have lower absolute energy requirements compared to larger, older fish, giving them a selective advantage in streams with low productivity and higher temperatures (Rosenfeld and Boss 2001). Hughes and Reynolds (1994) proposed that differences in energetic requirements of fish influenced the decrease in maximum body size along an upstream gradient.

Effects of competition on fish growth characteristics are related to fish density and size, and the size and quality of the space available (Brett 1979, Grant and Kramer 1990; Bohlin et al. 2002; Paukert and Willis 2004; Harvey et al. 2005), and salmonid density (i.e., density dependent growth) has been suggested as a mechanism that can regulate size structure and population numbers (Heath 1992; Elliott 1994). In the current study, however, the relationship between size structure and density of headwater populations of coastal cutthroat trout, the only salmonid in the study watersheds, was not significant. Mean length of coastal cutthroat trout was not strongly influenced by either biomass per m^2 (r^2 = 0.19, P = 0.74) and density (number of individuals per $m^{2;}$ r^2 = 0.22, P = 0.30).

In single-variable linear regression models, neither maximum pool depth nor mean July temperature alone explained more than 31% of the variation in survival among the 37 headwater populations coastal cutthroat trout in western Oregon, but when combined, these variables explained nearly two-thirds of the variation in survival (R^2 = 0.61, P < 0.001). The interaction of maximum pool depth and July temperature on the survival in this study may be explained by importance of deep pools for refuge during summer low-flow periods and the potentially negative effects of high water temperature during winter months. Adult cutthroat trout are more impaired and have less of a tolerance to increased water temperature than juveniles do (Heath 1963; Hunter 1973; Pauley et al. 1989).

The age, growth, and size structure of fish are influenced by temperature and available habitat. Streams located in higher elevations typically have colder winter water temperatures that can lead to later spawning times, increased incubation periods, and shorter growth seasons. Variation in habitat can cause among-population differences in mean fish size because of space requirements related to fish size, availability of refuge from summer low flows and turbulent spring runoff, and intraspecific competition related density dependent mechanisms.

This study documented variation of age, growth, and size structure across the range of coastal cutthroat trout in headwater watersheds in Oregon and identified biological and environmental variables associated with the observed trends. Although variation among watersheds was often minor, these data provide a comprehensive view of coastal cutthroat trout in headwater environments and provides information useful for comparisons with other coastal cutthroat trout populations and life-history types. Although studying isolate fluvial population of coastal cutthroat trout has provided us with useful quantitative information, further research focused on broad-scale patterns of age, growth, and size structure of all life history forms are needed to understand how changes in habitat might affect this subspecies.

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Table 1. Biological variables for 37 headwater watersheds in western Oregon containing coastal cutthroat trout.

Variable	Measurement	Source
Brody growth coefficient (K)	Estimated from the mean length for each age-group utilizing the von Bertlanffy growth formula with surface factor D = 1	Gresswell et al. 2005
Index of growth performance (P)	Estimated by combining the asymptotic weight ($w\infty$) and the Brody growth coefficient (K)	Pauly 1979
Relative growth rate	Actual length of fish at the end of the growth year minus length of fish at beginning of growth year (estimated by back-calculation using the direct proportion method), divided by the estimated length at the beginning of the growth year	Gresswell et al. 2005
Length at age	Length at age for the last full year of growth determined from age-length key	Devries and Frie 1996
Mean fish length	Individual fish fork length measured to the nearest millimeter, and averaged across the watershed	Anderson and Neuman 1996
Proportional Stock Density (PSD)	Numerical descriptor of percentage of fish $\geq$ minimum quality divided by minimum stock length based on all-tackle world record for given species or sub-species	Anderson 1976
Mean fish weight	Individual fish weight measured to the nearest gram, and averaged across the watershed	Anderson and Neuman 1996
Length-weight regression	Least-squares regression of individual fish weight in grams on fork length in mm for all fish within the watershed	LeCren 1951

Table 1. Continued.

Variable	Measurement	Source
Mean fish age	Individual fish age estimated by the scale method, averaged across the basin	Devries and Frie 1996
Maximum fish age	Maximum age obtained by any fish with in a watershed, estimated by the scale method	Devries and Frie 1996
Mean survival	Total mortality estimated by catch curves for fish 2 years and older, converted to survival by taking the natural log of total annual mortality	Ricker 1975

Table 2. Environmental variables for 37 headwater watersheds in western Oregon obtained from geographical information system (GIS) and field sampling.

Variable	Measurement	Source
Alkalinity	Negative ion concentration expressed in mg/L bicarbonate (HCO_3^-)	Bain and Stevenson 1999
Biomass, individual	Mean weight of all fish collected times the number of fish in the watershed	Anderson and Neuman 1996
Biomass per m^2	Mean fish weight times number of fish in watershed, divided by stream length	Anderson and Neuman 1996
Calcium concentration	Dissolved Ca^+ ion concentration per mg/L	Bain and Stevenson 1999
Conductivity	Electrical current in water sample, expressed in microSiemens (*u*S) per cm	Bain and Stevenson 1999
Drainage basin area	Estimated total basin area in m^2 calculated from GIS	Bain and Stevenson 1999
Maximum pool depth	Maximum depth of each pool summed over the watershed	
Mean basin aspect	Mean aspect of the entire basin, in degrees, derived from DEM	Gresswell et al. 1997
Mean basin elevation	Mean elevation in meters, derived from DEM	Gresswell et al. 1997
Mean basin slope	Mean slope of the entire basin, in degrees, derived from DEM	Gresswell et al. 1997
Mean January air temperature	Daily average air temperature for January (1980 to 1997) averaged across the basin using Zonal Statistical functions	www.daymet.com
Mean July air temperature	Daily average air temperature for July (1980 to 1997) averaged across the basin using Zonal Statistical functions	www.daymet.com

Table 2 Continued

Variable	Measurement	Source
Mean stream width	Average stream width of all units summed over the watershed	
Number of log jams	Number of unique log jams in each surveyed watershed	
Number of migration barriers	Number of barriers large enough to prevent migration within the watershed	Wofford et al. 2004
Number of vertical steps	Number of vertical steps ≥ 1 m, divided by the surveyed stream length	Guy et al. 2004
Percent pools	Proportion of total pool length to total surveyed stream length	
Percent stream canopy open	Percent of riparian cover open, derived from DEM	Gresswell et al. 2005
pH	Potential hydrogenii (pH) or hydrogen ion activity in a negative $\log^{10}$ of hydrogen ion (H^+) concentration in moles per liter	Bain and Stevenson 1999
Pool length	Total length of all pool units in meters	
Sodium concentration	Dissolved Na^+ ion concentration per mg/L	Bain and Stevenson 1999
Stream connectivity	Number of steps ≥ 1 m times the average step height	Guy et al. 2004
Total number of pools	Total number of pools in watershed	
Yield	Annual precipitation averaged across the watershed multiplied by the watershed area	Gresswell et al. 1997

Table 3. Component loading of biological and environmental variables and the variance explained by the first three factors of Principal Component Analysis (PCA).

Variable	PCA component axis 1	2	3	Total
Biological Variables				
Index of growth performance (P)	**0.94**	-0.09	0.20	
Length at age 1	**0.87**	-0.15	0.27	
Brody growth coefficient (K)	**-0.87**	0.08	-0.25	
Mean fish length	-0.31	**-0.73**	0.40	
Proportional Stock Density (PSD)	-0.32	**-0.70**	0.48	
Maximum age	-0.22	0.54	**0.69**	
Survival	-0.19	0.53	**0.67**	
Variance represented (%)	30.32	25.32	20.41	76.06
Environmental Variables				
Calcium concentration mg/l	**-0.96**	-0.05	-0.11	
Alkalinity mg/l	**-0.96**	-0.14	-0.08	
Conductivity *u*S	**-0.95**	0.18	-0.04	
July temperature ºC	**-0.82**	0.05	0.22	
pH	**-0.81**	-0.39	0.01	
Sodium concentration mg/l	**-0.79**	0.41	0.06	
Average step height ≥ 1 m	0.18	**-0.86**	0.19	
Connectivity	0.11	**-0.82**	0.04	
January temperature °C	0.16	**0.74**	0.03	
Mean basin elevation (meters)	-0.29	**-0.71**	-0.22	
Maximum pool depth (meters)	0.17	-0.21	**-0.78**	
Percent stream canopy open	0.26	0.10	**0.68**	
Variance represented (%)	37.08	25.94	10.12	73.14

Table 4. Simple linear regression models of single variables predicting the length at age 1, fish length, and survival of coastal cutthroat trout. Akaike's Information Criterion (AIC), AIC differences between a given model and the 'best' model (ΔAIC_c), and Akaike weights (w_i). Models with lowest AIC_c and highest w_i are those that 'best' fit the data. Akaike's Information Criterion was corrected for small sample size.

Model	AIC_c	ΔAIC_c	w_i
A) Mean length at age 1			
January air temperature	58.17	0.00	0.99
Calcium ions	68.27	10.10	0.01
Alkalinity	70.88	12.71	0.00
Average number steps ≥ 1 m	70.89	12.72	0.00
Mean stream width	70.89	12.72	0.00
July air temperature	71.46	13.29	0.00
Maximum pool depth	71.47	13.30	0.00
B) Mean fish length			
Average number steps ≥ 1 m	55.95	0.00	0.99
Mean stream width	66.29	10.34	0.01
Maximum pool depth	69.28	13.33	0.00
January air temperature	70.53	14.58	0.00
Alkalinity	71.52	15.57	0.00
July air temperature	71.69	15.74	0.00
Calcium ions	118.26	62.31	0.00
C) Mean survival			
Maximum pool depth	-107.97	-5.81	0.66
July air temperature	-104.97	-2.81	0.15
Average number steps ≥ 1 m	-102.38	-0.22	0.04
Alkalinity	-102.29	-0.13	0.04
Calcium ions	-102.16	0.00	0.04
January air temperature	-102.16	0.00	0.04
Mean stream width	-102.13	0.03	0.04

Table 5. Multiple linear regression models predicting the length at age 1, fish length, and survival o coastal cutthroat trout using predictor variables selected from habitat data collected at multiple spat scales. Models are a combination of the 'best' single variable models. Akaike's Information Criterion was corrected for small sample size. Only models with ΔAIC_c <7 are presented.

Model	AIC_c	ΔAIC_c	w_i
A) Mean length at age 1			
January air temperature, calcium ions	60.11	0.00	0.46
July air temperature, January air temperature	62.18	2.07	0.16
January air temperature, calcium ions, maximum pool depth	62.62	2.51	0.13
Maximum pool depth, January air temperature	62.66	2.55	0.13
July air temperature, January air temperature, maximum pool depth	63.26	3.15	0.10
B) Mean fish length			
Maximum pool depth, average number steps ≥ 1 m	55.18	0.00	0.51
July air temperature, average number steps ≥ 1 m, maximum pool depth	57.59	2.41	0.15
Calcium ions, average number steps ≥ 1 m, maximum pool depth	57.75	2.57	0.14
July air temperature, average number steps ≥ 1 m	58.26	3.08	0.11
Calcium ions, average number steps ≥ 1 m	58.72	3.54	0.09
C) Mean survival			
July air temperature, maximum pool depth	-113.77	0.00	0.54
July air temperature, maximum pool width, maximum pool depth	-111.48	2.29	0.17
July air temperature, January air temperature, maximum pool depth	-111.07	2.70	0.14
July air temperature, average number steps ≥ 1 m, maximum pool depth	-110.89	2.88	0.13

Table 6. Multiple regression parameter estimates, standard error (SE), and confidence intervals for the 'best approximating' models predicting length at age 1, fish length, and survival of coastal cutthroat trout from data collected in 37 headwater watersheds.

Parameter	Estimate	SE	95% confidence interval Lower bound	Upper bound
A) Mean length at age 1				
Intercept	79.60	1.55	76.46	82.74
Calcium ions	0.37	0.25	-0.15	0.88
January temperature	2.55	0.40	1.73	3.37
B) Mean fish length				
Intercept	107.98	1.63	104.66	111.29
Mean stream depth	13.60	3.42	6.64	20.56
No. steps ≥ 1 m	278.69	29.27	219.20	338.18
C) Mean survival				
Intercept	0.68	0.05	0.58	0.77
July temperature	-0.01	0.00	-0.02	-0.01
Mean stream depth	0.16	0.03	0.11	0.21

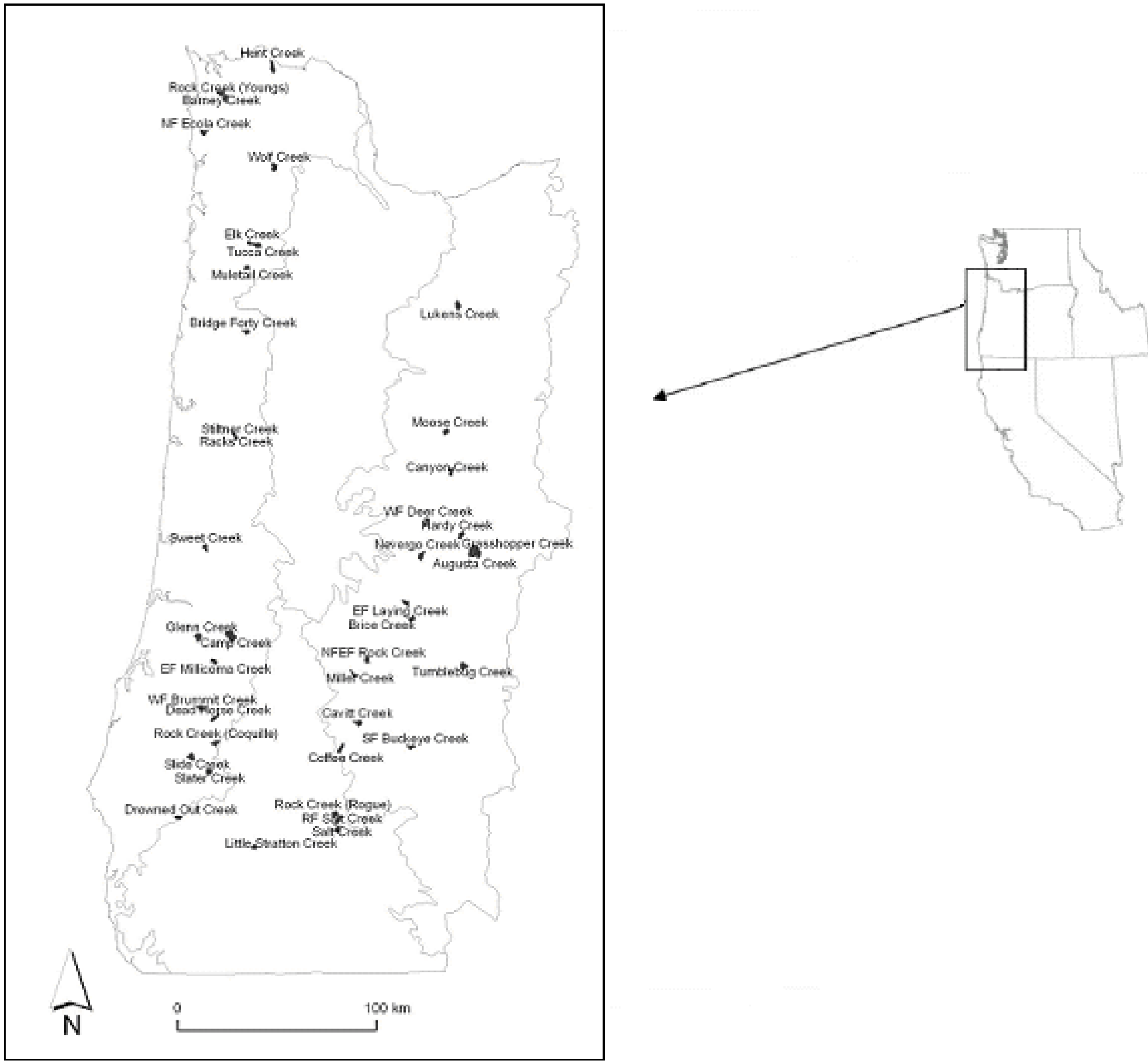
Figure Legends

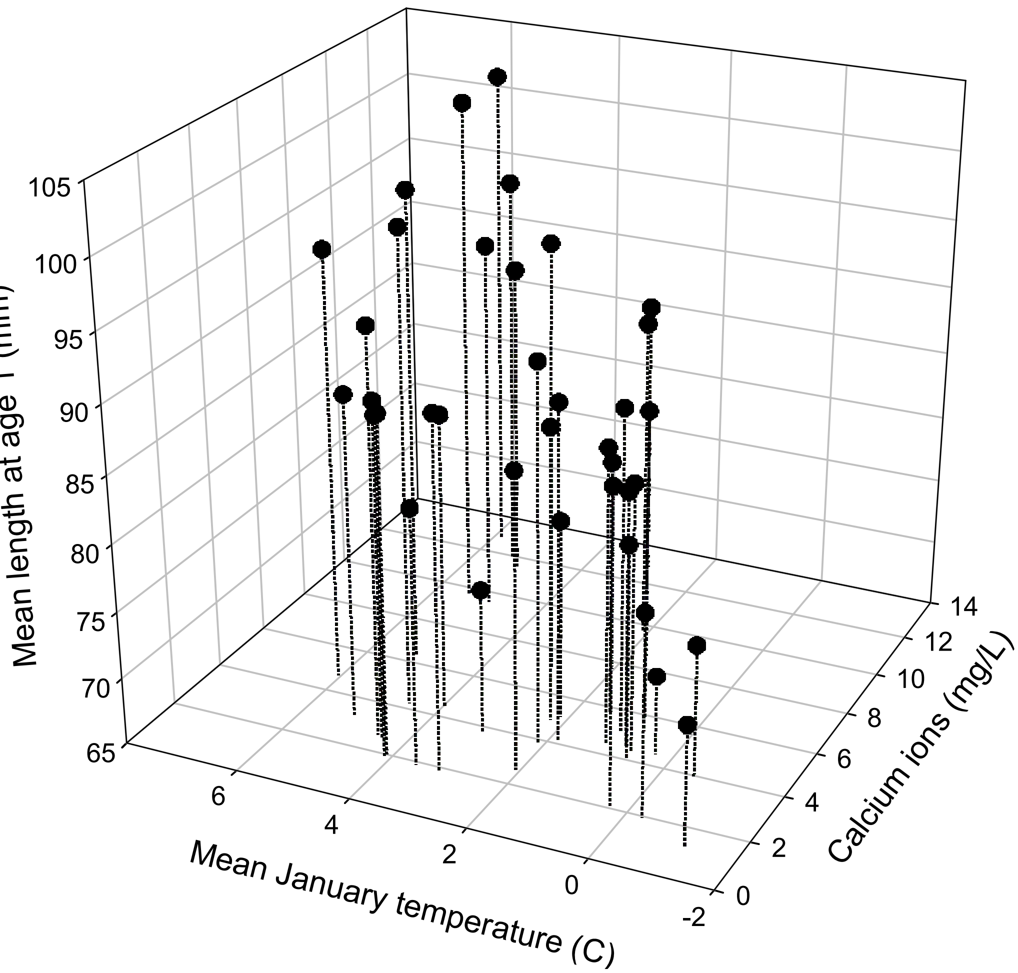
Figure 1. Map of western Oregon showing 37 sample watersheds containing only populations of coastal cutthroat trout and located above natural barriers

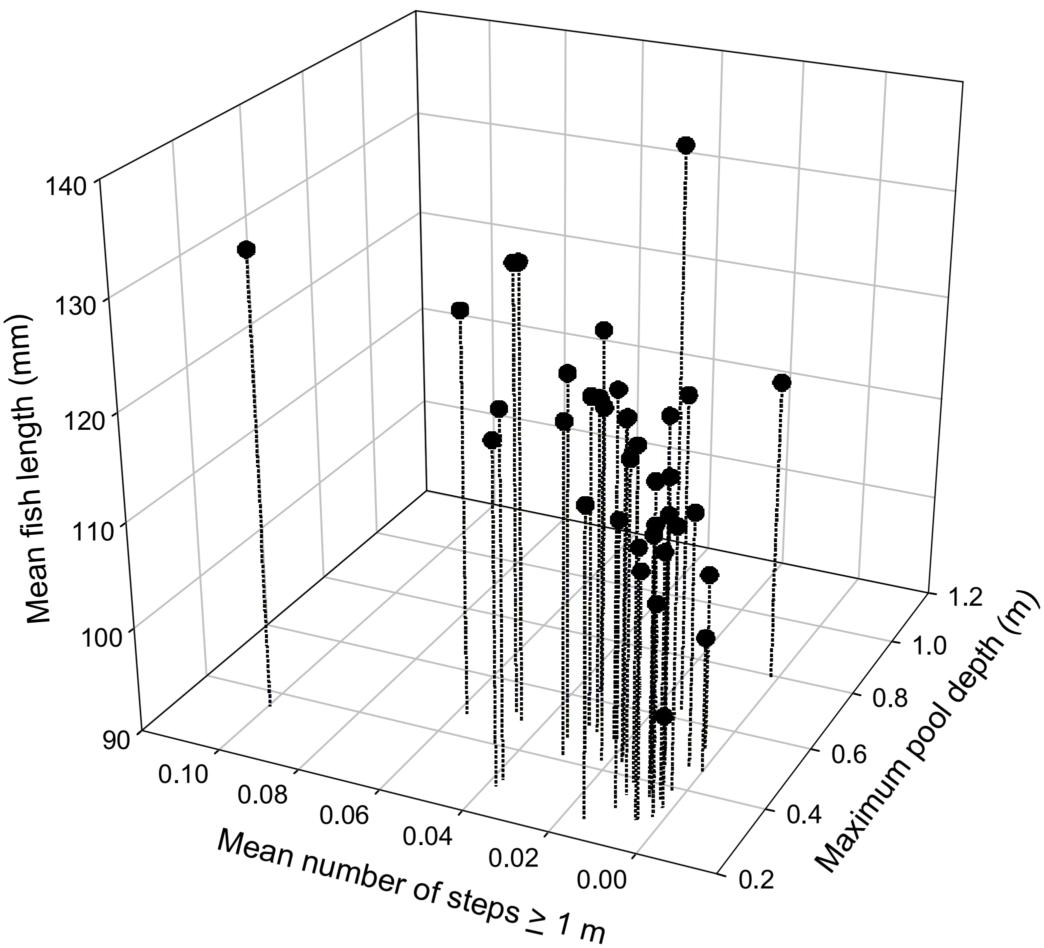
Figure 2. Scatter plot (3D) showing variables from AIC best-approximating model of length at age 1 of coastal cutthroat trout in headwater watersheds of western Oregon in with different mean January temperatures (C) and calcium ion concentrations (mg/L).

Figure 3. Scatter plot (3D) from AIC best-approximating model with mean number ofvertical steps≥ 1m and maximum pool depth (m) as predictor variables and mean fish length in 37 watersheds in western Oregon as the response variable.

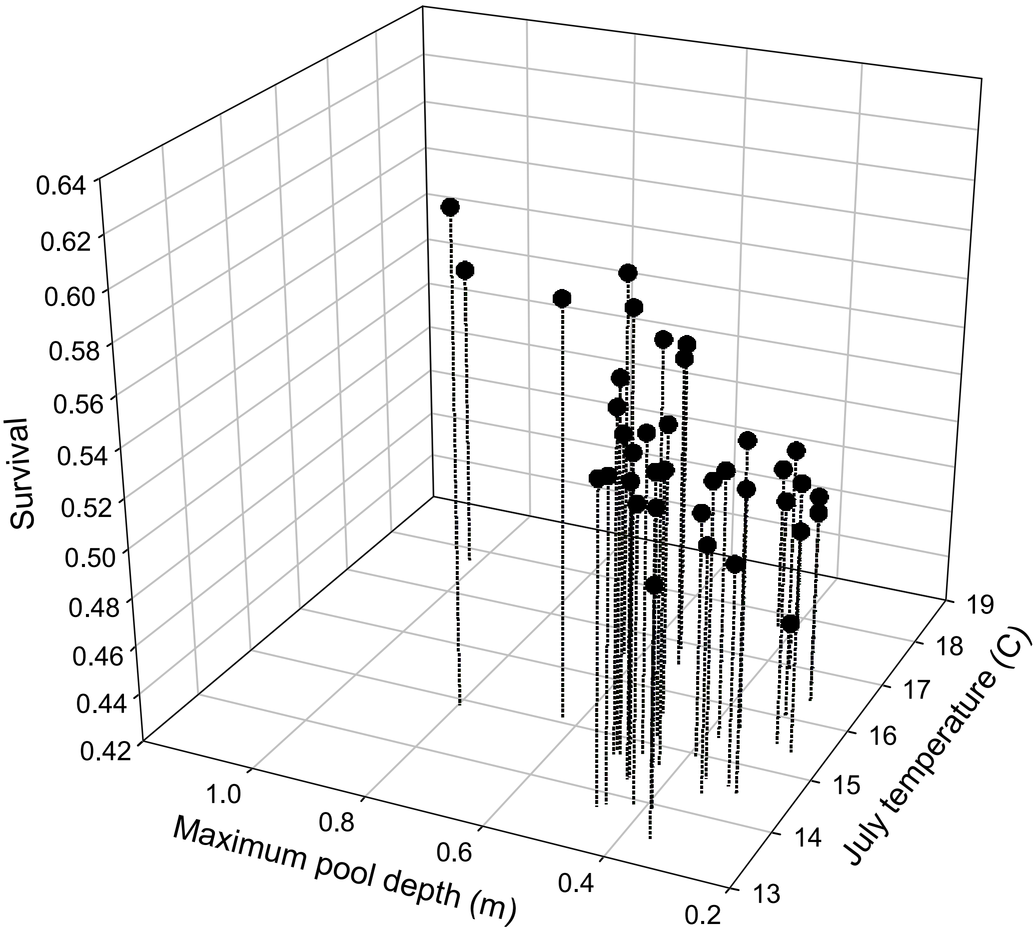
Figure 4. Scatter plot (3D) showing variables from AIC best-approximating model of survival of isolated coastal cutthroat trout in western Oregon as the response variable and maximum pool depth and mean July temperatures as predictor variables.


Hunt Creek
Rock Creek (Youngs)
Barney Creek
NF Ecola Creek
Wolf Creek
Elk Creek
Tucca Creek
Muletail Creek
Bridge Forty Creek
Lukens Creek
Stillmer Creek
Racks Creek
Moose Creek
Canyon Creek
WF Deer Creek
Hardy Creek
Sweet Creek
Nevergo Creek
Grasshopper Creek
Augusta Creek
EF Laying Creek
Brice Creek
Glenn Creek
Camp Creek
NFEF Rock Creek
EF Millicoma Creek
Tumblebug Creek
Miller Creek
WF Brummit Creek
Dead Horse Creek
Cavitt Creek
Rock Creek (Coquille)
SF Buckeye Creek
Coffee Creek
Slide Creek
Slater Creek
Drowned Out Creek
Rock Creek (Rogue)
RF Salt Creek
Salt Creek
Little Stratton Creek
N
0
100 km


Mean length at age 1 (mm)
105
100
95
90
85
80
75
70
65
Mean January temperature (C)
6
4
2
0
-2
Calcium ions (mg/L)
0
2
4
6
8
10
12
14



140
130
120
110
100
90
Mean fish length (mm)
0.10
0.08
0.06
0.04
0.02
0.00
Mean number of steps ≥ 1 m
0.2
0.4
0.6
0.8
1.0
1.2
Maximum pool depth (m)



Survival
0.64
0.62
0.60
0.58
0.56
0.54
0.52
0.50
0.48
0.46
0.44
0.42
Maximum pool depth (m)
1.0
0.8
0.6
0.4
0.2
July temperature (C)
13
14
15
16
17
18
19

Influence of Landscape-Scale Variables on the Age and Growth Structure of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in Headwater Streams

Chapter 4:

Conclusion

Management of fishes is enhanced by knowledge of population-specific age structure and growth rates. The ability to age fish populations accurately is necessary because it provides essential information needed to understand the life-history characteristics of fish, such as age-at-maturity, life span, and adaptations for environmental extremes (Chugunova 1963; Jearld 1983). Studying the growth of fish also provides information on the potential effects of harvest, habitat management, and environmental change (Hammers and Miranda 1991).

The findings of this thesis contribute to the understanding of the population structure of coastal cutthroat trout by providing new information on the variation of age, growth, size, and survival of headwater populations in western Oregon. This analysis of 37 coastal cutthroat trout populations located above barriers to migration also has identified a number of watershed-scale environmental variables that influence the age and growth structure. Comparisons with populations from across the range of the subspecies suggest that the observed variation in age and growth is influenced less by latitudinal gradients in growth than previously suggested. Instead, there is evidence that at this broad spatial scale, differences are more strongly related to life-history type and the habitats in which the populations are found.

Age estimation by the scale method was a useful, non-lethal procedure for aging coastal cutthroat trout from populations in headwater streams. Strict adherence to established protocols minimized the previously identified shortcomings of age estimation by this method and enhanced the opportunity for comparison to other studies. Number of degree-days was used as a metric for predicting if first annuli are present for headwater fluvial populations of coastal cutthroat trout. Our data showed a strong relationship between number of circuli to first annuli and mean stream elevation; young fish in lower elevation streams had a longer growing season, and thus formed an increased number of circuli to first annuli. Scale regeneration was common, and it appears to be influenced by the stream gradient, habitat type (lotic or lentic), and the age of the fish.

The age, growth, and size structure of coastal cutthroat trout in headwater watersheds in western Oregon is influenced by water temperature and pool depth. Streams located in higher elevations typically have colder winter stream temperatures that can lead to later spawning times, increased incubation periods, and shorter growth seasons. Variation in habitat can cause among-population differences in mean fish size as the result of size-related habitat requirements, availability of refuge from summer low flows and turbulent spring runoff, and reductions in intraspecific competition through density dependent mechanisms.

The overall fitness of a fish population can be illustrated by how well individuals grow, feed, and replace themselves. Survival of coastal cutthroat trout, like many other populations of fish, reflects the interaction of critical (lethal) summer temperatures and the availability of pockets of cooler refuge waters.

This study has described the variation of age, growth, and size structure across the range of coastal cutthroat trout in headwater watersheds in Oregon and suggested what biological and environmental variables best describe the observed trends. The methodology outlined in this thesis provides an alternative way of examining age and growth across a wider geographic range than most previous studies. Not only does it describe the natural variation of biological characteristics of coastal cutthroat trout across western Oregon, but it also demonstrates how these headwater populations have adapter and respond to environmental conditions.

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