SIZE VARIATION AND FITNESS CONSEQUENCES IN AGE 0 WESTSLOPE CUTTHROAT TROUT

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ABSTRACT

Phenotypic diversity is an important component of ecological diversity in fishes. Phenotypic diversity potentially leads to divergence and speciation via local adaptation and stabilization of population abundance in variable environments. Although benefits of being large are well documented, size variation may have benefits as well. Understanding the spatial distribution of size variation across important environmental gradients will contribute to understanding of relationships between inland salmonids and their environment. For age 0 westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in the Coeur d' Alene basin, Idaho, I found most size variation to occur at the broadest scale studied ($10km^2$) associated with water temperature and productivity gradients. Instream habitat variables but not age 0 size structure differed between wide and narrow valley streams. At the stream reach scale, habitats occupied by large and small age 0 trout differed, whereas at the habitat unit scale, those occupied by homogeneously- versus heterogeneously-sized individuals did not differ. Maintenance of population abundance and diversity may depend on diverse habitats at the reach scale whereas maintenance of meaningful habitat complexity may depend on management at the stream scale. I used the growth record available in sagittal otoliths to examine overwinter size-selective mortality and phenotypic adaptations in two streams that differed in temperature. I found overwinter selection for growth rate in 2001-02 but not in 2000-01. Direction of selection was different in the two streams, favoring fast growth in the warm stream and slow growth in the cold stream. Fish in the warmer stream varied more in emergence timing whereas fish in the colder stream showed compensatory growth characteristics that reduced intrapopulation size variation and increased average size. Populations at the extremes of critical environmental gradients may be less variable and therefore more sensitive and less resilient to disturbance, but may also represent intraspecific diversity that is important to conserve. Conservation of intraspecific variation will likely require the maintenance of high quality habitats across multiple environmental gradients, including landform, temperature, and productivity, and across the spatial scales at which those gradients occur.

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CHAPTER 1

INTRODUCTION

Phenotypic variation plays a critical part in many evolutionarily and ecologically essential processes (Skulason and Smith 1995). These include local adaptation that may increase individual fitness, response to temporal environmental change, population differentiation processes leading to speciation, and effects on biotic interactions such as reduction of intra- and interspecific competition through niche differentiation (e.g. Nikol'skiy 1969; Utter 1981; Skulason and Smith 1995). Organism size has been recognized as an important phenotypic characteristic mediating ecological processes such as metabolism, growth, production rate, reproductive condition and commitments, and constraints on body function (Policansky 1983; Stein et al. 1987). Size variation may provide multiple benefits to a population, including resilience in variable environments and reduction in competition through niche differentiation (Werner and Gilliam 1984; Mahon and Portt 1985; Good et al. 2001). Phenotypic variation can be generated by genetic or environmental mechanisms (Kirpichnikov 1981; Berven and Gill 1983; McDowall 1994). Size variation in fish includes both genetic (Gjedrem 1976; Reznick 1981; Sumpter 1992; Nicieza et al. 1994; Smoker et al. 1994; Kinnison et al. 1998) and environmental (e.g. Shuter et al. 1980; Trippel and Beamish 1989; Beacham and Murray 1990; Rieman and Myers 1992; Benoit and Pepin 1999) components. Environmental variation represents the range of non-genetically based phenotypes displayed among individuals across environmental gradients. Plasticity represents the extent of an individual’s phenotypic variation expressed in response to environmental gradients experienced by that individual (Schlichting 1989; West-Eberhard 1989; Adkison 1995). Processes generating phenotypic variation and relationships to life history characteristics are critical to the resilience and persistence of organisms in variable environments (Schlichting 1989). Successful fish conservation and management requires recognition and understanding of phenotypic variation and processes generating that variation (Gresswell et al. 1994; Healey and Prince 1995).

SIZE AND SIZE VARIATION

Organism size has been well recognized as an important phenotypic characteristic mediating various ecological processes, including metabolism, growth, production rate, reproductive condition and commitments, and constraints on body function (Peters 1983; Policansky 1983; Schmidt-Neilsen 1984; Werner and Gilliam 1984; Stein et al. 1987). Body size helps to explain organism distribution across habitats (Larscheid and Hubert 1992), and is a significant factor mediating ontogenetic niche shifts (Werner and Gilliam 1984). Interspecific and intraspecific competition and predation relationships can change dramatically as an organism grows and its role in a community changes (Werner and Gilliam 1984; Stein et al. 1987).

"Bigger-is-better" is a well-documented paradigm in fish ecology (Litvak and Leggett 1992; Chambers 1993; Hare and Cowen 1997; Sogard 1997). In young fish, offspring size is positively associated with intraspecific competitive ability (Abbott et al. 1985), timing of development and ontogenetic behavior shifts (Mikheev et al. 1994), and probability of survival through early stages of development (Elliott 1989; Elliott 1990; Smith and Griffith 1994), including the first winter (Hunt 1969; Werner 1984; Holtby 1988; Quinn and Peterson 1996). The importance of juvenile size has been reviewed by Reznick (1981) and Werner and Gilliam (1984). Miller et al. (1988) proposed a framework based on fish size that integrates observed relationships among juvenile fish ecology, survival and recruitment.

However, the "bigger-is-better" paradigm for juvenile fishes may be oversimplified or result from study design limitations. Leggett and Deblois (1994) concluded that when only larval susceptibility to predation was considered, larger size was beneficial, but inclusion of encounter and predator attack probabilities shifted the advantage toward smaller individuals. Litvak and Leggett (1992) found that when age and associated learning was controlled for, predation on larval capelin *(Mallotus villosus*) was size-dependent with larger individuals being the preferred prey. McCormick and Molony (1993) pointed out that many size fitness studies included organisms across ages and therefore developmental states. Greater age was associated with benefits of learned survival behaviors and advanced physical and physiological condition, giving larger fish age- rather than size-associated advantages. McCormick and Molony (1993) demonstrated with goatfish (*Upeneus tragula*) larvae that body length may not be associated with other fitness characteristics including body fat and carbohydrate content, Fulton's condition factor, growth rate, or burst swimming speed.

Big *may not always* be best. In some situations, small may be best. Predators may prefer larger prey (Litvak and Leggett 1992), particularly by avian and terrestrial predators (Harvey and Stewart 1991; Power 1987). Larger prey may also be slower to leave cover and resume feeding after predator threat, limiting growth potential as their fitness value increases with increasing size (Grant and Noakes 1987; Reinhardt and Healey 1999).

Actively feeding and recently fed juveniles may incur increased vulnerability to and higher mortality from predators (Lankford et al. 2001). Nielsen (1994) found that coho salmon (*Oncorhynchus kisutch*) with relatively slow somatic growth contributed more energy to immature egg formation than did average or fast-growing individuals. Whether early energy contribution to egg formation leads to increased fecundity has not been demonstrated (Nielsen 1994).

Size variation has value as well. Niche separation through morphological or behavioral diversification is a well-accepted paradigm of competition theory (e.g. Skulason and Smith 1995; Landry et al. 1999) and size-based or ontogenetic niche shifts are well-documented (Werner and Gilliam 1984; Mittelbach and Chesson 1987; Erkinaro et al. 1997; Ruzycki and Wurtsbaugh 1999). Different size classes corresponding to year classes of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) consumed different taxa and different sizes of food items (Bozek et al. 1994). Similar diet differentiation may also occur within size classes. Inferior competitors may switch tactics to maintain fitness. Metcalfe et al. (1988) found that age 0 Atlantic salmon (*Salmo salar*) diverged in their feeding strategy in late summer, with some individuals demonstrating increased appetite and others with decreased appetite. Size divergence going into winter may have reduced competition for limited overwintering habitats and food supplies and reduced overwintering mortality of less competitive individuals. Jonsson et al. (1988) identified four phenotypes of Arctic char (*Salvelinus alpinus*) in Lake Thingvallavatn, Iceland, that differed in body size and food preference. Piscivorous and planktivorous individuals were identical genetically; piscivorous individuals were likely faster-growing recruits from the juvenile planktivorous population. In this system, competition among individuals may have been reduced through trophic differentiation. Similarly, Taylor and Bentzen (1993) concluded that size differentiated smelt (*Osmerus mordax*; “dwarf” and “normal-sized”) diverged sympatrically into planktivorous and piscivorous feeders, potentially to reduce foraging competition. Larger individuals may have feeding advantages in some circumstances, since they are more likely to win in competitive interactions, hold territories that provide a food supply (Keeley and McPhail 1998) and are able to consume a wider size range of prey (Grossman 1980). However, smaller individuals have an advantage during food shortages since food requirements are lower (Persson 1985; Hamrin and Persson 1986).

Size-mediated habitat differentiation may also reduce competition. For example, L'Abee-Lund et al. (1993) found that juvenile Arctic char shifted from epibenthic to pelagic habitats as individual, and predator size increased. Nielsen (1992) identified four phenotypes of coho salmon differentiated by size, habitat, behavior, and growth rate. Growth rates and fitness differed between habitats. However, diversification allowed slower-growing individuals an alternative strategy for growth in an environment with reduced competition. Variation in body size may allow for greater abundances through competitive segregation, as found by Chandler and Bjornn (1988) with juvenile steelhead (*Oncorhynchus mykiss*). They found heterogeneously-sized groups of age 0 steelhead at higher densities than homogeneously-sized groups, supporting the niche-packing theory that diverse habitat may support more diverse organisms at higher density than homogeneous habitat (Klopfer and Mac Arthur 1960).

Size variation may also demonstrate the availability of more than one strategy for maximizing fitness. For example, although large size has been associated with increased reproductive success, Gross (1985) concluded that smaller jack Pacific salmon (*Oncorhynchus* spp.) males may enjoy fitness equal to larger males by using a “sneaker” strategy rather than the fighting strategy employed by larger males. Intermediate-sized males are at a competitive disadvantage since they are less successful at either strategy.

In variable environments, there may be no one best size. For example, Good et al. (2001) found size-selective mortality to operate on smaller Atlantic salmon fry during one year and on larger fry the next year, suggesting that no single size may be selected for in variable environments. Variation may provide recruitment stability and long-term survival in a variable environment (den Boer 1968; Lomnicki 1980). Conversely, populations with limited size variation may be more vulnerable to size-dependent disturbances.

Factors affecting fitness characteristics such as growth, survival, and reproductive success may vary with age class, population, environment, and species. The importance of size and size variation may vary as well. For example, Bradford et al. (2001) found no size-selective overwinter mortality in age 0 chinook salmon (*Oncorhynchus tshawytscha*) in a small tributary to the Yukon River, an exceptionally harsh environment with low temperatures and long winters. They suggested that overwinter size-selective mortality may be more important in more moderate environments, whereas in stressful environments overwinter mortality rates of age 0 individuals are high but equally so across all sizes and survival is dependent on stochastic factors. Schultz et al. (1998) found a more northern stock of Atlantic silverside (*Menidia menidia*) to be more tolerant of extreme cold winter temperatures and Meyer and Griffith (1997) suggests that size-selective mortality may occur in any environment but may be more likely under relatively low-frequency severe environmental conditions.

SPATIAL SCALE

Instream habitat and water quality conditions reflect landscape characteristics at multiple scales within a drainage. Instream water temperature is a function of landscape features such as elevation, solar aspect, and valley width, and may also be associated with stream size. For example, Larscheid and Hubert (1992) found water temperature and fish size to be correlated with elevation and Bozek and Hubert (1992) found trout (*Oncorhynchus* sp.) species distribution to be correlated with stream size and water temperature. Lotic productivity reflects watershed conditions including geology, rainfall, aspect, vegetation, as well as stream size and valley width. Vannote et al. (1980) identified predictable changes in lotic systems with size as formulated in the river continuum theory. Valley width can influence off-channel habitat and large woody debris availability and channel type (Rot et al. 2000). Instream habitat measures including reach width, velocity, substrate composition, and gradient have been correlated with elevation and stream size (Lanka et al. 1987).

Temperature and nutrient concentration have been correlated with distance from the headwaters (Hughes and Gammon 1987). This distance has also been linked to size of juvenile brown trout *(Salmo trutta)* by Hayes (1995) and sockeye salmon (*Oncorhynchus nerka*) by Woody et al. (2000). Mean aspect and basin area explained two-thirds of the variation in timing of spawning and length of spawners of Yellowstone cutthroat trout (*O. c. bouvieri*; Gresswell et al. 1997). Rainbow trout (*Oncorhynchus mykiss*) standing crop has been correlated with watershed aspect (Li et al. 1994). Frissell et al. (1986) proposed a hierarchical structure for classifying stream habitats, including five scales from watersheds to microhabitats. Watershed characteristics, including climate, soils, and geology, and segment-level characteristics, including position in the drainage network and valley width (confinement), influence instream productivity through direct and indirect effects on temperature and nutrient availability.

Organism variation and ecological processes occur at multiple spatial scales in response to environmental gradients occurring at different scales (Morris 1987; O'Neill et al. 1988; Carlile et al. 1989; Taylor 1991; Healey and Prince 1995; Lewis et al. 1996; Rabeni and Sowa 1996; Cooper et al. 1998). The relative importance of environmental and genetic factors controlling phenotypic response may vary with temporal and spatial scale of variability in the environment and their interactions (Riddell and Leggett 1981). Because different processes operate at different scales (Addicott et al. 1987; Menge and Olson 1990), the relative importance of competition, predation, and abiotic factors likely changes with scale and species (Menge and Olson 1990). Examples of scale dependency include

Young's (1999) finding that the proportion of coho salmon jack spawners did not differ in relation to local stream habitat variables such as gradient, distance from the ocean, and elevation, but instead to the broader scale variable of basin identity. Age 0 and age 1 Atlantic salmon varied in feeding and growth at a relatively fine spatial scale (20 m reach length) in response to flood events (Arndt et al. 2002). Different factors regulated an Arkansas darter (*Etheostoma cragini*) population at each of four scales, including pool, reach, segment, and watershed. Consideration of physical and biotic processes at all four scales was necessary to understand the dynamics of this population (Labbe and Fausch 2000).

Although relationships have been identified among scales and specific watershed-instream characteristics, relationships between the scales at which landscape patterns occur and their causal mechanisms are not well understood. Horne and Schneider (1995) suggested that physical processes and the resulting biological variation occur at the same scales. If so, causation may be inferred by matching scales of variation and dominant processes. Conversely, Levin (1992) suggests that ecological patterns may be determined by causal mechanisms occurring at broader scales, or they may be the net response to multiple cumulative processes occurring at finer spatial scales. Understanding of scale effects requires that phenomena be studied at the appropriate scale(s; May 1994). And, since responses may be scale-specific, inferences are limited to the scales studied (Cullinan and Thomas 1992).

ROLE OF ENVIRONMENTAL VARIATION

The environmental factors most important in producing phenotypic variation in fishes have not been identified conclusively (van Noordwijk 1989). However, all aquatic organisms are sensitive to temperature, pH, ion concentration, and pressure as they affect physiological processes (Stearns 1989). Environmental influences on salmonid phenotypic variation are reviewed by Thorpe (1994). A wide range of environmental conditions tends to produce a wider range in character traits (Endler 1973). Because fish exhibit higher intraspecific phenotypic diversity than most taxa but have only average genetic diversity (Healey 1986; Allendorf et al. 1997), they must be more responsive to environmental variation than other aquatic taxa (Allendorf and Leary 1988). This suggests that focus only on measurable molecular genetic diversity may fail to conserve a significant component of intraspecific fish diversity (Allendorf and Leary 1988).

The processes generating size variation are incompletely understood, but important instream characteristics include temperature, food availability (Claytor et al. 1991; McDowall 1994), and habitat characteristics affecting predation, competition, and shelter from high flows. Habitat complexity (Baltz et al. 1991) and intra- and interspecific competitor density (Dong and DeAngelis 1998) may be particularly important in controlling size variation. Growth rates are highly sensitive to changes in physical factors such as water temperature and food availability (Nicieza et al. 1994). Because growth rates and organism size influence many life history characteristics, including mortality, age at maturity, competition and predation, stream productivity can also influence species and community structure and therefore biodiversity (Werner and Gilliam 1984). Fish growth, age and size at maturation, and migratory life history type have been linked to aquatic productivity (Policansky 1983; Gross et al. 1988; Rieman and Myers 1992).

Conductivity can generally be used as an effective surrogate for nutrient availability for streams within a basin. It has been positively correlated with primary production (e.g. Chetelat et al. 1999) as well as fish growth. Examples include lake trout (*Salvelinus namaycush*) growth, mean size, fecundity, and size at maturity (Trippel and Beamish 1989; Trippel 1993; Trippel and Beamish 1993), brown trout growth rate and standing crop (McFadden and Cooper 1962), brook trout (*Salvelinus fontinalis*) weight (Donald et al. 1980), sea lamprey (*Petromyzon marinus*) growth rate (Holmes 1990), and fish production and biomass (Scarnecchia and Bergerson 1987).

Fish growth is directly correlated with stream temperature (Donald et al. 1980; Elliott 1984; Holtby 1988; Mills 1988; Vondracek et al. 1988; Copp 1990; Elliott 1990; Holmes 1990; Johnson et al. 1992), but inversely correlated with temperature above optimum thermal tolerances (Myrick and Cech 1996). Temperature modulation of development producing significant phenotypic variation is probably a universal example among ectotherms (Smith-Gill 1983).

At finer spatial scales, age 0 size variation may be associated with habitat complexity since a more diverse environment may accommodate size-based ontogenetic habitat shifts and associated processes (Baltz et al. 1991). Although “habitat complexity” has been used for a variety of applications in the ecological literature, it incorporates concepts of habitat diversity *and* interactions between organisms and their habitats. A complex habitat may accommodate diversity at one or multiple biotic scales, for example species, age classes, or variants within an age class by providing diverse niches (Klopfer and Mac Arthur 1960; Schoener 1974), as well as potentially supporting multiple ecological functions (for example, provision of food and predator refuge) within a scale. Diverse age 0 salmonid habitat may accommodate diverse body sizes as well as meet age 0 needs, such as refuge from predation and harsh environments and foraging opportunity (Mason and Chapman 1965; Chapman 1966; Fausch 1984; Power 1987; Harvey 1991; Fausch 1993). Habitat complexity influences size, structure, distribution, and stability of a population (Sedell et al. 1990; Pearsons et al. 1992) and may also increase a population's resistance to (Poff and Ward 1990; Pearsons et al. 1992) and recovery from disturbance (Connell and Sousa 1983). Harvey and Nakamoto (1997) found habitat complexity to mediate competition between size classes of juvenile rainbow trout.

The effect of density on growth is unclear. Increased competition as a result of high density may limit individual growth and therefore fish size and size variation in a population or cohort. For example, Johnson et al. (1992) found high brook trout density in a confined pool produced a homogeneously sized population of stunted fish. Effects of fish density on growth and size structure have been documented (e.g. Jobling and Reinsnes 1986; Grant 1993; Knight et al. 1999; Railsbeck and Rose 1999; Roni and Quinn 2001). However, several authors found that density did not limit juvenile salmonid growth (Moore and Gregory 1988a; Rieman and Myers 1992; Hayes 1995), particularly if individuals were free to emigrate from high-density or food-limiting situations (Keeley 2001). Dong and DeAngelis (1998) found size variation increased with density whereas Elliott (1984; 1990) found size variation decreased with egg density and therefore potentially with fry density.

Local adaptation allows organisms to better match their environment, maximizing fitness. Factors affecting fitness vary with environmental conditions, and life history characteristics may therefore reflect spatial patterns and environmental gradients. For example, some environments may limit growth, yet adaptive responses resulting in compensatory growth may produce a countergradient response (Conover and Schultz 1995; Imsland et al. 2001). Short growing seasons at higher latitudes and elevations may limit body size, but a countergradient response may have evolved to increase growth rates in these environments relative to populations with longer growing seasons (Conover 1990; Conover and Present 1990; Schultz et al. 1996; Conover et al. 1997; Schultz et al. 1998). Where cold temperatures limit growth, physiological adaptations including higher growth rate and energy storage efficiency may increase temperature tolerance (Nicieza and Metcalfe 1997). Yamahira and Conover (2002) found adaptations to both reduced temperature and shortened growing season in Atlantic silverside and tidewater silverside (*M. peninsulae*), including shifted reaction norms in populations associated with lower temperatures, and increasing maximum growth rate with latitude.

STUDY GOALS

The goals of this work are to address, for age 0 westslope cutthroat trout within a subbasin, the questions: 1) where is size variation, 2) what causes it, and 3) does it matter? Specifically, I sought to quantify and characterize the distribution of size variation across spatial scales, to test environmental correlates likely to be causative factors in generation of size variation, and to explore fitness aspects of size variation. Chapter 2 characterizes the distribution of size variation across three scales, broad areas within a subbasin, among neighboring streams, and within streams, and examines relationships between size variation and two instream factors likely to affect growth and therefore size variation, temperature and productivity, as well as several watershed characteristics, including aspect, distance from the headwaters, elevation, and valley width, that may be expected to affect instream temperature. Chapter 3 is an empirical study of relationships between habitat complexity and age 0 westslope cutthroat trout size variation at the finer scales. Chapter 4 explores relationships between age 0 size and fitness and life history characteristics such as size-selective overwinter mortality and relationships between life history characteristics and the nature of the growth environment, specifically, life history diversification in moderate environments and adaptive mechanisms in harsh environments. Chapter 5 concludes with consideration of relationships between my findings and relevant ecological literature, discussion of implications for management and conservation of inland salmonids, and recommendations for future research.

CHAPTER 2

LENGTH VARIATION IN AGE 0 WESTSLOPE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI LEWISI*) ACROSS SPATIAL SCALES AND ENVIRONMENTAL GRADIENTS

ABSTRACT

Phenotypic diversity is an important component of ecological diversity in fishes, potentially leading to speciation via local adaptation and stabilizing populations in variable environments. The benefits of larger body size in salmonids for survival, migratory success, competitive ability, and predator avoidance are well documented. However, in some circumstances, small may be better or there may be no one best size. I examined mean body size (CLen) and interquartile range of mean size (CIQR; size diversity) in age 0 westslope cutthroat trout in the Coeur d' Alene basin, Idaho, among areas (10^2 km^2 – area scale), among streams within areas (10^1 km^2 – stream scale), and among sites within streams (10^0 km^2 – site scale). I explored relationships between size and size variation and instream gradients of temperature and productivity (measured as conductivity). I also explored spatial patterns of size variation by examining the relationship between size variation and four landscape gradients that may affect temperature: aspect, elevation, headwater distance, and valley width. The most variation in CLen and CIQR was found among areas (61% and 64% respectively), with lesser amounts of variation among streams (23% and 16%, respectively) and sites (13% and 14%, respectively). Both instream variables as well as elevation and aspect explained significant variation in mean size, whereas only temperature and elevation explained significant variation in size variation. Distribution of variation in length variables most closely matched conductivity, temperature, aspect, and elevation, supporting the view that productivity and temperature influence size variation at the same or broader spatial scales as landscape and instream patterns. Elevation was the only landscape variable explaining significant variation in stream water temperature. Differences in life history characteristics associated with growth may vary across temperature and productivity gradients as well. Conservation of the full range of variation in westslope cutthroat trout may require high quality habitats across these

gradients and at multiple spatial scales. Populations in cold streams with limited size variation may be highly sensitive and have low resilience to disturbance. Identifying the spatial scales of diversity and associated environmental gradients are important in understanding conservation needs of stream fishes. These may need to be considered when defining evolutionarily significant units (ESUs) for species protected under the U.S. Endangered Species Act.

INTRODUCTION

Phenotypic variation, the intraspecific variation in life history, morphology, and behavior, plays a critical part in many evolutionarily and ecologically essential functions (Skulason and Smith 1995), and therefore may be critical to conserve. Processes driven by phenotypic variation include the ability to adapt to local conditions and disturbance regimes, population differentiation that leads to speciation, and the ability to reduce intra- and interspecific competition through niche differentiation (e.g. Nikol'skiy 1969; Utter 1981; Skulason and Smith 1995). Plasticity in some traits may allow adjustment to variable environments while maintaining stability in traits closely linked to survival and fitness (Caswell 1983; Stearns 1983; Thompson 1991). Causes, consequences, and evolutionary potential of phenotypic plasticity are important questions in the ecology and conservation of organisms in variable environments (Schlichting 1989). Successful fish conservation and management may require recognition and understanding of phenotypic variation and processes generating that variation (Gresswell et al. 1994; Healey and Prince 1995).

Organism size has been well recognized as an important phenotypic characteristic, mediating various biological processes, including metabolism, growth, production rate, reproductive condition and commitments, and constraints on body function (Peters 1983; Policansky 1983; Schmidt-Neilsen 1984; Werner and Gilliam 1984; Stein et al. 1987). Through these relationships, body size has important effects on organism fitness, ultimately affecting various evolutionary processes. The benefits of large juvenile size include increased first-year survival (Hunt 1969; Werner 1984; Holtby 1988; Elliott 1989; Elliott 1990; Smith and Griffith 1994; Quinn and Peterson 1996), intra-specific competitive advantage (Abbott et al. 1985; Persson 1985), and reduced vulnerability to predation (Parker 1971; Pepin and Shears 1995; Claessen et al. 2002). However, there are also advantages to being small. Both aquatic and terrestrial predators prefer larger prey (Power 1987; Harvey 1991; Litvak and Leggett 1992). In addition, aggressive feeding and growth have drawbacks. Actively feeding or satiated individuals may have a higher risk of predation (Lankford et al. 2001), and under risk of predation, larger individuals with higher fitness may be slower to leave cover and resume feeding, limiting future growth potential (Grant and Noakes 1987; Reinhardt and Healey 1999). In some circumstances, there may be no one best size, and size variation within a population has value. Size-based or ontogenetic niche shifts are well-documented (Werner and Gilliam 1984; Mittelbach and Chesson 1987; Erkinaro et al. 1997; Ruzycki and Wurtsbaugh 1999), and may serve to reduce intraspecific competition within a population through morphological differentiation and niche separation (e.g. Skulason and Smith 1995; Landry et al. 1999). Size-mediated habitat, food, and reproductive strategy differentiation have each been documented in larval fishes (e.g. Gross 1985; Jonsson et al. 1988; Metcalfe et al. 1988; Nielsen 1992; L'Abee-Lund et al. 1993; Taylor and Bentzen 1993; Bozek et al. 1994). Size variation may provide recruitment stability and long-term survival in temporally variable environments, as well (den Boer 1968; Lomnicki 1980; Chandler and Bjornn 1988; Good et al. 2001).

Relationships between fish size and environmental conditions, such as temperature and food availability, have been well-documented (Claytor et al. 1991; McDowall 1994; Nicieza et al. 1994). Environmental variation represents the range of non-genetically based phenotypes displayed among individuals across environmental gradients (Schlichting 1989; West-Eberhard 1989; Adkison 1995). Salmonids express higher than average phenotypic diversity and may be more responsive to environmental factors affecting growth than other fishes (Healey 1986; Allendorf and Leary 1988; Allendorf et al. 1997). Conductivity, generally an effective surrogate for nutrient availability for streams within a basin, has been positively correlated with primary production (e.g. Chetelat et al. 1999) as well as fish growth, mean size and weight, and biomass (McFadden and Cooper 1962; Donald et al. 1980; Scarnecchia and Bergerson 1987; Trippel and Beamish 1989; 1993; Holmes 1990; Trippel 1993). Growth is directly correlated with temperature in numerous fish species, including salmonids (Donald et al. 1980; Elliott 1984; Holtby 1988; Mills 1988; Vondracek et al. 1988; Copp 1990; Elliott 1990; Holmes 1990; Johnson et al. 1992). Smith-Gill (1983) suggested that the linkage between temperature variation and significant phenotypic variation is probably universal among ectotherms. Fish size variation can be generated by environmental or genetic mechanisms or their interaction (Kirpichnikov 1981; Berven and Gill 1983; McDowall 1994). Genetic components of fish growth and size divergence have also been documented (e.g. Gjedrem 1976; Reznick 1981; Sumpter 1992; Nicieza et al. 1994; Smoker et al. 1994; Kinnison et al. 1998).

Instream variables important to aquatic organisms are controlled by landscape characteristics and processes occurring at multiple spatial scales. Frissell et al. (1986) developed a hierarchical stream habitat classification system that identified landscape characteristics influencing instream temperature and nutrient availability, including watershed characteristics such as climate, soils, and geology, and segment-level characteristics such as position in the drainage network and valley width (confinement). Individual habitat characteristics vary across multiple and different spatial scales in response to the identities and scales of occurrence of their controlling landscape factors. For example, Larscheid and Hubert (1992) found water temperature and fish size to be correlated with elevation, and Hughes and Gammon (1987) found temperature and nutrient concentration to be correlated with distance from the headwaters. Organism life history characteristics have also been linked to landscape characteristics. For example, mean aspect and basin area explained two-thirds of the variation in spawning timing and length of spawners of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*; Gresswell et al. 1997). Organismal response therefore occurs at multiple scales in response to the scale-dependency of habitat (Morris 1987; O'Neill et al. 1988; Carlile et al. 1989; Taylor 1991; Healey and Prince 1995; Lewis et al. 1996; Rabeni and Sowa 1996; Cooper et al. 1998). Labbe and Fausch (2000) found that a population of Arkansas darters (*Etheostoma cragini*) was regulated by different factors at each of four spatial scales, and that consideration of ecological relationships at all four scales was necessary to explain survival probability of individuals in this population.

In this study, I sought to identify the spatial scales and environmental gradients associated with size and size variation of age 0 westslope cutthroat trout. Although historically and currently one of the most widespread of the inland trout subspecies, westslope cutthroat trout is in decline throughout much of its range (Lee et al. 1997) and in 2000 was proposed for listing under the U.S. Endangered Species Act. I chose to study age 0 fish because early life history stages play a disproportionately important role in determining population recruitment (Werner and Gilliam 1984; Van Winkle et al. 1993). Natural selection operates most intensively on the most vulnerable life stages, and competition, predation and survival are critical size-mediated processes for age 0 fish (Stein et al. 1987). To better understand watershed influences on instream productivity and temperature gradients, landscape variables associated with these instream characteristics were also selected for inclusion. Relationships between the scales at which landscape patterns occur and their causal mechanisms are not well understood. Horne and Schneider (1995) suggested that physical processes and the resulting biological variation occur at the same scales. Conversely, Levin (1992) suggested that ecological patterns may be determined by causal mechanisms occurring at broader scales, or they may be the net response to multiple cumulative processes occurring at finer spatial scales. This study will contribute to the understanding of relationships between broad scale landscape patterns and finer scale instream and biotic responses. Understanding relationships between fish diversity and landscape characteristics rather than instream characteristics may also be more useful to land managers charged with conserving aquatic resources. Understanding of the extent, spatial distribution, and causal processes of phenotypic variation in cutthroat trout and other inland salmonids remains limited (Gresswell et al. 1994). I selected the Coeur d' Alene (CDA) basin of northern Idaho as my study area since it offers relatively diverse geology, topography, and other landscape characteristics affecting instream temperature and productivity gradients and therefore potentially fish size. My hypotheses were: 1) age 0 size variation is correlated with instream temperature and productivity and watershed gradients associated with temperature, and 2) age 0 size variation and associated environmental variables occur at the same spatial scales.

STUDY AREA

The study was conducted in the Coeur d' Alene (CDA) basin of northern Idaho, USA (Figure 2.1), a region of low mountains vegetated by coniferous forest dominated primarily by Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*) and other tree species (Bailey 1995). Elevation ranges from 600 to 1850 m. Climate includes severe winters of heavy snow, rain-on-snow, and rain. Annual precipitation is 50 to 100 mm (20 to 40 in; NOAA 2003). Geology is dominated by Precambrian Belt sedimentary rock containing basalt sills and granite sheets (Alt and Hyndman 1989). The majority of the basin is managed by the Idaho Panhandle National Forest. Logging and mining in the basin began in the mid-1800s (Maclay 1940) and have influenced much of the basin. Logging and recreation are the predominant land uses today. Many drainages have been moderately to heavily impacted by road construction and timber harvest during the past 50 years, particularly at lower elevations.

Twelve of 19 study streams drain to the North Fork of the CDA River, four streams drain to the Little North Fork of the CDA River, and three streams drain to Wolf Lodge Creek. All ultimately drain into Lake Coeur d' Alene and the Columbia River. Study streams are second- or third-order, moderate-gradient (2-6%), with gravel or cobble substrate and high water quality.

Fish fauna of study streams is limited to native westslope cutthroat trout, torrent sculpin (*Cottus rhotheus*), shorthead sculpin (*Cottus confusus*), and to non-native brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*). Bull trout (*Salvelinus confluentus*) are native to the system but are believed to be extirpated. Anadromous species do not have access to this system due to natural migration barriers below Lake Coeur d' Alene. Westslope cutthroat trout abundance has been depressed in some streams in the study area due to historical overharvest and habitat degradation (Dunnigan 1997; Abbott 2000; N. Horner, Idaho Department of Fish and Game, personal communication).

METHODS

Field Collections

Because trout abundance is relatively low across my study area, I selected streams that contained higher than average westslope cutthroat trout abundance based on data from 1994-1996 for 84 streams (Dunnigan 1997; Abbott 2000; B. Rieman, unpublished data) to ensure that adequate sample sizes were obtainable. Selected streams had relatively easy road or trail access. In order to address the spatial scale objectives of my study, multiple sites per stream (site scale; 10^0 km^2) were selected in 2 to 4 adjacent streams (stream scale; 10^1 km^2) distributed in groups (area scale; 10^2 km^2; Figure 2.1) throughout the study area. Streams were also selected to represent wide environmental gradients. Within each stream, an upper site was located as high in the drainage as possible while still being large enough to obtain an adequate sample size of age 0 fish (see below). Lower sites were generally selected immediately above the confluence with a receiving stream. In a few cases where study streams were larger than average, the lower site was placed higher in the drainage to maintain similar stream sizes across all study streams. Middle sites were located approximately halfway between the lower and upper site per stream. In three cases, only two sites were sampled and in two cases, only one site was sampled, due to presence of a hydrologic barrier precluding upstream fish passage (one stream), difficult site access (three streams), or low fish density (one stream).

At each collection site, a sample of 35 age 0 individuals was collected as well as all other westslope cutthroat trout ages encountered. Bootstrapping analyses of larger data sets suggested that a sample of 35 individuals accurately describe the size distribution at a site. Age 0 fish size varied among sites and across the sampling period and collection methods can be size selective (Nielsen and Johnson 1983). Smaller individuals are relatively slow and easy to hand collect, but are relatively unresponsive to electrical current. Larger individuals are quicker and able to evade hand nets, but are more responsive to electrical current. I used both methods as appropriate. Visually located small individuals were hand-collected, and then the surrounding area was sampled using a backpack electrofisher (Type VII, Smith-Root, Inc., Vancouver, Washington). All habitats with characteristics identified by Lentz (1998) as potential suitable habitats for age 0 westslope cutthroat trout were systematically sampled using the backpack electrofisher. Voltage was varied by stream to compensate for water conductivity differences. Collections for spatial analysis were made during July and August of 2000 and 2001. Some sites were resampled to obtain temporal growth data. These data were used to correct dependent variables for differences due to sampling date (see below). These collections were made between July and October of each year. Westslope cutthroat trout of all age classes were collected and length frequency histograms were used in identifying the maximum length of age 0 fish per site. Individuals of uncertain age were collected for age confirmation from otolith analyses. All collected fish were anesthetized, measured (total body length), and released.

Temperature was recorded using calibrated instream HOBO thermographs (HOBO H1 TEMP datalogger, Onset Computer Corporation). Due to equipment limitations, only 40 of 71 sites received HOBOs during the two years. HOBOs were placed annually at each site as soon as possible after snowmelt and were generally retrieved in late September or October. At each site, a HOBO was anchored to the bottom of the stream and shaded with cobbles in a slow or still water pocket or eddy characteristic of age 0 habitat. Due to differences in date of HOBO placement and HOBO malfunction, temperature data were available for somewhat different time periods between years and between sites. Daily average water temperatures for the time period in which data were available for all sites during both years were averaged within year, so that valid between-year and between-site comparisons could be made. In order to evaluate temperature variation among potential HOBO placement locations within a site, 7 HOBOs, were placed at the lower site on Lonesome Creek (a lower elevation stream) and the upper site on Tom Lavin Creek (a higher elevation stream). Age 0 trout habitats typically consist of isolated or partially isolated stream margin areas characterized by low water velocity, often separated from the main channel flow by a sharp change in water velocity and in some cases physical obstructions as well (Moore and Gregory 1988b; Lentz 1998). Within each of these sites, three HOBOs were placed in shady age 0 habitats, three in sunny habitats, and one in the main flow.

Conductivity was measured with a YSI Model 30 SCT conductivity meter three times per site during each summer. Two-year averages were used in all analyses. Elevation at each site was estimated to the nearest 3 m (10 ft) from 1:24,000 topographic maps. Headwater stream distance was measured from the upstream source as indicated on 1:24,000 maps downstream to each site and converted to meters. Average aspect of the stream channel through each site was estimated from topographic maps and converted to a reversed Day scale (Day and Monk 1974), from 1 (northeastern) to 16 (southwestern). Valley width was paced at each site and converted to meters.

Analyses

Fish length frequencies were plotted for each site and used to identify the maximum length of age 0 fish at each site. In general, a 5 to 10 mm gap existed between age 0 and age 1 fish, so differentiation of the two age classes was clear. Aging based on length groups was confirmed by otolith analysis. Collections were made during a 10-week period in 2000 (with 37 sites in a 7-week period), and a 5-week period in 2001 (with 29 sites in a 3-week period).

To compensate for differences in fish size among sites due to date of sampling, a correction factor was applied to total length and interquartile range data for each sample. Corrected total length (CLen) and corrected interquartile range (CIQR) were used in all analyses. A subsample of 13 sites during 2000 and 11 sites during 2001, representing the full range of environmental gradients found in the stream sample, was sampled more than once during each collection period and used to characterize growth rates (Appendix 2.1, Tables 2.8 and 2.9). For each site within year, total body length was regressed on collection date, and the slopes from each regression were averaged within each year (Table 2.1). The average regression slope was used to correct total length at all sites to the 221st day of the year (August 8, 2000 and August 9, 2001), the midpoint of all sampling efforts in 2000 and 2001. In 2000, regression slopes ranged from 0.1 to 0.5 mm/day (mean = 0.26 ± 0.11mm/day), and in 2001, slopes ranged from 0.1 to 0.4 mm/day (mean = 0.29 ± 0.10 mm/day). CLen for each year was calculated as follows:

$$\text{2000: CLen} = \text{Total length} + 0.26\,(221 - \text{Sample Day of the Year})$$
$$\text{2001: CLen} = \text{Total length} + 0.29\,(221 - \text{Sample Day of the Year}).$$

In 2000, the earliest two samples collected were corrected by 14 days by adding 12.2% and 12.8% of original body length and the latest sample was corrected by 58 days by adding 27.7% of original body length. In 2001, the earliest two samples collected were corrected by 29 days by adding 28.2% and 28.5% of original body length and the latest two samples were corrected by 8 days by adding 6.2% and 6.9% of original body length. To assure that correction produce a bias in the data, I examined correlations between date of collection and all independent variables. Correlation between collection date and an environmental variable would have introduced this pattern into size date through the collection date. All coefficient of determination values were low, with a maximum of 0.141 with headwater distance and all other r^2 values below 0.09.

Because correction of total length assumes constant growth of all individuals and therefore does not allow for size diversification (or homogenization) during the sampling period, total length and interquartile range were corrected separately. Raw total length data were used to calculate interquartile range of total length for each time series site. A correction factor was calculated for Interquartile range in a treatment similar to that for total length (Table 2.1). Slopes for 2000 ranged from -0.1 to 0.1mm/day. The mean regression slope of 0.05 ± 0.07 mm/day was used in correcting CIQR in 2000. Slopes for 2001 ranged from 0.1 to 0.3 mm/day. The mean regression slope of 0.12 ± 0.06 mm/day was used in correcting CIQR in 2001.

Normality of the data was confirmed through examination of box and whisker plots and normal probability plots; skewness and kurtosis coefficients were calculated using Systat (Systat Version 8.0, SPSS, Inc. 1998, Standard Version). Effect of year of sampling on size variables was assessed through a paired t-test on sites sampled during both years. The distribution of size variation among scales was analyzed in nested analyses of variance (ANOVA) with CLen and CIQR as dependent variables and area, stream(area), site(area*stream), and year (not nested) as independent variables. The percentage of the total mean square error attributable to each scale variable was calculated. To explore spatial scale relationships between environmental gradients and size variation, ANOVA was conducted on each environmental gradient. The percentage of total mean square error was calculated for each scale. These results were compared to similar analyses for CLen and CIQR.

Correlations among landscape variables were examined to identify redundancies. Relationships of instream temperature and landscape variables were examined through regression analyses. Finally, relationships of size variables with landscape gradients were examined through stepwise regression; regressions were conducted separately with instream (temperature, conductivity) and landscape variables (aspect, elevation, headwater distance, valley width). Regression analyses were conducted at the site, stream, and area scales by averaging over the next finer scale. Significance level used for instream and landscape variables to enter and stay in regression models was $p < 0.10$. ANOVA and regression analyses were conducted in SAS (SAS Institute, Inc., Release 6.12 TS060, Copyright 1989-96).

To obtain an estimate of age 0 density, I scored each site on the difficulty of collecting requisite subsamples (based on collection reach length and time required), from 1 = low density to 3 = high density. I regressed CLen and CIQR on these density classes separately and with instream and landscape variables. I also regressed length correction slopes (growth rates per stream) on density.

RESULTS

Mean, maximum, and minimum stream temperatures were similar between flowing water, shaded, and sunny habitats within each stream (Table 2.2). Sunny units were not warmer. Variation among units within location (sunny, shady) was generally low. Habitat units appeared to have more stable daily temperature patterns than the flowing water sites since daily temperature fluctuations were greater in the flowing water sites. Daily average temperatures varied among sunny units more than among shaded units, particularly for average maximum temperature. Average maximum temperature tended to vary more among units than did mean or minimum average temperatures. Temperatures in Tom Lavin Creek were lower and less variable than in Lonesome Creek.

Average stream temperature was significantly higher in 2000 than in 2001 ($t=8.76$, $p<0.0001$, $N=13$). Therefore, temperature within year was used in all regression analyses that included temperature as a variable. Elevation was the only landscape variable explaining significant variation in temperature ($r^2=0.321$, $p<0.008$, $N=21$ and $r^2=0.476$, $p<0.002$, $N=19$ in 2000 and 2001, respectively).

Forty-one sites were sampled in 2000. Thirty sites were sampled in 2001, of which 23 had been sampled in 2000. Neither CLen nor CIQR differed significantly between 2000 and 2001 (CLen: paired $t=0.61$, $p<0.56$, $N=23$ and CIQR: paired $t=1.26$, $p<0.22$, $N=23$). In analyses of variation among spatial scales, year accounted for 17% and 18% of variation in CLen (Figure 2.2a) and CIQR (Figure 2.2b), respectively.

Meaningful variation in CLen and CIQR was seen at area, stream, and site scales (Table 2.3). The majority of variation in CLen and CIQR, 47 and 52%, respectively, occurred at the area scale (Figures 2.2a, 2.2b). CLen scale analyses included a within-site scale that interquartile range did not; however, only 1% of total variation was attributable to that scale. Mean fish size ranged from 31.6 to 40.0 mm at the area scale (Figure 2.3a), 26.8 to 44.1 mm at the stream scale (Figure 2.3b) and 26.3 to 49.1 mm at the site scale (Figure 2.3c). CIQR ranged from 2.3 to 7.6 mm at the area scale (Figure 2.4a), 1.2 to 10.1 mm at the stream scale (Figure 2.4b), and –0.2 to 15.1 mm at the site scale (Figure 2.4c). The negative interquartile range value is an artifact of the length correction process. Although elevation effects are discussed in more detail below, fish tended to be larger and more variable in size at lower elevations and at most scales (Figures 2.3, 2.4).

Fish length, instream temperature and productivity, and landscape variables differed somewhat in the distribution of variation among spatial scales (Figure 2.5). All variables except headwater distance and valley width had the most variation at the area scale. Headwater distance and valley width had the most variation at the stream scale with the remainder relatively evenly divided between the site and area scales. Distribution of variation in length variables among spatial scales most closely corresponded to aspect and conductivity, secondarily to temperature and elevation, and least to headwater distance and valley width.

Most landscape variables were not significantly correlated with each other. Headwater distance was significantly correlated with elevation and valley width (Table 2.4). All four variables were included in analyses since inter-variable correlation explained less than half of the variation in each variable.

Temperature and conductivity appeared significant to CLen at the site and stream scales but only temperature was significant at the area scale (Table 2.5). Temperature and conductivity together explained 58.1 and 29.6% of the variation in CLen at the site and stream scales, respectively; temperature explained 68.7% of the variation in CLen at the area scale. Neither variable was able to enter the model at the site or area scales for CIQR, and only temperature was significant to CIQR at the stream scale, explaining 33.5% of the variation in CIQR (Table 2.6). Because of the limited number of thermographs, only 40 of 71 sites included the variable temperature. Instream analyses may have had limited power to explain variation in size variables at the area scale, but not at the site scale since temperature was significant with a smaller sample size at the stream scale.

Landscape variables were less effective at explaining variation in CLen than were instream variables. Elevation and aspect appeared in models at the site and stream scales, together explaining 29.6 and 31.7% of the variation in CLen, respectively. No variables were able to enter the model at the area scale (Table 2.5).

Elevation was the only significant variable to CIQR, and was so at all three scales, explaining 25.4, 35.2, and 76.8% of the variation in CIQR at site, stream, and area scales, respectively (Table 2.6). The site scale differs from the stream and area scales in that it represents a longitudinal gradient within a stream. Fish size was larger and more variable at lower sites within a stream (Table 2.7).

I found no relationship between CLen and density ($p<0.17$, $r^2=0.041$, slope = 1.49, N=48) or CIQR ($p<0.85$, $r^2=-0.000$, slope = -0.123, N=48). In stepwise regressions with instream and landscape variables, density was not a significant variable to CLen or CIQR with instream or landscape gradients at any scale. However, regression of fish growth rates for streams used in correcting length data on density produced a significant negative relationship ($p<0.004$, $r^2=0.464$, slope=-0.076, N=16).

DISCUSSION

Size differences were identified at three spatial scales, with the most variation found at the area scale. Although adult westslope cutthroat trout can vary dramatically in size, most variation is attributed to differences in contribution between adfluvial, fluvial, and resident populations (Averett and MacPhee 1971; Shepard et al. 1984). Few studies of size variation in age 0 fish size have been conducted. Unlike my findings, Shepard et al. (1984) examined age 0 westslope cutthroat trout growth in tributaries of the Flathead River, Montana, and concluded that growth was similar among tributaries. My results suggest that adjacent streams can be similar or vastly different depending on the nature of their environments. Differences in age 0 size among nearby streams may be due to subtle differences in elevation and temperature but are more likely a function of other variables, for example productivity (conductivity) that appeared to vary substantially at the stream scale. Size differences among areas can be explained by differences in temperature.

Size variation occurred primarily at the area scale associated with elevation and temperature in this study. Lower elevation sites were more likely to produce a wider range of age 0 sizes. Several mechanisms may explain the observed pattern of increasing size variation downstream. Although age 0 salmonids are highly mobile in both upstream and downstream directions, likelihood of movement does not appear to be size-based, and distance moved is greater downstream than upstream, particularly in small, high gradient streams (Kahler 1999). Smaller age 0 individuals from upstream may be able to reach lower sites and contribute to size diversity there, but it is less likely that larger individuals would be able to move several kilometers upstream to in sufficient numbers to influence population size structure of upper sites (Kahler 1999). Varying temperature with elevation could produce a size variation gradient across multiple spatial scales through effects on growth rate and timing and duration of emergence. I observed age 0 fish at lower sites to emerge 9-15 days earlier than at upper sites. The differences I observed in size variation were due primarily to the presence of larger individuals at warmer sites, extending the length range at those sites. Minimum size at productive and unproductive sites was more similar, which could be a function of late emergence but could also be a result of migration from upstream. Size variation within a site should be correlated with habitat complexity (Baltz et al. 1991), and habitat characteristics affecting competition (e.g. density) and predation (Power 1987) should determine size variation.

Size variation can be produced by environmental or genetic variation. Although genetic structuring in westslope cutthroat trout commonly occurs among streams or adjacent populations (Allendorf and Leary 1988), the CDA drainage appears to have relatively little genetic structuring among streams or broader spatial scales such as my area scale (B. Rieman, unpublished data; Spruell et al. 1999). The apparent genetic structuring of the CDA would not be expected to produce the size variation pattern observed of variation primarily at the area scale and secondarily at the stream scale. Even the within-stream variation (site scale) I observed would not be expected with the genetic structuring of the CDA since longitudinal patterns in genetic diversity have not been demonstrated. The phenotypic patterning I observed in age 0 fish can most easily be explained by the phenotypic plasticity characteristic of *Oncorhynchus* spp. (Thorpe 1989; Taylor 1991; Healey and Prince 1995) in response to the pattern of environmental gradients I observed within the CDA.

My results suggest that although density does not appear to be limiting fish size, density may be limiting growth rate. High fish density is generally thought to reduce growth rates and limit individual size (Van Den Avyle 1993) and therefore be inversely correlated with fish length. I found the opposite in a simple regression analysis with only density, and found no significant relationship of CLen with density when analyzed with instream or landscape environmental gradients. However, density may also increase competitive pressure and therefore encourage phenotypic diversification. Growth rate is negatively correlated with body size (Ricker 1979). Both density and fish size could explain the reduced growth rate of lower, warmer, more productive streams in my study. If density is limiting growth, system productivity may be compensating for density limitation of fish growth in these streams, and high fish density in unproductive streams such as the upper site of Tom Lavin Creek may compound growth rate limitations of an unproductive environment. Introgression by rainbow trout could influence growth and therefore the length pattern I observed of larger fish at lower elevations within and among streams, since rainbow trout may spawn and emerge earlier than cutthroat trout under some circumstances. Rainbow trout introgression is thought to occur primarily from downstream (Hitt 2002), and occurs primarily in downstream tributaries in the Coeur d' Alene (B. Rieman, unpublished data; P. Spruell, University of Montana, unpublished data). However, hybridization between rainbow and cutthroat trout has been associated with reduced, rather than increased growth. Allendorf and Leary (1988) demonstrated that age 0 F1 hybrids grew more slowly than pure westslope cutthroat trout, and Hawkins and Foote (1998) found that coastal cutthroat steelhead (*Oncorhynchus mykiss*) hybrids had reduced early growth and survival compared to parental stock. Rainbow trout also develop more slowly than do cutthroat trout, so that in spite of potentially earlier emergence, age 0 hybrids may not have a size advantage over pure cutthroat trout (Hawkins and Foote 1998). For these reasons, it is unlikely that rainbow trout introgression explains size patterns observed in my study.

Elevation and aspect may be expected to influence water temperature, yet Pearson's correlations between these variables and my mean daily average temperature variable were not high. My variable, averaged over days and the summer growth period, may not reflect the full effects of elevation and aspect on water temperature or the thermal environment experienced by fish. For example, length of the growing season may correlate better with elevation and aspect than with my temperature metric. L'Abee-Lund et al. (1989) found a relationship between water temperature and length of the growing season. Elevation may also be associated with landform and channel type (Rosgen 1994) and indirectly affect water temperature. Based on my findings, instream temperature obtained from seasonally placed instream recorders may fail to capture meaningful aspects of a fish's thermal environment. Over broad scales, elevation was most effective at predicting fish size. However, at a finer scale, elevation may fail to provide accurate information regarding fish size in some instances, since for example, influence of groundwater on water temperature varies at relatively fine scales.

Processes maintaining diversity within species may occur at different scales, and conservation of that diversity depends on consideration of those differences (May 1994). Elucidation of fish population structure through examination of genetic and phenotypic variation within and among populations can help to define meaningful units for conservation (Lomnicki 1980). Patterns common in westslope cutthroat trout, however, of significant genetic variation at the population/stream scale (Allendorf and Leary 1988), are not apparent in the CDA drainage (Knudsen and Spruell 1999, B. Rieman, unpublished data). The examination of age 0 size variation in the CDA identified diversity at finer scales than genetic information could provide. If variation in size of age 0 fish leads to important diversity in life history, fuller exploitation of available habitats or more resilient or abundant populations, maintenance of that variation will be an important goal for conservation and management. The extent of size variation within streams varied within and among areas. If size variation is associated with population resilience, focused attention may be required to identify, understand, and protect streams and systems with naturally low size variation and therefore resilience. If “bigger is better” for age 0 fish, these same populations with only small individuals may be exceptionally vulnerable to catastrophic events or chronic habitat degradation resulting in small population sizes. Understanding of population structure is critical to conservation goals such as maintenance of gene flow frequencies, potential for local adaptation, and identification of diversity-generating environmental processes.

In order to maintain phenotypic diversity of fishes, the range of environments and habitats that produced that diversity must be maintained (Healey and Prince 1995). I have demonstrated that patterns in age 0 size variation are consistent with instream and temperature gradients likely to influence the growth and size diversification of age 0 westslope cutthroat trout. Most of the variation in age 0 size and important environmental gradients associated with it cannot be represented within individual streams or even among streams in one area of a larger basin. The potential diversity represented by age 0 size can be conserved only through representation of multiple streams and populations distributed across distinct areas of the basin. This is consistent with the findings of Gresswell et al. (1997), that considerable life history variation in Yellowstone cutthroat trout occurs among streams in response to watershed characteristics, and Allendorf and Leary (1988), that considerable genetic variation in westslope cutthroat trout occurs at the stream scale. Conservation of westslope cutthroat trout across their temperature and elevation range may be challenging as current habitat conditions in lower elevation streams and reaches of streams tend to be in poorer condition and introgression rates with rainbow trout may be higher. Consideration of important environmental gradients may need to be considered when evolutionarily significant units (ESUs) are defined for taxa protected under the U.S. Endangered Species Act. This may also suggest that a conservation strategy of more, smaller areas of high quality habitat may be more effective than fewer, larger areas at conserving intraspecific diversity in this subspecies.

Although the relationship of size, particularly juvenile size, to survival and life history has been a focus in the literature, empirical relationships of size and variation in size of juvenile westslope cutthroat trout to fitness and the resilience and persistence of whole populations remains to be explored. Size has been associated with overwinter survival and size-selective mortality (Hunt 1969; Smith and Griffith 1994), yet one of the coldest, least productive sites included in this study (Tom Lavin Upper) has high abundance of relatively uniformly small age 0 westslope cutthroat trout. During two years of study, I did not document overwinter selectivity favoring fast growth that would be expected to be associated with large size at this site (Chapter 4). No growth rate selectivity was documented during one year and selectivity favoring slower growth rate was documented during the second year. However, compensatory growth mechanisms also appear to be present in age 0 fish at this site (*sensu* Nicieza and Metcalfe 1997). The role of size variation in age 0 salmonid population stability (*sensu* Lomnicki 1980) remains to be explored. The role of age 0 growth in influencing life history type, as suggested by Jonsson and Jonsson (1993), in the CDA, which contains resident, fluvial, and adfluvial individuals, is not understood. In addition, characterizing the role of habitat complexity, including identification of important components and scales, in generating size variation needs to be explored. Although scales and environmental gradients associated with age 0 size structure are important to identify for conservation purposes, other ecological processes and phenotypic traits must be acknowledged, understood, and conserved. Because size influences many aspects of life history, other phenotypic traits and life history characteristics may follow similar patterns to those observed for size variation. Scales and distribution of critical resources, such as spawning gravels and winter refuge habitats, sources of life history types, and disturbance regimes are also important to conserve. Age 0 size structure should influence many aspects of westslope cutthroat trout life history and population dynamics; understanding the full implications of that variation, however, remains an important challenge.

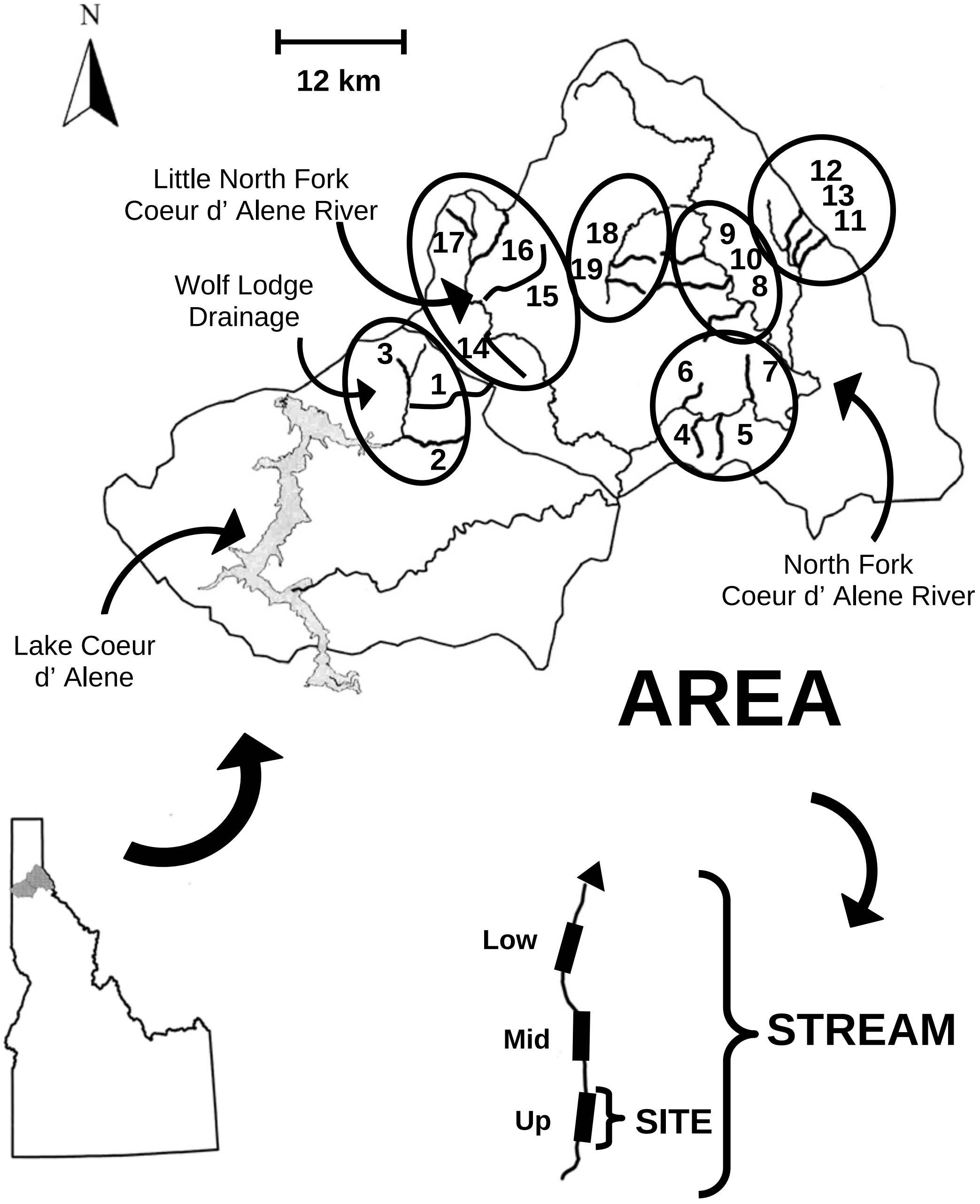


Figure 2.1. Study area in the Coeur d' Alene River basin, northern Idaho, U.S.A., 2000-2001, showing study design at three spatial scales: area, stream, and site. Study areas are identified by ovals, study streams within areas are numbered. Streams names are: 1. Marie, 2. Cedar, 3. Lonesome, 4. Coal, 5. Graham, 6. Scott, 7. Brown, 8. Yellowdog, 9. Miners, 10. Flat, 11. Cabin, 12. Clinton, 13. Rampike 14. Skookum, 15. Cascade, 16. Iron, 17. Tom Lavin, 18. Halsey, 19. Little Elk.

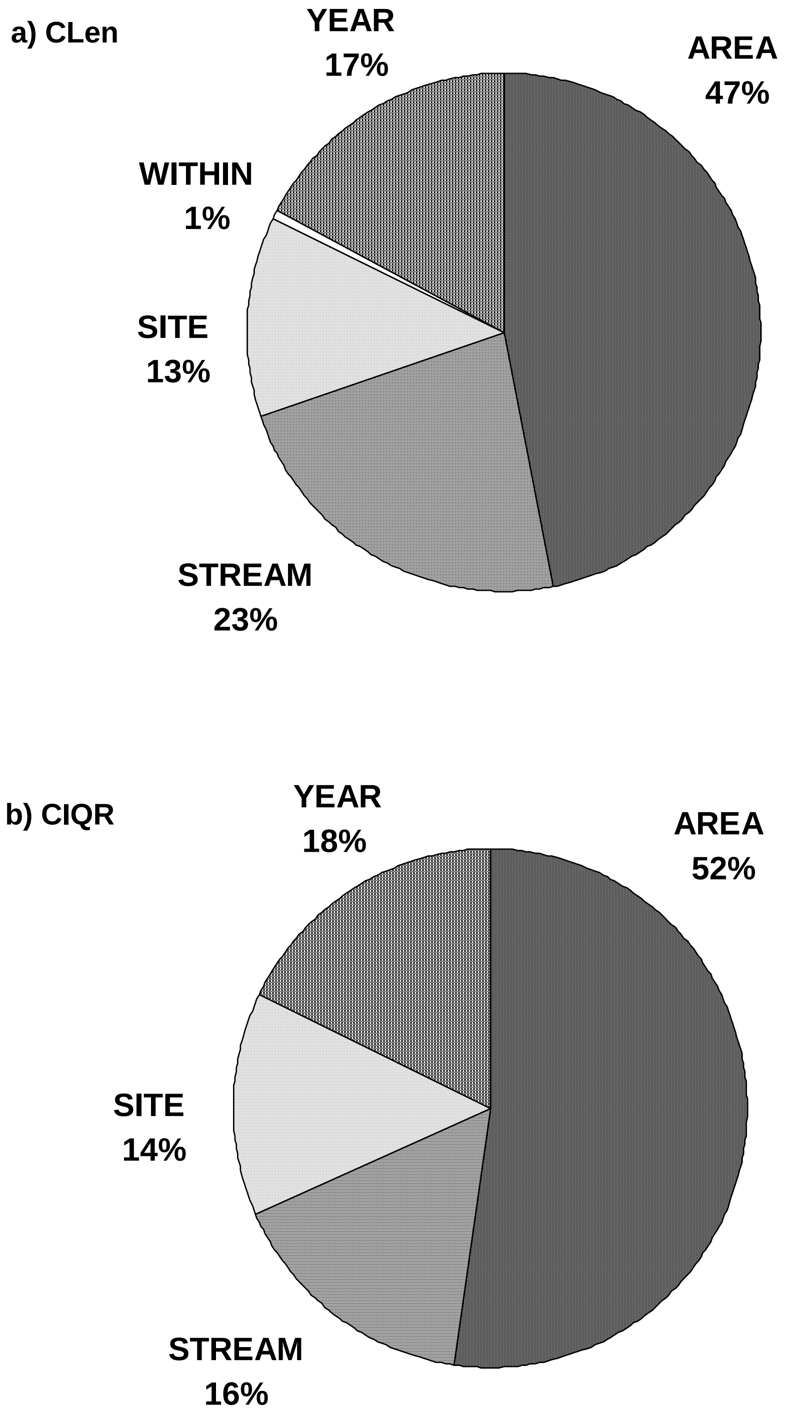


Figure 2.2. Distribution of variation in a) corrected total length (CLen) and b) corrected interquartile range (CIQR) of total length. CLen has an additional scale of variation, within site.

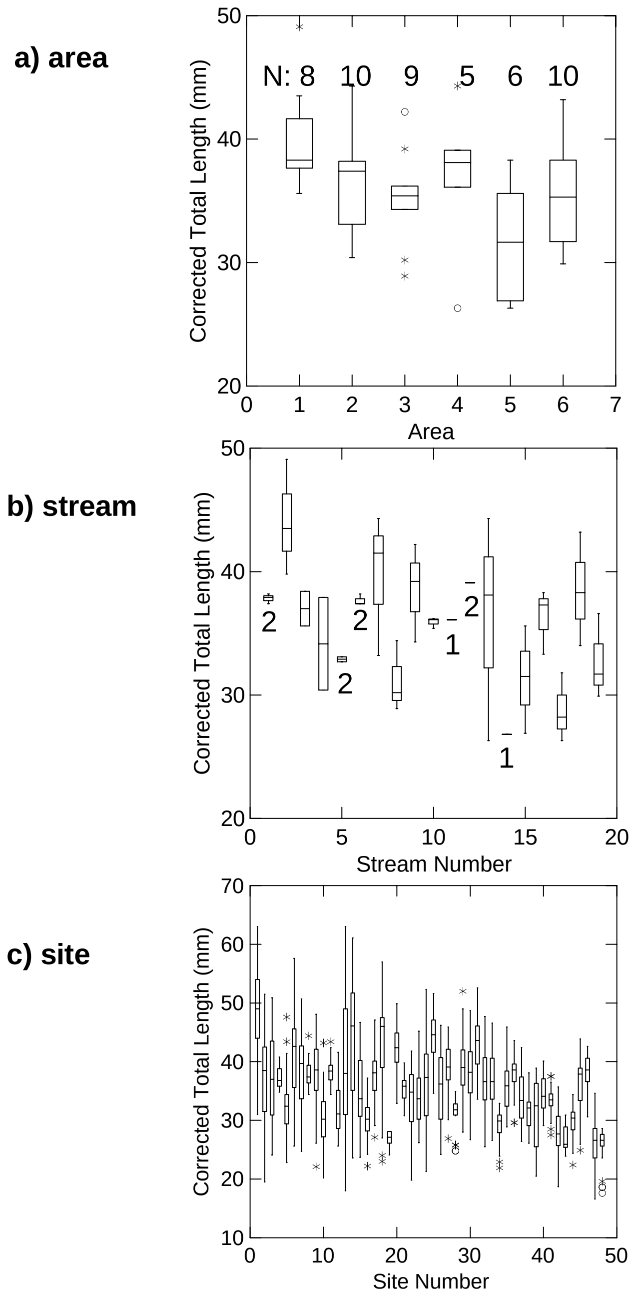
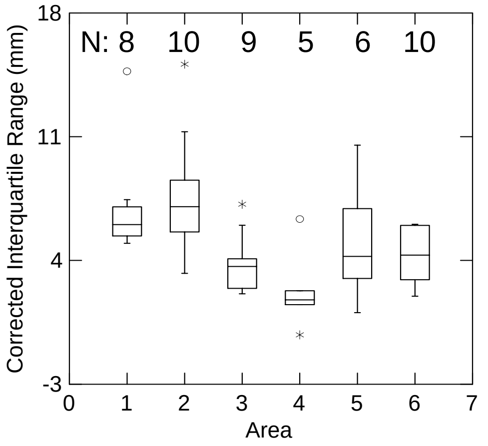
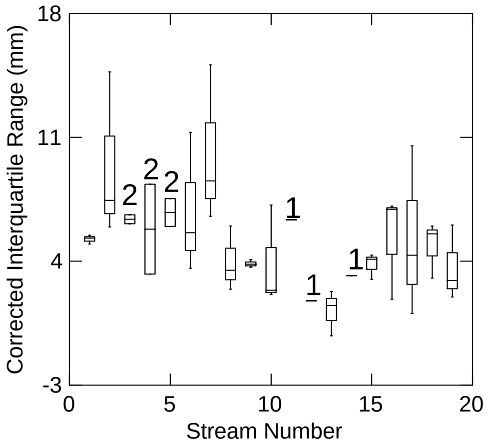


Figure 2.3. Boxplots of corrected total length (CLen) at a) area, b) stream, and c) site scales. Boxes represent the interquartile range, the line across the box represents the median value, and vertical lines extending from the box show highest and lowest values, excluding outliers. Outliers (asterisks) represent values that are 1.5 to 3.0 times the interquartile range. Areas and streams within areas are ordered by elevation. Streams are not ordered by elevation across areas since areas overlap in elevation. Stream numbers are as listed in Figure 2.1. Sample size is indicated at the top of a) for all areas and on top of specific data bars where N is other than 3 in b).

a) area



b) stream



c) site

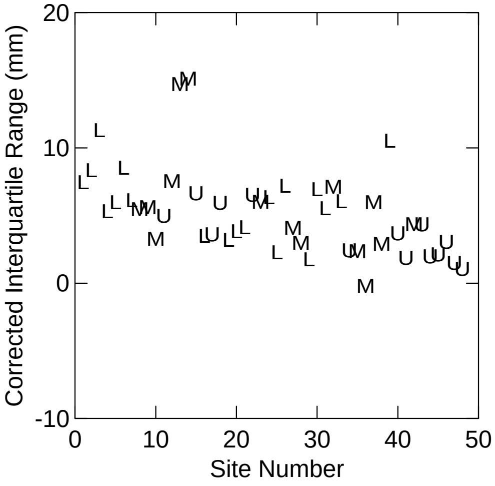


Figure 2.4. Plots of corrected interquartile range (CIQR) of total length of age 0 westslope cutthroat trout, Coeur d’ Alene River drainage, 2000-2001, at a) area, b) stream, and c) site scales. Plots a) and b) are boxplots; graphing conventions are as described in Figure 2.3. For plot c) sites are low (L), middle (M), and upper (U).

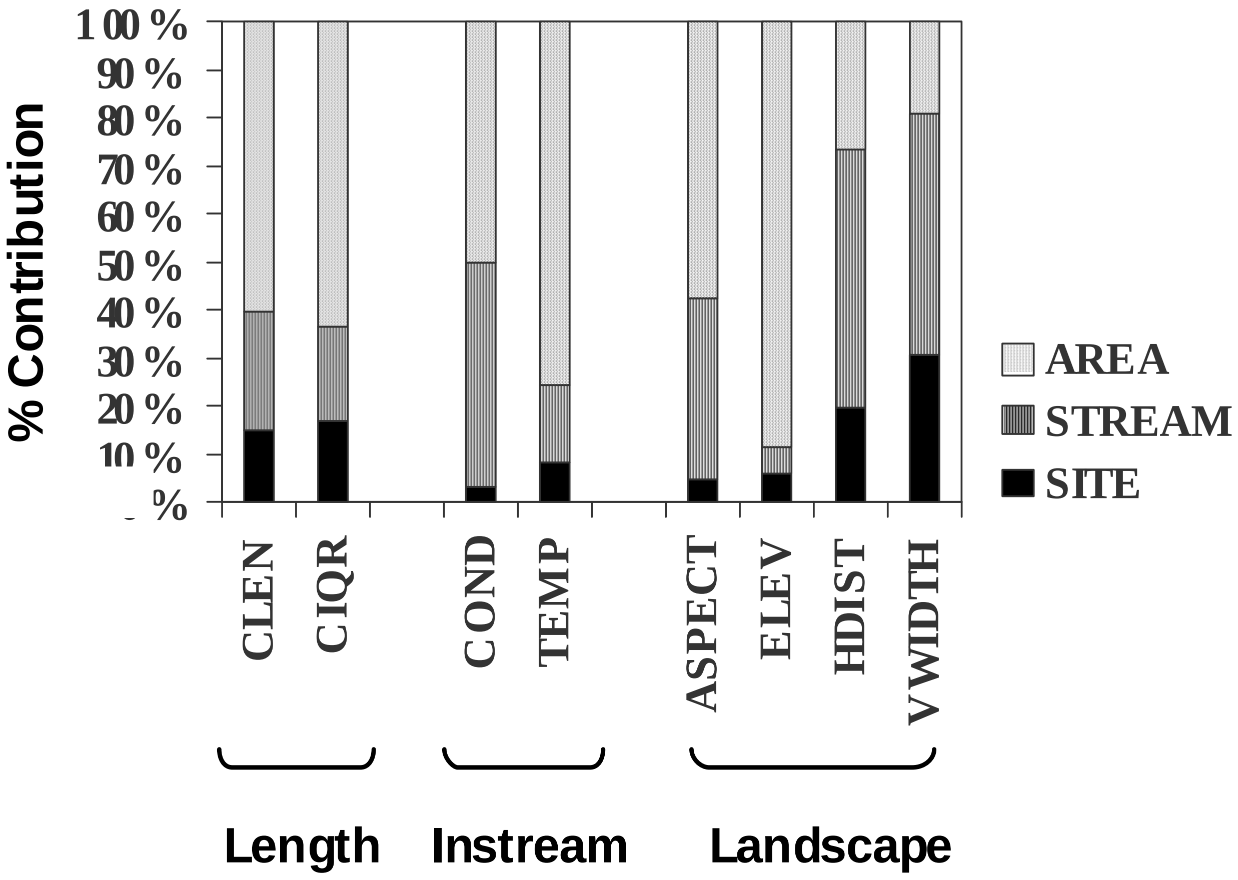


Figure 2.5. Distribution of variation in corrected total length (CLen) and corrected interquartile range (CIQR) of total length of westslope cutthroat trout, instream productivity variables, and landscape variables in the Coeur d' Alene River drainage, 2000-2001. Cond = conductivity, temp = temperature, elev = elevation, hdist = headwater distance, vwidth = valley width.

Table 2.1. Streams and regression coefficients used in calculating mean length and interquartile range correction factors for 2000 and 2001.

			CLen			CIQR	
Stream, Site	**N**	**Slope (mm/day)**	**p**	**Adjusted r^2**	**Slope (mm/day)**	**p**	**Adjusted r^2**
2000							
Cedar Lower	3	0.4	0.10	0.95	-0.1	0.13	0.92
Cedar Middle	3	0.2	0.06	0.99	0.1	0.34	0.49
Cedar Upper	3	0.2	0.15	0.59	0.0	0.89	0.00
Halsey Lower	2	0.3			0.1		
Iron Lower	2	0.2	0.25	0.70	0.1		
Iron Middle	2	0.3			0.1		
Iron Upper	2	0.3			0.1		
Lonesome Lower	3	0.1	0.12	0.93	0.0	0.89	0.00
Lonesome Upper	3	0.1	0.03	0.99	0.0	0.67	0.00
Tom Lavin Upper	2	0.2			0.1		
Yellowdog Lower	2	0.5			0.1		
Yellowdog Middle	2	0.3			0.1		
Yellowdog Upper	2	0.3			0.0		
2000 Average		0.26			0.05		
2001							
Brown Lower	4	0.4	0.02	0.98	0.1	0.25	0.33
Cedar Lower	4	0.3	0.01	0.99	0.1	0.04	0.88
Cedar Upper	3	0.3	0.16	0.94	0.1	0.06	0.98
Coal Lower	3	0.4	0.03	1.00	0.1	0.08	0.97
Coal Middle	3	0.3	0.07	0.99	0.1	0.32	0.53
Iron Lower	3	0.4	0.01	1.00	0.1	0.15	0.89
Iron Upper	3	0.3	0.10	0.98	0.1	0.05	0.99
Lonesome Lower	4	0.2	0.02	0.97	0.1	0.09	0.73
Lonesome Upper	4	0.1	0.19	0.92	0.1	0.29	0.61
Tom Lavin Upper	3	0.2	0.21	0.90	0.1	0.13	0.92
Yellowdog Upper	2	0.4	0.18	0.97	0.3	0.12	0.93
2001 Average		0.29			0.12		

Table 2.2. Daily mean, maximum, and minimum water temperature (^{o}C) and standard deviation (SD) of shaded and sunny age 0 westslope cutthroat trout habitats and flowing water. N refers to number of HOBO temperature measurements averaged for sun and shade locations.

Location	**N**	**Mean (SD)**	**Minimum (SD)**	**Maximum (SD)**
Lonesome Creek				
Flow	1	12.8	9.4	17.4
Sun	3	12.89 (0.04)	9.93 (0.23)	16.30 (0.69)
Shade	3	12.84 (0.03)	9.67 (0.23)	16.93 (0.57)
Tom Lavin Creek				
Flow	1	9.6	8.7	10.6
Sun	3	9.49 (0.08)	8.62 (0.08)	10.47 (0.14)
Shade	3	9.53 (0.05)	8.64 (0.05)	10.57 (0.10)

Table 2.3. Summary statistics for corrected total length (CLen) and corrected interquartile range (CIQR) across site, stream, and area spatial scales.

Scale	**Section**	**Min (mm)**	**Max (mm)**	**Range (mm)**	**SD**	**N**
Site	CLen	26.3	49.1	22.8	5.13	48
Stream	CLen	26.8	44.1	17.3	4.16	19
Area	CLen	31.6	40.0	8.4	2.72	6
Site	CIQR	-0.2	15.1	14.9	3.16	48
Stream	CIQR	1.2	10.1	8.9	2.24	19
Area	CIQR	2.3	7.6	5.3	2.00	6

Table 2.4. Pearson correlation and (probability of occurrence) matrix for landscape variables.

	Elevation	**Headwater Distance**	**Valley Width**
Aspect	0.156 (0.29)	-0.167 (0.26)	0.075 (0.61)
Elevation		-0.436 (0.002)	-0.198 (0.18)
Headwater Distance			0.597 (0.0001)

Table 2.5. Regression model results for CLen at site, stream, and area scales, with instream (conductivity, temperature) and landscape variables (aspect, elevation, headwater distance, valley width). Significance level to enter and stay in model: $p < 0.10$.

Scale	Model Component	Slope	r^2	p	N
SITE	*INSTREAM*				
	Temperature	2.51	0.332	< 0.007	
	Conductivity	0.08	0.248	< 0.005	
	MODEL		0.581	< 0.0004	21
	LANDSCAPE				
	Elevation	0.25	0.243	< 0.0004	
	Aspect	-0.01	0.053	< 0.08	
	MODEL		0.296	< 0.0004	48
STREAM	*INSTREAM*				
	Temperature	1.83	0.305	<0.10	
	Conductivity	0.06	0.280	<0.07	
	MODEL		0.586	<0.05	10
	LANDSCAPE				
	Aspect	0.44	0.160	<0.09	
	Elevation	-0.02	0.158	<0.08	
	MODEL		0.317	<0.05	19
AREA	*INSTREAM*				
	Temperature/MODEL	1.61	0.687	<0.09	5
	LANDSCAPE				
	None able to enter model				6

Table 2.6. Regression model results for CIQR at site, stream, and area scales, with instream (conductivity, temperature) and landscape variables (aspect, elevation, headwater distance, valley width). Significance level to enter and stay in model: $p < 0.10$.

Scale	Model Component	Slope	r^2	p	N
SITE	*INSTREAM*				
	None able to enter model				21
	LANDSCAPE				
	Elevation/MODEL	-0.00	0.254	< 0.0003	48
STREAM	*INSTREAM*				
	Temperature/MODEL	0.98	0.335	<0.08	10
	LANDSCAPE				
	Elevation/MODEL	-0.01	0.352	<0.008	19
AREA	*INSTREAM*				
	None able to enter model				5
	LANDSCAPE				
	Elevation/MODEL	-0.02	0.768	<0.03	6

Table 2.7. Mean (SD) corrected total length (CLen) and corrected interquartile range (CIQR) differences of age 0 westslope cutthroat trout among sites, 2000-2001. L=lower sites, M=middle sites, U=upper sites.

Section	CLen difference (mm)	CIQR difference (mm)	N
L-M	2.67 (4.23)	0.64 (4.10)	15
M-U	2.94 (4.85)	2.57 (3.34)	13
L-U	5.23 (4.92)	2.78 (3.07)	14

APPENDIX 2.1

TEMPORAL DATA

Table 2.8. Total length (mm) and interquartile range (mm; in parentheses) for streams sampled multiple times during 2000 and used to produce corrected total length (CLen) and corrected interquartile range (CIQR) variables used in analyses.

Stream	Site	Collection Day of the Year			
		201-207	221-235	257-274	276-286
Cedar	Lower	33.2 (8.0)		58.2 (10.0)	63.5 (9.0)
Cedar	Middle	38.3 (11.0)		48.8 (17.3)	52.7 (15.5)
Cedar	Upper	33.8 (11.0)	44.1 (9.0)	52.6 (8.5)	49.6 (10.0)
Halsey	Lower		46.6 (6.5)		58.8 (11.3)
Iron	Lower		38.5 (7.0)	52.5 (8.0)	49.0 (9.3)
Iron	Middle		37.6 (7.0)		51.2 (10.0)
Iron	Upper		33.8 (2.0)		47.8 (7.0)
TomLavin	Upper		29.6 (2.0)	38.8 (4.0)	
Lonesome	Lower	38.6 (6.5)		47.7 (8.8)	49.5 (6.5)
Lonesome	Upper		41.5 (5.0)	44.8 (9.3)	46.8 (6.8)
Yellowdog	Lower		32.0 (4.0)	52.8 (8.0)	
Yellowdog	Middle		36.2 (6.5)	50.5 (10.8)	
Yellowdog	Upper		31.0 (3.0)	43.2 (4.0)	

Table 2.9. Total length (mm) and interquartile range (mm; in parentheses) for streams sampled multiple times during 2001 and used to produce corrected total length (CLen) and corrected interquartile range (CIQR) variables used in analyses.

Stream	**Site**	**Collection Day of the Year**				
		170-171	**197-201**	**218-228**	**260-264**	**286**
Brown	Lower		30.6 (3.5)	42.5 (9.8)	57.1 (9.8)	61.4 (9.5)
Cedar	Lower	27.7 (2.8)	38.8 (3.0)	46.0 (7.8)	55.8 (12.0)	
Cedar	Upper		27.3 (3.8)	39.4 (7.0)	45.7 (10.0)	
Coal	Lower		23.9 (2.0)	34.8 (6.0)	46.1 (9.0)	
Coal	Middle		24.3 (1.0)	31.0 (7.5)	42.4 (8.0)	
Iron	Lower		27.5 (3.0)	34.2 (5.0)	49.9 (7.0)	
Iron	Upper		25.1 (0.0)	28.2 (2.0)	44.8 (5.5)	
Lonesome	Lower	27.2 (2.0)	33.5 (5.3)	35.2 (4.0)	45.7 (12.5)	
Lonesome	Upper		31.4 (3.0)	37.2 (6.5)	40.7 (7.5)	
TomLavin	Upper			32.6 (4.0)	42.6 (6.3)	43.2 (6.8)
Yellowdog	Upper		22.1 (0.0)	28.6 (7.0)		

CHAPTER 3

HABITAT COMPLEXITY – LENGTH VARIATION RELATIONSHIPS IN AGE 0 WESTSLOPE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI LEWISI*)

ABSTRACT

Phenotypic variation plays a critical part in many evolutionarily and ecologically essential functions, including adaptation to local conditions and disturbance regimes, speciation, and reduction in intra- and interspecific competition. Organism size influences many ecological processes, including competition, predation, habitat selection, and reproductive success. However, no one size may be most successful: size variation allows for niche differentiation and therefore reduction in competition, and can stabilize population abundance in variable environments. Habitat complexity may support or generate size variation by providing diverse habitats for diverse organism sizes. Organism-habitat relationships may be scale dependent; scale must therefore be considered in habitat studies. I examined relationships between body size and habitat complexity in age 0 westslope cutthroat trout in the Coeur d' Alene River subbasin of northern Idaho at stream, reach, and habitat unit scales. At the stream scale, I found that habitat units in narrow valleys were more likely to be generated by boulder rather than woody debris or scour processes, dominated by larger substrates, smaller, shallower and more variable in depth, and less likely to contain sculpins (*Cottus* sp.) or have access to terrestrial predators than those in wide valleys. Habitat unit types were less diverse in narrow valleys. Habitat differences were not associated with differences in age 0 size structure; habitat unit age 0 density was significantly higher in narrow valley streams. At the reach scale, habitat units containing large fish were larger and deeper, had greater aquatic and terrestrial predator access and were more diverse than habitat units containing small individuals. Large and small individuals used different types of habitat. At the unit scale, I did not find consistent relationships between habitat characteristics or fish density and fish size diversity. The link between size diversity and habitat complexity at the reach scale and ontogenetic changes in

habitat suggest that maintenance of population abundance, productivity, and diversity may depend on the availability of diverse habitats at this scale. Although diverse habitats supporting a variety of sizes are available in both wide and narrow streams, processes responsible for producing that habitat diversity appear to vary. Management at the stream scale may therefore be necessary to conserve important habitat generating processes. Understanding processes linking intraspecific diversity and its habitat template across scales will likely be important to the conservation of intraspecific diversity in inland salmonids such as westslope cutthroat trout.

INTRODUCTION

Phenotypic variation, the intraspecific variation in life history, morphology, and behavior, plays a critical role in many evolutionarily and ecologically essential functions, including adaptation to local conditions and disturbance regimes, speciation processes, and reduction in intra- and interspecific competition through niche differentiation (e.g. Nikol'skiy 1969; Utter 1981; Healey and Prince 1995; Skulason and Smith 1995). Phenotypic diversification mechanisms include genetic and environmental processes and the interaction between them (Berven and Gill 1983). Environmental diversification includes local adaptation, the evolution of genetic and phenotypic characteristics that allow an organism to better match its environment and increase fitness (Templeton 1994). Plasticity allows for phenotypic variation in specific characteristics that are not genetically controlled, such that an organism is able to succeed in a variety of environments or in a temporally variable environment (Stearns 1989; Scheiner 1993). Understanding connections between biodiversity and habitat complexity and the spatial scales at which critical habitat features occur contribute to our understanding of species dynamics and ecological processes connecting an organism to its environment, as well as our ability to manage and conserve threatened species and functional habitats.

Organism size has been recognized as an important phenotypic characteristic mediating ecological processes such as metabolism, growth, production rate, and reproductive condition and commitments (Policansky 1983; Stein et al. 1987). In many cases, big may be better, offering juveniles an advantage in intra- and interspecific competitive and predation relationships and likelihood of survival (e.g. Hunt 1969; Abbott et al. 1985; Holtby 1988; Elliott 1989; Elliott 1990; Mikheev et al. 1994; Smith and Griffith 1994; Quinn and Peterson 1996) and as reviewed by Reznick (1981) and Werner and Gilliam (1984). However, in some cases smaller may be better since larger individuals may be preferred prey (Power 1987; Harvey 1991; Litvak and Leggett 1992) and smaller individuals may better withstand some environmental stresses (Connolly and Petersen 2003). In other situations, there may be no one best size. Niche separation through size or other diversification is a well-accepted paradigm of competition theory (e.g. Skulason and Smith 1995; Landry et al. 1999) and size-based or ontogenetic niche shifts are well-documented (Werner and Gilliam 1984; Mittelbach and Chesson 1987; Erkinaro et al. 1997; Ruzycki and Wurtsbaugh 1999). Size variation may maintain recruitment stability and abundance and therefore long-term population survival in a variable environment (den Boer 1968; Lomnicki 1980).

Ecological processes that affect size variation and distribution in a population include size-selective mortality, organism mobility, and habitat characteristics affecting growth and survival (e.g. Rieman and Myers 1992; Mullen and Burton 1995; Sogard 1997; Kahler 1999; Knight et al. 1999; Einum and Fleming 2000). Habitat selection by age 0 salmonids is driven by the need to maximize net energy intake, competition for food and space, and risk of predation (Mason and Chapman 1965; Chapman 1966; Fausch 1984; Power 1987; Harvey 1991; Fausch 1993). Numerous habitat characteristics affect one or more of these primary factors. Focal velocity, presence of and distance from cover, and depth may be the more important factors controlling size-related habitat use (Chapman 1966; Everest and Chapman 1972; Griffith 1972; Nielsen 1992). Other factors that have been linked to size structure of age 0 salmonids include substrate and territory size (Moore and Gregory 1988b; Grant and Kramer 1990). In addition, biotic factors such as density, competition (Chapman 1966), and predation may influence size structure and habitat use (Litvak and Leggett 1992; Rice et al. 1993; Claessen et al. 2002). The habitat complexity relationship with age 0 salmonid size structure is reviewed in greater detail in Appendix 3.1.

Local size variation depends on the generation and spatial distribution of differently-sized individuals. Complex habitats may provide more niches and therefore support more biodiversity than simpler habitats (Klopfer and Mac Arthur 1960; Schoener 1974) and as reviewed by Downes et al. (1998) and Bell et al. (1991). “Habitat complexity” incorporates concepts of habitat diversity as well as degree of interaction between component parts (Bisson et al. 1981). Distribution of size variation is dependent on the spatial distribution of habitat diversity as well as organism mobility. When probabilities of predation, displacement or physical damage (e.g. from high water velocity), and competitive displacement are low relative to benefits gained by moving, individuals may move to higher quality habitat or as their needs change with size or age (e.g. Luecke 1986; Kahler 1999; Ruzycki and Wurtsbaugh 1999). Size-mediated habitat selection, including ontogenetic niche shifts, have been well-documented (Werner and Gilliam 1984). Salmonids may follow the ideal-despotic distribution theory of Fretwell (1972), a modification of the ideal free distribution (Fretwell and Lucas 1970) which describes organisms as “ideal” in their knowledge of resource distribution with equally “free” access to those resources, such that organism distribution will exactly match resource density. The ideal-despotic distribution theory applies to organisms that are ideal in their knowledge of resource distribution, but not free;

access is despotic, i.e. controlled by territorial behaviors such that competitively dominant individuals occupy the most desirable positions. Size variation may mediate habitat selection of age 0 salmonids in response to both intra- and inter-cohort size distributions.

Aquatic processes and biotic diversity occur across multiple spatial scales in response to environmental gradients at different scales (Morris 1987; O'Neill et al. 1988; Carlile et al. 1989; Milne 1991; Taylor 1991; Healey and Prince 1995; Rabeni and Sowa 1996; Cooper et al. 1998). Habitat complexity available to a specific group of individuals may be distributed within or among habitat units. Organism movements such as migration, straying, invertebrate drift, and ontogenetic niche shifts that may be local- or broad-scale are one method of interconnection and movement of organisms and materials among and within scales (Schlosser 1991; Fausch et al. 2002). Moore and Gregory (1988b) identified four lateral stream habitat types with characteristics required by age 0 cutthroat trout, isolated pools, stream margins, side channels, and backwaters. Differences among unit types such as these or the relative distribution of unit types among reaches or streams may affect size variation within a reach as well as within a habitat unit. Many organisms operate at multiple scales to fulfill their full life history (Labbe and Fausch 2000). Because habitat characteristics occur at different scales and habitat use is size-mediated, size-dependent ecological processes therefore are likely to occur across multiple scales as well.

One broad scale landscape feature likely to have significant effects on age 0 population characteristics is landform. Valley constraint affects the physical, hydrological, and biological characteristics of a stream. Wide valley unconstrained reaches are “response segments,” experiencing significant morphological response to changes in sediment supply from upstream whereas narrow valley constrained reaches are “transport segments” that are morphologically resilient, rapidly conveying sediment to downstream reaches (Montgomery and Buffington 1997). Wide valley floors therefore tend to reflect fluvial processes whereas narrow, high gradient streams reflect both fluvial processes and landforms external to the channel such as landslides and bedrock outcrops (Grant and Swanson 1995). Wide valley channels are more likely to have secondary channels and to contain higher volumes of large woody debris (Grant and Swanson 1995; Rot et al. 2000). Lamberti et al. (1989) found wide valley reaches retained leaves and dissolved nutrients longer, and that stream characteristics such as heterogeneity in stream hydraulics, geomorphic complexity, woody debris, and lateral habitats contributed to organic material retention. Wide valley reaches had two to three times more channel units, higher discharge, and off channel habitats that provided a higher diversity of fish habitats and refuge during high water (Gregory et al.

1989). Age 0 cutthroat trout abundance and density have been found to be greater in wide valley than narrow valley reaches, and abundance has been linked to habitat structure characteristics such as riparian canopy and channel morphology (Moore and Gregory 1988b; Gregory et al. 1989; Lentz 1998).

Size variation can be generated at multiple scales and by multiple processes. My study goal was to explore relationships between size variation in age 0 westslope cutthroat trout and habitat complexity across multiple scales. My hypotheses were: 1) habitat use by age 0 westslope cutthroat trout is size-mediated, 2) more diverse habitats therefore support greater size variation, and 3) habitat fish size relationships vary across spatial scales since they are dependent on habitat characteristics that are scale-dependent. I incorporated three spatial scales: stream, reach, and habitat unit, using different and complementary approaches per scale. At the stream scale, I compared habitat diversity and age 0 size variation among streams differing in valley width. If streams differing in valley width also differ in age 0 habitat and habitat diversity, and habitat use is size-mediated, then age 0 size variation would be expected to vary at the stream scale. At the reach scale, I compared habitat characteristics of habitat units occupied by large, medium, and small fish. If fish of different sizes use different habitats, reaches with more diverse habitats would therefore support greater size variation. At the habitat unit scale, I compared habitat unit characteristics of units occupied by homogeneously- and heterogeneously-sized groups of fish. Size-selective habitat use would suggest that more diverse habitat units would support greater size variation. At each scale, I identified and compared habitat characteristics expected to differ among fish differing in size based on size-dependent habitat needs related to predation risk, space, and energy conservation (see Appendix 3.1 for a review of age 0 habitat use). Comparing the relative presence and strength of habitat size relationships among scales should indicate the scales of greatest importance to habitat diversity size variation relationships.

STUDY AREA

The study was conducted in the Coeur d’ Alene (CDA) River basin of northern Idaho, U.S.A. (Figure 3.1), a region of low mountains vegetated by coniferous forest dominated primarily by Douglas-fir (*Pseudotsuga menziesiii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*; Bailey 1995). Elevation ranged from 600 to 1850 m. Climate includes severe winters of heavy snowfall, rain-on-snow events, and rainfall of 0.5-1.0 m (20-40 in)yr^{-1}. Geology is dominated by Precambrian Belt sedimentary rock likely containing basalt sills and granite sheets (Alt and Hyndman 1989). The majority of the basin is owned by the federal government and managed by the U.S. Department of Agriculture Forest Service. Logging and mining in the basin began in the mid-1800s (Maclay 1940) and logging and recreation are predominant land uses today.

Fish fauna of study streams include native westslope cutthroat trout, torrent sculpin (*Cottus rhotheus*), shorthead sculpin (*Cottus confusus*), and non-native rainbow trout (*Oncorhynchus mykiss*). Bull trout (*Salvelinus confluentus*) are native to the system but are believed to be extirpated. Westslope cutthroat trout abundance has been depressed in some streams in the study area due to historic overharvest and habitat degradation (Dunnigan 1997); N. Horner, ID Department of Fish and Game, personal communication). Study streams are second- or third-order, moderate-gradient (2-5%), typically gravel or cobble substrate with relatively low embeddedness, and high water quality. I chose streams representative of narrow and wide valley conditions that had moderate to high westslope cutthroat trout abundance, and avoided streams that were difficult to access or had unusual levels of human disturbance.

METHODS

Three wide valley and three narrow valley reaches in six streams were selected for study (Figure 3.1). However, during the study I found that the valley floor of one “wide valley” stream, Halsey Creek, contains an unusual bench in the study reach that prevents channel movement across most of the valley in this area. For this reason, it was excluded from all valley width analyses. For four of six streams, the selected reach used was the section immediately above the confluence with its receiving stream. For the other two sites, reaches were selected higher in the watershed. In all cases reaches were selected such that watershed area above the study reach was similar in drainage area among the six streams. Primary selection criteria were 1) narrow or wide valley, 2) relatively high population abundance, 3) limited impacts of timber harvest, road construction, and other anthropogenic influences, 4) easy access, 5) similar in temperature and productivity regimes (see Chapter 2).

To characterize differences between streams and valleys, valley floor width was paced, active channel width, wetted width, and maximum depth were measured, side channels were counted, and side channel wetted width and maximum depth were measured along five transects per reach. The valley floor width index of Grant and Swanson (1995), calculated as the ratio of the width of the valley floor (at 3 m above the low flow water surface) to the active channel width was used to characterize channel width.

Fish collection

Within a study reach, all potential age 0 habitats were sampled using a backpack electrofisher, beginning at the lower end and proceeding upstream. Age 0 habitat was based on (Lentz 1998), who found age 0 trout to be limited to habitats defined by a narrow depth zone, gravel, cobble, or larger substrates, and slow velocity areas typically located in lateral areas along stream margins. When an age 0 individual was located either visually or by electrofishing, habitat unit boundaries were determined, defined as the water's edge along the shoreline, emergent rocky or woody substrate, or a line of water velocity against which age 0 fish would be unable to maintain position and would therefore be displaced downstream from the unit. Within the habitat unit, all westslope cutthroat trout were collected and lengths were recorded, and habitat characteristics were measured or recorded as described below. I attempted to collect all cutthroat trout seen, whether they were in an age 0 habitat unit or not, to define the size structure of the population and the upper limit of age 0 length. Forty habitat units in 2000 and 30 habitat units in 2001 were sampled per stream.

Reach length required to locate the requisite number of habitat units was paced and stream scale age 0 cutthroat trout density was calculated from the total number of age 0 fish captured and reach length.

Habitat characterization

For each habitat unit, habitat characteristics expected to differ by age 0 size, based on the existing literature (see Appendix 3.1) were recorded (Table 3.1). Two individuals classified each categorical variable independently and differences were negotiated until agreement was reached. Predator access was estimated separately for aquatic and terrestrial predators. Aquatic predator accessibility, for potential cutthroat trout and sculpin predators, was considered relative to presence of structural debris present and water depth in the habitat unit that would limit aquatic predator maneuverability, and access into the unit. Access was considered precluded if the majority of the unit contained cover, depth was insufficient for an aquatic predator to maneuver, or if access to the unit was blocked by depth or structure. Terrestrial predator accessibility was considered relative to presence of deep water or structural debris that would provide overhead cover. Canopy was considered open if the unit would receive full sun during most or all of the day, partial if it would receive full sun for half or less of the day, and closed if it would never receive sun (when leaves were present in the case of units shadowed by deciduous vegetation).

Habitats were categorized by type based on location within the channel (Figure 3.2); unit types likely differ in characteristics such as flow, substrate, size, and accessibility. Most types were classified and described prior to fieldwork based on an elaboration of the types described by Moore and Gregory (1988b). Additional types were recognized in the field and added to the potential list as they were identified during data collection. Habitat units are typically areas sheltered from the main flow. Unit source, or the hydrologic characteristic responsible for creating the sheltered unit, was categorized as due to bedrock/boulder, large woody debris, or scour, where scour referred to an underwater obstruction formed by the shape of the streambed such that an eddy of slow water was created downstream. If the unit was created by more than one source, the most important influence was recorded. Dominant substrate was the size of substrate composing the highest percentage of the unit habitat area. Overall habitat diversity of each habitat unit was described as diverse or uniform based on the variation in depth, water velocity, and cover present in the unit. Sculpins were considered potential competitors since most sculpins observed in study streams were too small to prey on age 0 trout (Johnson et al. 1983). Presence or absence of sculpins was noted based on observations during electroshocking for trout and habitat unit characterization.

Habitat unit area was calculated for each unit from unit width and length measurements. Six depth measurements from randomly selected locations were taken for each unit and used to calculate the mean and coefficient of variation of depth. I hypothesized that coefficient of variation of depth would relate to age 0 size diversity at the unit (within unit) scale and mean depth would reflect habitat availability for larger fish at the reach (among units) scale.

Age 0 density was calculated from the number of fish per unit and unit area and included as a habitat variable in unit and reach analyses since it may mediate habitat use.

Analyses

The upper length limit of age 0 individuals was determined from length frequency histograms within stream and year, with confirmation by otolith analyses (Chapter 2). Age 0 fish were classified across years as small (<33 mm), medium (33-48 mm), or large (>48 mm) by examining the length frequency histogram for all individuals and selecting break points that divided fish into roughly equal size ranges and sample sizes. Individuals were classified across rather than within collection years since my focus was size-selective habitat use rather than inter-annual differences in habitat use. Because sampling occurred later in the year during 2000 than 2001, most fish collected in 2000 were classified as medium or large whereas during 2001 most individuals were classified as small or medium. Therefore, analyses were not always able to distinguish between differences due to year and fish size. In some cases, I analyzed medium-sized fish only to examine variable differences due to year of sampling, since medium-sized fish were collected during both years and could be used to test for differences due to year.

For each spatial scale, age 0 size habitat relationships were examined for each habitat variable individually and in a combined CART analysis (see below). Continuous variables were analyzed using the general linear model for analysis of variance (ANOVA) in SAS (SAS Institute, Inc., Release 6.12 TS060, Copyright 1989-96). When sample size was sufficient, year of sampling, stream identity, and interaction terms were included as covariates. Categorical variables were analyzed in one-way chi square goodness-of-fit tests by treating one member of the contrasting pair (stream scale: wide versus narrow; reach scale: large versus small fish; unit scale: heterogeneous versus homogeneous units) as observed frequencies and the other member as expected frequencies. Although researchers disagree on definition and treatment of low cell counts in chi-square tests, most agree that chi square statistics are inflated for cell counts of five or lower (Ott 1984 and references therein). When low cell counts were encountered, categories were combined when possible. When combining categories was not possible and cell counts were five or less for 20% or more of cells, I applied Yates' continuity correction (Garson 2003). A significance level of $p<0.10$ was used in all comparisons.

Analyses were conducted separately and differed among scales. At the stream scale, I tested for differences in habitat and age 0 size characteristics between reaches in wide and narrow valleys by pooling habitat unit data within each reach. Drawing inferences at this scale regarding relationships between habitat and size variation would require finding significant differences in habitat characteristics and correlated fish size or size variation between wide and narrow valley streams. Habitat units in Halsey Creek were excluded from stream-scale analyses as explained earlier. At the reach scale I contrasted habitat use by large, medium, and small fish by comparing habitat differences among habitat units. Only units containing a single size category were used in analyses. Demonstration of size-mediated habitat use and differences in habitat characteristics among units would suggest relationships between habitat and size variation at this scale. At the unit scale I contrasted habitats occupied by homogeneously- and heterogeneously-sized fish to test whether habitat characteristics within habitat units differed between those occupied by homogenous and heterogeneous sizes of fish. Only habitat units occupied by more than one age 0 individual were used in analyses. “Homogenous” units contained individuals of only one size category whereas “heterogeneous” units contained individuals of more than one size category. Inferences regarding habitat size variation relationships at this scale would be direct since significant test results would indicate differences in habitat associated with age 0 size variation.

CART is a recursive partitioning approach conceptually similar to logistic stepwise regression that can be used with mixed data types including classification data (Turner in review). Because CART analysis is nonparametric, it works well when predictive variables are nonadditive (as in the case of substitutable resources), interactions are not simply multiplicative, and relationships are multivariate or nonlinear (Urban 2002). It also works well for applications where broad patterns and multiple potential outcomes are sought in complex or “noisy” data, for example in predicting species occurrences or explaining habitat use differences among organisms (Vayssieres et al. 2000). The disadvantage of the CART approach is that since it is by nature exploratory, it is not designed for hypothesis testing and results must be confirmed by more traditional approaches (Rieman et al. 1997). I used CART to build predictive models relating habitat characteristics and fish size at the stream, reach, and unit scales, respectively: 1) valley width (narrow versus wide), 2) fish size (large versus small), and 3) habitat unit fish size composition (heterogeneous versus homogeneous). I also used CART to characterize habitat unit type (seven types). All classification and regression tree analyses were conducted using the program CART, version 5.0.9.148 (Salford Systems).

In some analyses, low frequency of occurrence for some dominant substrate categories necessitated combining categories; sand, silt, and organic material were combined into one category of substrates associated with low water velocity and bedrock, boulder, and claypan were combined into one category of substrates associated with high water velocity.

RESULTS

Stream Scale

Streams with wide valleys tended to have lower channel slopes and higher sinuosity (Table 3.2). Narrow valleys tended to be lower in elevation, have slightly higher conductivities, and wider wetted channel widths. I did not find any differences in maximum depth, number of side channels, or age 0 density (number fish/linear meter).

Size characteristics of age 0 fish differed between narrow and wide valleys, but differences were not consistent across sampling years (Table 3.3; additional detail given in Appendix 3.2, Table 3.8). Mean fish length did not vary between wide and narrow valleys streams. Coefficient of variation in length was significantly higher in narrow valley units when pooled over the 2 years of sampling; however, the direction of differences in length variation was reversed between years. Number of age 0 fish per habitat unit was significantly higher in wide valley habitat units in 2001 but there was no difference in 2000. Age 0 habitat unit density was significantly higher in narrow valley habitat units during both years. Only the model for age 0 length, in which year was significant but valley width was not, explained a significant amount of variation ($p<0.10$) in the dependent variable (Table 3.3).

Habitat unit depth and area differed between valley widths and among streams (Table 3.3; additional detail given in Appendix 3.2, Tables 3.8, 3.9). Habitat units in wide valleys tended to be larger and deeper than habitat units in narrow valleys. Although the interaction term between valley width and year of sampling was significant for unit area and mean depth, interactions were due to differences in magnitude and were consistent in direction in these relationships.

Habitat unit source, type, dominant substrate, sculpin presence, and terrestrial and aquatic predator access differed significantly between narrow and wide valleys (Figure 3.3 a-e; see Appendix 3.2, Tables 3.9, 3.10 for additional data detail). Units in narrow valleys were more likely to be generated by boulders and to have larger substrates, restricted access to aquatic predators, and the partially-isolated pool habitat unit type. Wide valley streams were more likely to have diverse within-unit habitat, lateral habitat, slow-water riffle, and channel-wide pool habitat unit types to contain sculpins, and to be restricted to terrestrial predators.

CART analysis results were generally consistent with ANOVA and chi-square test results for individual habitat variables. Unit source was the most definitive at explaining differences between narrow and wide valleys (r^2=0.651). When source was removed from the model, several other habitat variables contributed to discrimination of units in wide and narrow valleys, including dominant substrate, mean depth, sculpin presence, unit type, and unit area. However, without inclusion of unit source, the coefficient of determination analog decreased to 0.393. Because unit type was difficult to interpret in a CART analysis, I conducted an analysis with it excluded from the model. The coefficient of determination analog was slightly lower without unit type (r^2=0.379), but the tree remained difficult to interpret (Figure 3.4). Units with characteristics that were relatively unique to wide streams were unusually deep or dominated by small substrates, whereas units with characteristics that were relatively unique to narrow valley streams were dominated by boulders, shallow without sculpins, or located in side-channels.

Reach Scale

Habitat units occupied by larger fish tended to be larger and deeper and tended to have more fish per unit but lower age 0 density (Table 3.4). Dominant substrate, aquatic predator access, terrestrial predator access, and unit type differed significantly between habitat units occupied by large and small fish (Figure 3.5; see Appendix 3.2, Table 3.12 for additional data detail), with units occupied by small fish were more likely to be pea gravel and less likely to be fine substrates or boulder, less likely to have full aquatic or terrestrial predator access, more likely to have partial aquatic predator access, more likely to have diverse within-unit habitat, and more likely to be partially isolated pool or slow-water riffle pool types and less likely to be lateral habitat or channel-wide pool types.

CART analyses for 2000 identified unit area, mean depth, dominant substrate, and age 0 density as meaningful habitat variables (r^2= 0.288). Large fish were more likely to be associated with larger, deeper units, pea gravel or cobble substrate and greater age 0 density. CART did not identify habitat variables that differed between units occupied by small and medium-sized fish during 2001 (r^2=0.069). An analysis of large (2000) versus small (2001) fish was difficult to interpret but identified differences in aquatic and terrestrial predator access and unit area (Figure 3.6; r^2=0.635), with small fish most likely to be in habitat units with partial terrestrial and aquatic predator access. Larger fish were not associated with particular predator access or unit area characteristics. A combined analysis contrasting habitat characteristics of large (2000), medium (2000, 2001 combined), and small (2001) fish identified terrestrial and aquatic predator access as significant variables (r^2=0.308). Large fish were more apt to be in units with no terrestrial predator access and no or full aquatic predator access whereas small fish were most apt to be in units with limited or full terrestrial predator access and partial aquatic predator access. Removal of these variables shifted habitat emphasis to unit area and mean depth (r^2=0.234) with larger fish more likely to be in deeper and larger habitat units and small fish more likely to be in shallower smaller habitat units.

Habitat Unit Type

Most habitat unit types had limited terrestrial predator access and partial canopy closure, were dominated by cobble substrates, and contained sculpins and did not differ greatly in coefficient of variation in depth or age 0 fish length; other characteristics varied somewhat among unit types (Table 3.5). The most frequently occupied unit types were lateral habitat, partially isolated pool, and slow-water riffle. Fish size characteristics varied among habitat unit types as well (Tables 3.5, 3.6), with slow-water riffles containing significantly smaller fish than average, channel-wide pools containing more fish per unit but lower age 0 density, isolated pools containing fewer fish than average per unit, and fast-water riffles with higher than average age 0 density. Larger individuals were most likely to be found in deeper unit types, large pool margin, fast water riffle, channel-wide pool, and lateral habitat and smaller individuals more likely to be found in the shallower unit types, partially isolated pool and slow-water riffle (Table 3.6).

Although habitat variables included in the CART model explained a meaningful amount of total variation among unit types (r^2=0.421), CART was not effective at differentiating among unit types since considerable overlap existed in most habitat characteristics and several unit types. The two most common habitat types, lateral habitat and partially isolated pool, were highly varied in their habitat characteristics. CART successfully characterized several of the less common types that had unusual characteristics, as identified above, including channel-wide pools with considerably larger than average area and isolated pools with no aquatic predator access.

Age 0 fish density differed among habitat unit types. Channel wide pools had lower than average age 0 density and fast water riffles had considerably higher that average age 0 density (Table 3.5).

Unit Scale

I did not identify strong relationships between any habitat variables and age 0 size mixture (heterogeneous versus homogeneous). Unit area was significantly different but the relationship was inconsistent across years with units containing homogenous groups larger in 2000 and smaller in 2001 (Table 3.7). No categorical habitat variables were significantly different between units occupied by homogeneously- and heterogeneously-sized fish mixtures (see Appendix 3.2, Tables 3.16, 3.17 for additional data detail).

CART analyses of habitat differences between units containing heterogeneously versus homogeneously sized individuals was confounded by the size-based habitat differences identified earlier. An analysis containing all fish sizes and combinations categorized separately (homogeneous units: large, medium, or small and heterogeneous units: all sizes, small plus medium) identified several variables including unit area, age 0 density, mean depth, unit habitat diversity, and coefficient of variation in depth as important in distinguishing between units occupied by heterogeneous and homogeneous fish mixtures; however, the correlation coefficient analog was relatively low for this model (r^2=0.245) and the classification tree was difficult to interpret (Figure 3.7). Analyses of habitat differences due to fish mixture separated by size identified only unit area as a significant variable for small- and medium sized-fish, with heterogeneous mixtures more likely to be in units with larger area (r^2=0.345). However, heterogeneous mixtures were also more likely to contain more fish (Appendix 3.2, Table 3.16), suggesting that fish density may be confounding the relationship between fish mixture and unit area. For medium- and large-sized fish, CART analysis identified only age 0 density as a significant variable with homogenous mixtures more likely to be in units with lower fish density.

DISCUSSION

My results support a scale dependent relationship between habitat and age 0 size variation. I found strong relationships between habitat characteristics and age 0 size at the reach scale but not at other scales included in the study. My results support all three of my hypotheses, that habitat use is size-mediated, age 0 size variation is associated with habitat diversity, and habitat size variation relationships are scale-dependent. Findings at the stream and unit scales may provide additional information regarding processes generating size variation at the reach scale.

I found habitat use by large and small age 0 fish differed, consistent with the findings of Grant and Kramer (1990) and Moore and Gregory (1988b), that age 0 salmonids shift habitats ontogenetically. Larger individuals defend larger territories, require greater water flow for food delivery, and are more able to tolerate faster flows (Mason and Chapman 1965; Huntingford and de Leaniz 1997; Lentz 1998). I found that large and small individuals tended to occupy different unit types, with larger fish more likely to be in the channel-wide pools and lateral habitats. Channel-wide pools are unusually large and deep, containing more fish than average but at a lower than average density. This type may be occupied primarily by larger fish since it offers considerable access to aquatic predators and was often occupied by older age classes of westslope cutthroat trout. Lateral habitats and partially isolated pools are relatively similar, but lateral habitats tend to be deeper and higher velocity, with greater access to aquatic predators, making them less desirable for smaller individuals. Partially isolated pool units tended to have a high coefficient of variation of depth, providing depth habitat for a variety of age 0 sizes, but also tend to have slower flows than lateral habitats and may therefore be less desirable for larger individuals with greater energetic demands (Mason and Chapman 1965; L'Abee-Lund et al. 1993; Bardonnet and Heland 1994; Huntingford and de Leaniz 1997). Slow-water riffles are slow and relatively shallow. Larger age 0 fish may be more at risk to terrestrial predators such as dippers (*Cinclus mexicanus)* and herons (*Ardea* sp.; Harvey and Stewart 1991) and therefore may avoid shallower units offering limited cover from terrestrial predators, and may also find food delivery rates to be inadequate in slow-water riffles.

Predation risk may be one factor driving size-mediated distribution of age 0 cutthroat trout, consistent with the findings of Power (1987) and Harvey and Stewart (1991), that small age 0 trout were more vulnerable to aquatic predators and larger age 0 individuals were more vulnerable to terrestrial predators. At the reach scale, I found small fish less likely to occupy deeper habitat units with greater aquatic predator access and larger individuals more likely to be in deeper units where depth may have provided cover from terrestrial predators. Size-dependent distribution of age 0 trout among unit types may also support a link to predation risk since I observed a strong relationship between fish size and unit type mean depth. Because units in narrow valley streams tended to be smaller and shallower than in wide valley streams, cover and substrate sources of refuge from terrestrial predators may be important in narrow valley streams.

My findings confirm a relationship between habitat diversity and size variation and suggest that important age 0 habitat diversity occurs among rather than within habitat units. I did not find habitat differences at the unit scale between units occupied by homogeneous and heterogeneous groups of age 0 individuals, suggesting that ontogenetic niche shifts may be accommodated primarily through movement among habitat units. Initial habitat selection by age 0 salmonids is apparently random with respect to habitat quality; early emergents establish territories quickly in the first acceptable habitat they encounter rather than selecting for higher quality habitats (Huntingford and de Leaniz 1997). Most units in my study apparently accommodated a limited range of sizes, and larger fish moved when habitat was no longer adequate. At the unit scale, larger more diverse units may have supported more individuals at higher density, consistent with Chandler and Bjornn (1988), who found in a laboratory study that age 0 salmonids occurred at higher densities in heterogeneous size mixtures than in homogenous size mixtures. Niche-packing theory suggests that when resources are limited, one would expect efficient “packing” of habitat units with mixtures containing larger fish in larger deeper units than homogeneously smaller groups (Klopfer and Mac Arthur 1960; Grant and Kramer 1990). When resources are not limiting, competitive interactions become less important and habitats are used less efficiently (Lonzarich and Quinn 1995). I found within-unit density to be greater in units occupied by heterogeneous groups of medium- and large-sized individuals than in homogeneously-sized individuals. However, I did not find a consistent relationship between density and group composition, consistent with the expectation that this phenomenon should be more likely at relatively high densities, and thus relatively limited at the densities I observed.

As age 0 resource needs increase with size, some habitat units may no longer be adequate, consistent with the self-thinning model of salmonid distribution that suggests that individuals must control more resources and therefore larger areas as they grow to meet their increasing resource needs (Grant and Kramer 1990; Grant 1993). Smaller fish may require smaller territories and may therefore occupy smaller habitat units or occur at higher densities in any units. I found density to be significantly higher in units containing small fish than in units containing large fish. The willingness of age 0 salmonids to move among habitat units and in response to limited food supply has been well-documented, e.g. by (Wilzbach 1985; L'Abee-Lund et al. 1993; Kahler 1999). Although Fretwell (1972) suggests that salmonids most closely follow the predictions of the ideal-despotic theory distribution, that individuals have perfect knowledge of resource distribution but competitively dominant individuals control the best resources, my results suggest that in relatively low density reaches, size-based differences age 0 resource use and availability of empty habitat units may reduce the role of intraspecific competition (despotic influence) in habitat selection within units. Age 0 salmonids still may be neither ideal in their ability to detect patterns in resource distribution, nor free since other factors such as perception of predation risk as discussed above may affect their distribution relative to available resources. Age 0 salmonid distribution may be function of size-mediated habitat use with habitat variation distributed primarily among rather than within habitat units where movement among units is mediated by the relative inadequacy of the current unit and risk associated with movement among habitat units.

My finding of habitat differences at the stream scale between wide and narrow valleys may contribute to understanding of processes influencing size variation at finer scales. I did not find significant differences in age 0 size variation at the stream scale, suggesting that diverse habitats are available in both wide and narrow valley streams. However, I did find differences in channel gradient and sinuosity between streams in wide and narrow valleys as well as instream habitat differences in habitat unit type, depth, size, dominant substrate, terrestrial predator access, source, and presence of sculpins. Physical and hydrodynamic differences between wide and narrow valleys produce stream reaches with different characteristics, which in turn affect instream conditions including fish habitats (Moore and Gregory 1988b; Gregory et al. 1989; Lentz 1998). Stream-scale differences between landforms suggest that important habitat generating processes at this scale, responsible for the diversity of habitat units identified at the reach scale, differ between wide and narrow valleys. Relationships between patterns and causal mechanisms, and the scales at which they occur, are not well understood. In Chapter 2, I found that temperature and productivity, environmental gradients closely linked to growth, displayed the same scales of variation as age 0 size variation, in support of Horne and Schneider (1995), that biological variation and causal processes responsible for generating that variation occur at the same scales. However, this study may help to clarify relationships between causal processes, environmental gradients, and organism response, supporting Levin (1992), that broader spatial scales may confine ecological patterns, both physical and biological, at finer scales.

Habitat unit differences between wide and narrow valley streams follow from differences in channel characteristics, primarily gradient. Lower gradient valleys and stream channels characteristic of wider valleys are “response segments” that retain finer substrate materials. The greater role of large woody debris in generating age 0 habitats would be expected to be more important in these channels rather than large substrate materials such as boulders and rubble more important to the “transport segments” of narrower valleys (Montgomery and Buffington 1997; Rot et al. 2000). Smaller dominant substrate size and more frequent sculpin presence in wide valley streams may be associated with lower gradients and therefore lower water velocities. Smaller dominant substrates were more common in wide valley units than in narrow valley units and sculpins are able to inhabit lower water velocities characteristic of lower gradient streams since they are benthic rather than drift feeders (Daniels 1987). Habitat units were more diverse in type in wider channels, primarily because these channels had higher frequencies of the channel-wide pool and slow water riffle types. These two habitat types were characteristic of lower gradient, slower waters, such that age 0 individuals were able to utilize the entire channel.

Inclusion of CART analysis in the study allowed for evaluation of the relative importance of and relationships between categorical and continuous variables. Independent variables toward the top of a CART tree are most effective at explaining variation in the dependent variable (Urban 2002) and therefore are of greatest importance to the relationship of interest. When one habitat variable was significantly more effective at discriminating between dependent variable classes, removal of that variable allowed for identification of lesser but still potentially meaningful additional variables, as well as habitat variables serving overlapping ecological functions. CART was not effective at handling variables with more than two or three classes, such as habitat unit type (seven classes) and the unit scale size variation variable, each analysis failed to produce ecologically interpretable trees or explain significant variation. Because CART works best with large sample sizes (Vayssieres et al. 2000), sample sizes in some of my analyses may have been inadequate for successful resolution of dependent variables. CART may also have limited ability to discriminate when a large number of meaningful independent variables interact and overlap. Although CART is effective at identifying variables serving the same function (e.g. refuge from predators), no analytical method is capable of effectively relating independent variables when they serve multiple and potentially conflicting functions (e.g. refuge from predators, food delivery, and refuge from high flows). Based on my results, CART appears to be most effective at characterizing one class relative to all other potential classes. CART was generally consistent with chi-square and ANOVA analyses of individual variables in identifying those of greatest importance, supporting its use in studies of this kind and the validity of its results.

Although wide and narrow valley streams both support a range of age 0 fish sizes, they appear to do so through different mechanisms. I suggest that this has important implications for management at this scale. For example, wide valley streams appear to provide greater habitat variation through their interaction with the floodplain and the ability of age 0 individuals to use the entire channel in lower gradient reaches of these streams. These streams also appear to depend more on woody debris for generation of age 0 habitat units since bedrock and boulder substrates are generally not available to form low-velocity lateral habitats. Large woody debris (LWD) has been well-documented as a critical component of stream structure and function, contributing to channel stability, and habitat generation, and providing nutrients and substrates for aquatic invertebrates (e.g. Bisson et al. 1987). In wide valley streams, LWD appears to serve the critical function of creating low velocity lateral habitat for age 0 salmonids. In narrow valley streams, boulders serve this function, although LWD may contribute by creating lower gradient reaches, in which boulder substrates act to form particular habitat units. Because processes contributing to the generation of size variation at the reach scale appear to occur at the stream scale, maintenance of size variation in age 0 trout may require attention to processes at that larger scale. Examples of activities in wide valleys streams that may affect habitat and therefore age 0 size diversity would include riparian timber harvest such that instream recruitment of large woody debris is precluded, road construction resulting in channel confinement and separation of the channel from its floodplain, and channelization reducing sinuosity and increasing channel gradient. In addition, watershed activities increasing bedload could result in reduced water depth in all habitats as well as loss of deeper habitat types. In extreme cases, flow may become subsurface during dry periods or years, as I have seen in the Coeur d’ Alene and other subbasins in Idaho.

Continued efforts to understand processes responsible for generating and supporting intraspecific diversity in inland trout and ecological and evolutionary significance of that diversity will contribute to the conservation of these taxa (Healey and Prince 1995). This study identified several habitat characteristics correlated with size diversity primarily at the reach scale, suggesting that habitat complexity at this scale may have a role in generating and maintaining size variation. Exploration of habitat complexity at larger spatial scales, including the role of disturbance processes, identification of primary gradients (e.g. productivity; see Chapter 2), and ultimately the habitat mosaic of conditions across scales (Thompson et al. 2001) will also be important. I emphasize the need for greater consideration of complexity and its components in conservation approaches to inland salmonids. An approach to stream conservation that incorporates important concepts of spatial scale, patch structure, individual variation, organism/habitat interaction, and identification of variation-generating processes will contribute to better understanding of the evolutionary and ecological processes that must be conserved concomitant with species conservation. Our understanding of organism habitat relationships, expanded to include these concepts, will enable us to evaluate organism response and ability to adapt to stress, whether adaptation is predictable in a changing environment, and how diversity affects system resilience (Michener et al. 2001). A biocomplexity approach may also contribute to the maintenance of diversity and connectivity as these systems are affected by global climate change and other novel anthropogenic sources of disturbance.

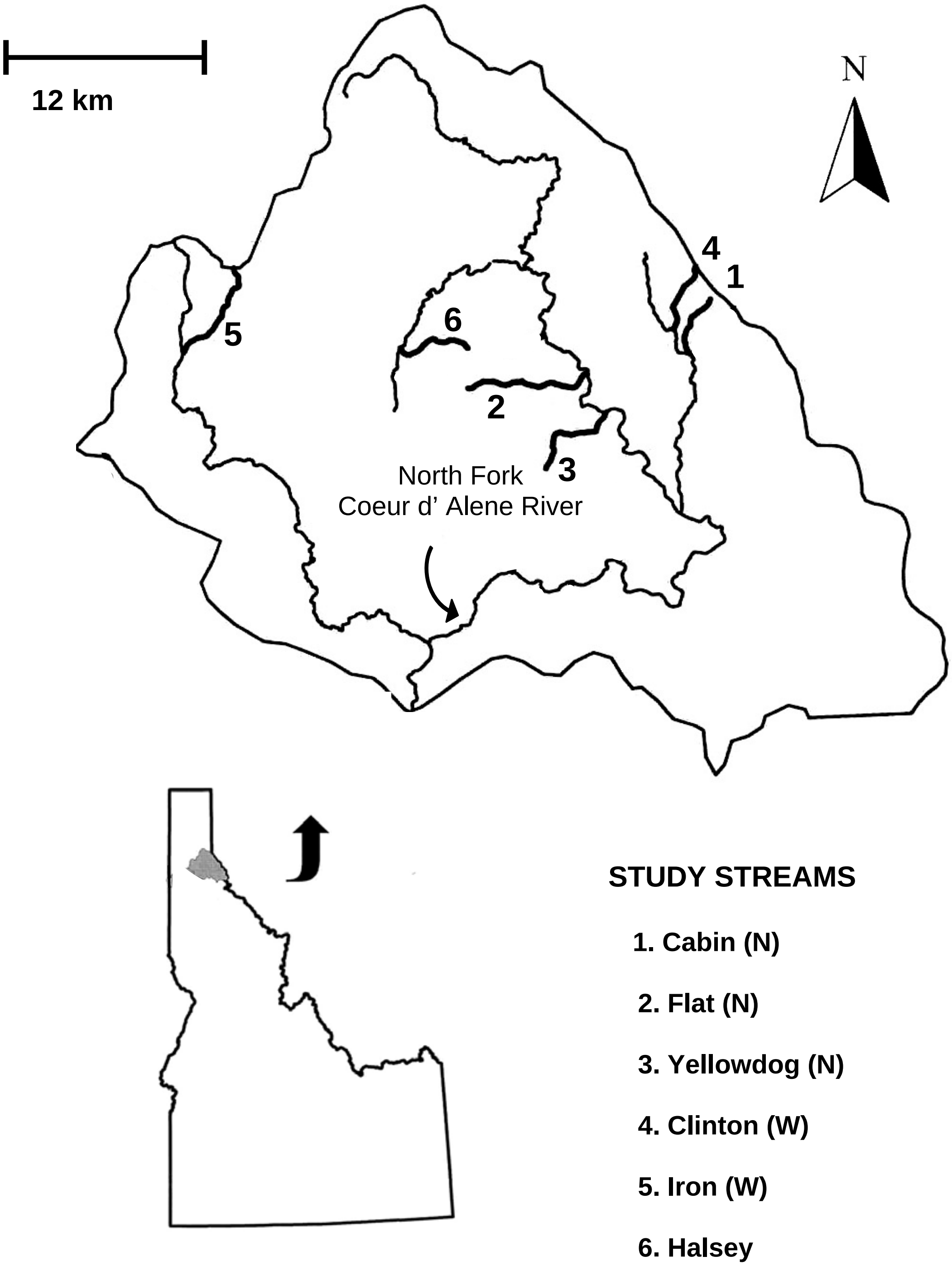


Figure 3.1. Study area in the North Fork Coeur d' Alene River subbasin, northern Idaho. N = narrow, W = wide valley width.

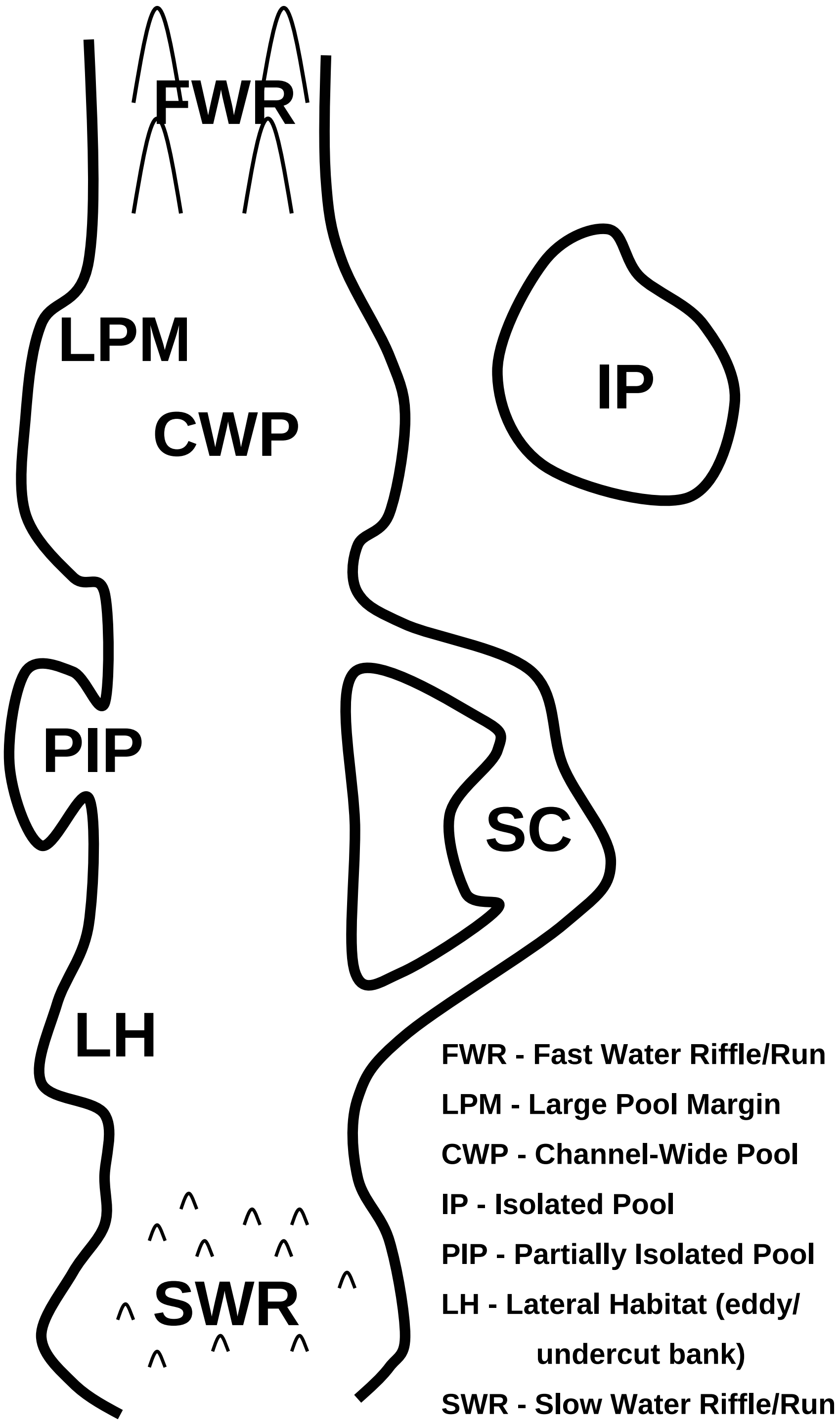


Figure 3.2. Habitat unit types used in the study. Habitat unit location in the main channel versus side channels (SC) was also recorded.

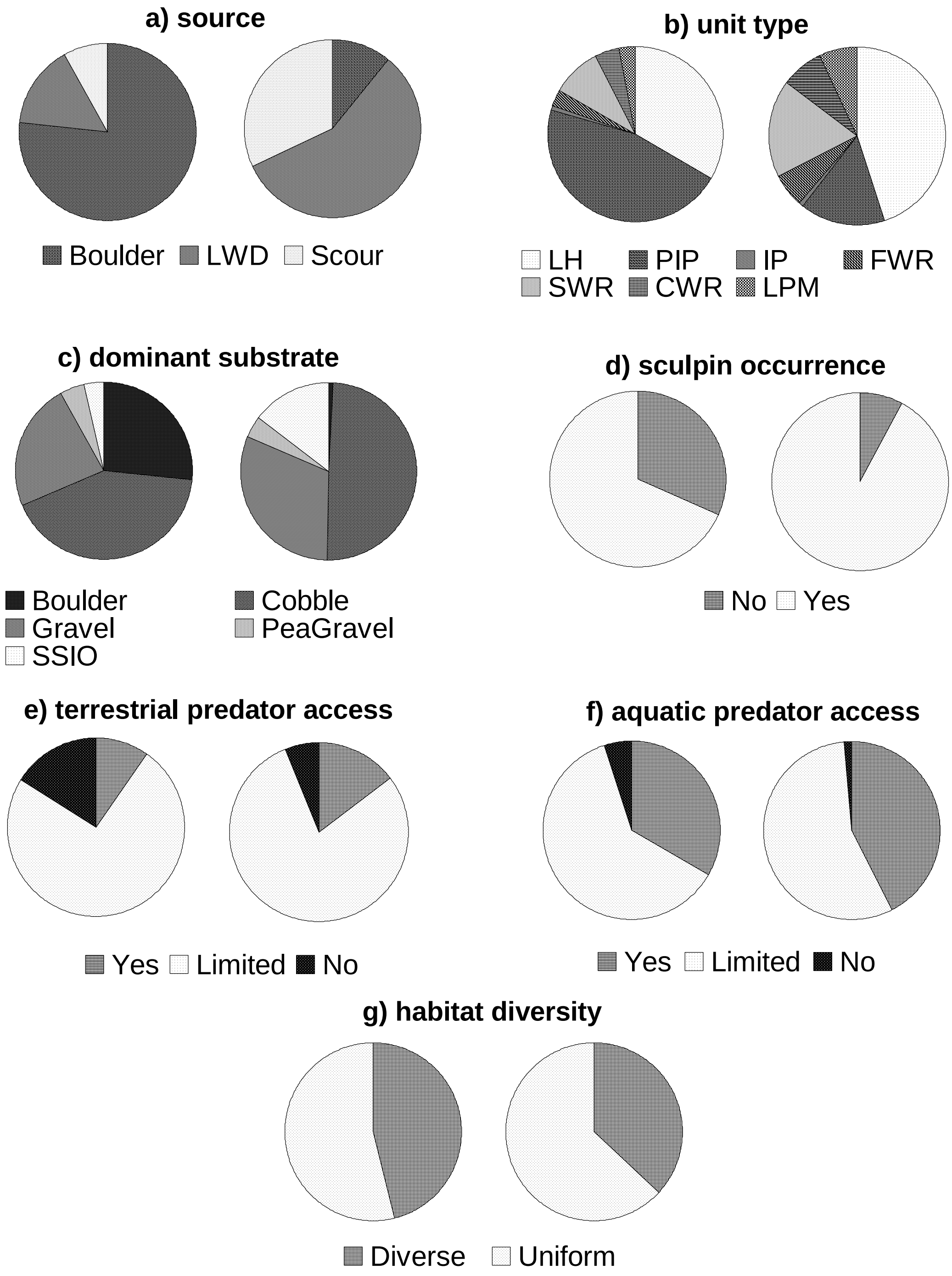


Figure 3.3. Habitat characteristics a) source, b) unit type, c) dominant substrate, d) sculpin occurrence, and e) terrestrial predator access, f) aquatic predator access, g) habitat diversity, differing significantly between wide and narrow valleys. Pie charts display proportion of habitat units with each habitat characteristic. For each pie chart pair, narrow valley averages are on the left and wide valley averages are on the right.

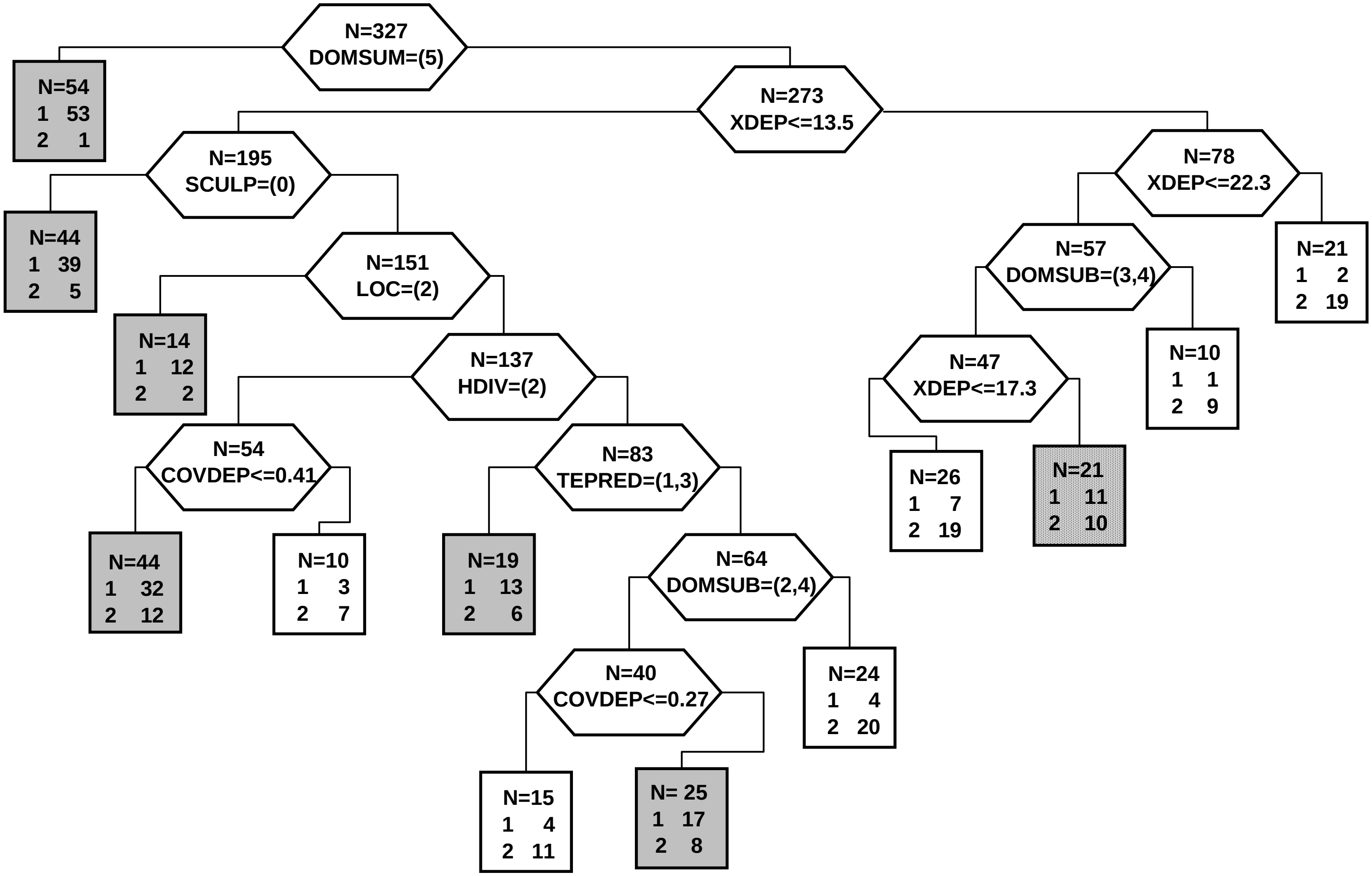


Figure 3.4. CART habitat analysis of units in narrow (class 1) and wide (class 2) valley habitat units. Classes and number of units/class are listed for each terminal node (rectangles). Hexagons contain branching criteria; units not meeting criterion branch to the right. Terminal nodes dominated by narrow valley, wide valley, and mixed units are gray, white, and dense hatch, respectively. Habitat variables are as described in Table 3.1 and the text.

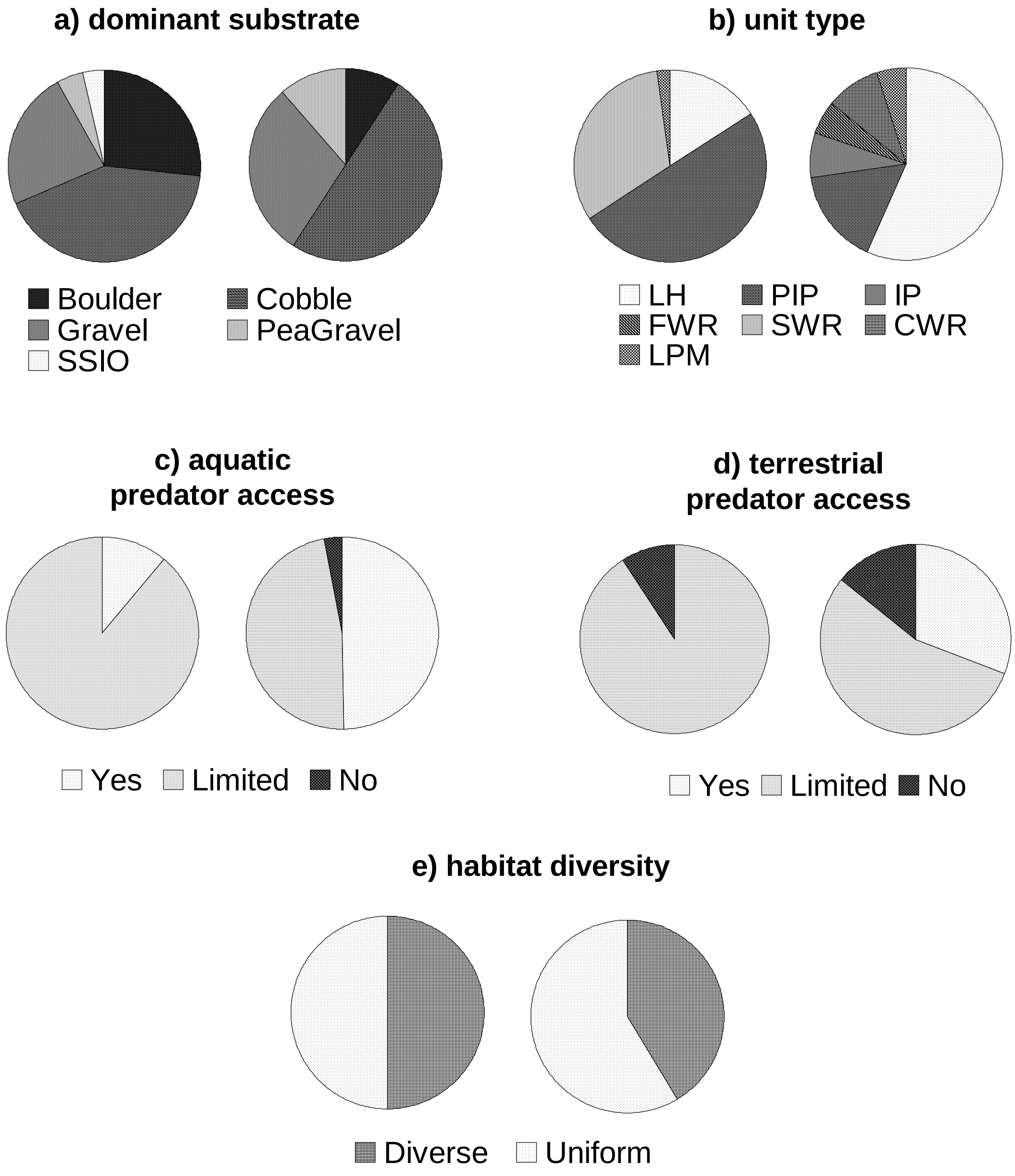


Figure 3.5. Habitat characteristics a) dominant substrate, b) unit type, c) aquatic predator access, d) terrestrial predator access, and e) habitat diversity, differing significantly in habitat use by large and small age 0 fish. Pie charts display proportion of habitat units with each habitat characteristic. For each pie chart pair, habitat use by small fish is on the left and habitat use by large fish is on the right.

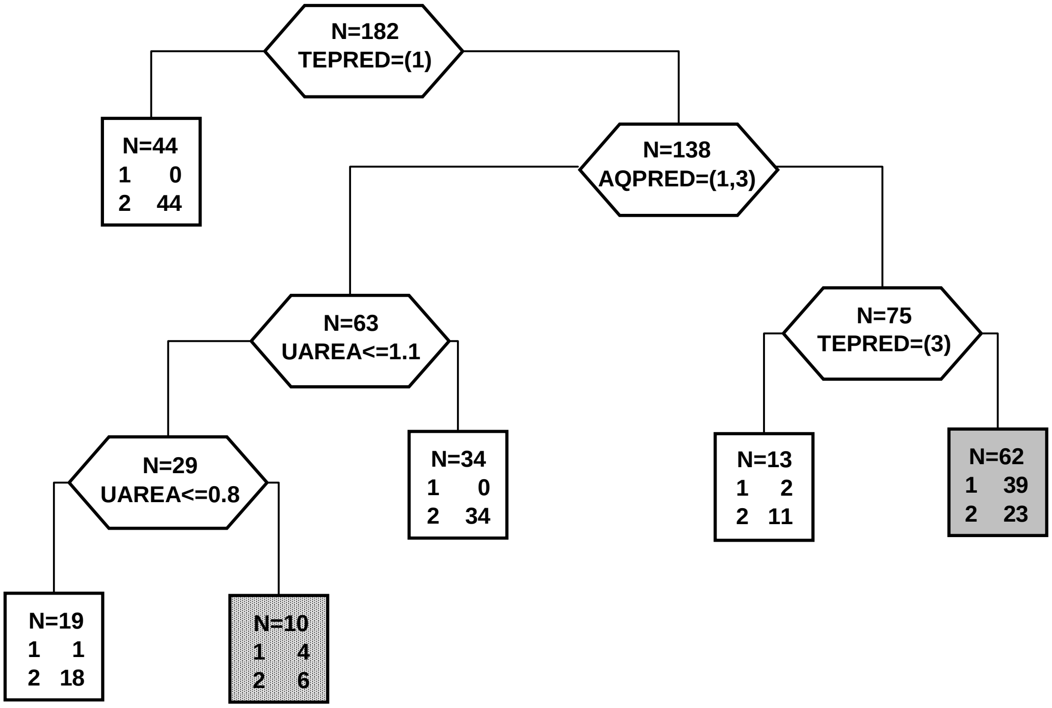


Figure 3.6. CART habitat analysis of units occupied by small (class 1) and large (class 2) fish. CART tree conventions and habitat variables are as described in Figure 3.4, Table 3.2, and the text. Terminal nodes dominated by small, large, and mixed sizes are white, gray, and dense hatch, respectively.

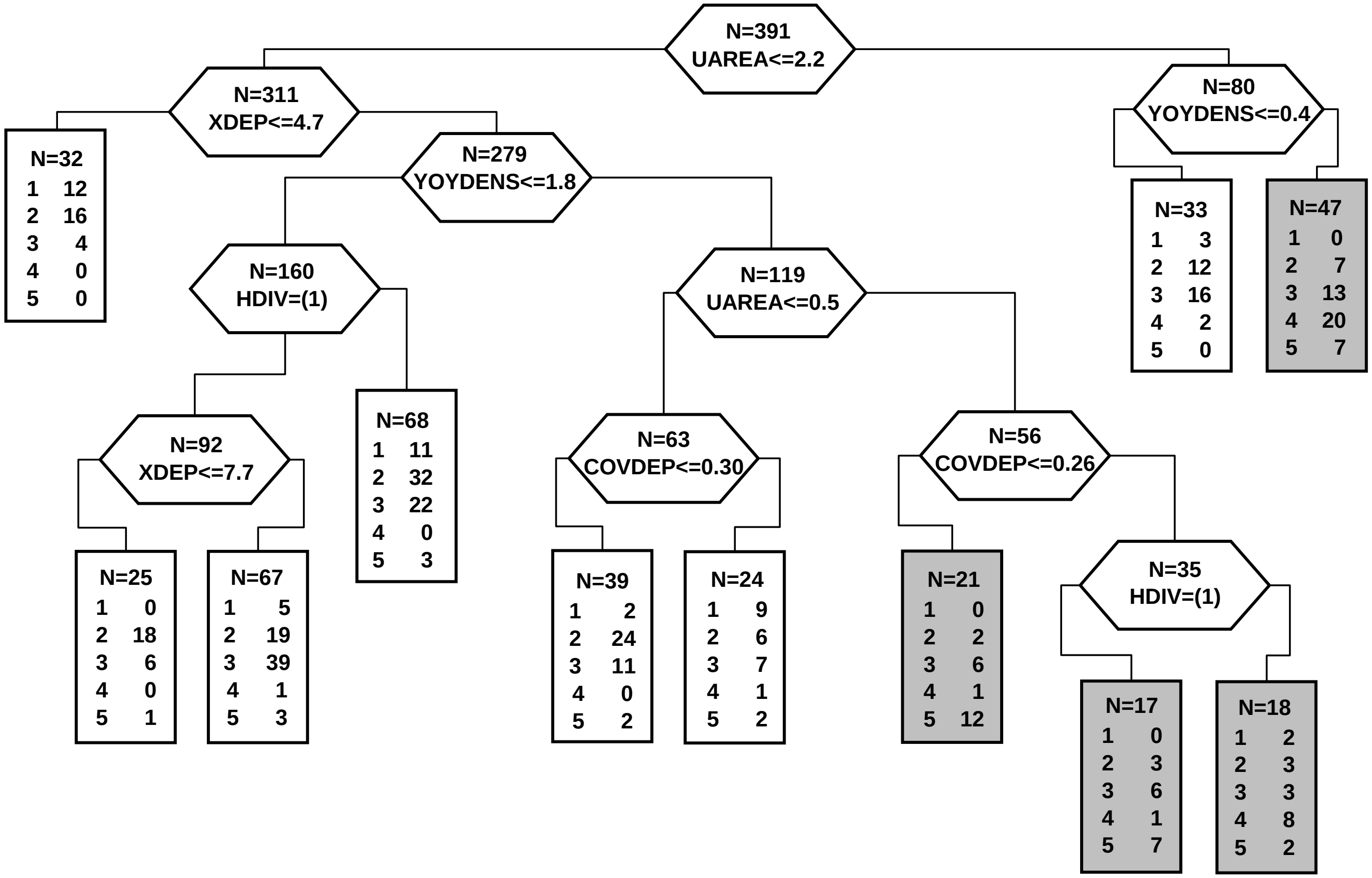


Figure 3.7. CART habitat analysis of units occupied by homogeneously and heterogeneously-sized individuals. Class codes: 1=small, 2=medium, 3=large, 4=small+medium, 5=all sizes. Terminal nodes containing significant numbers of heterogeneous units (classes 4,5) are shaded. Other CART tree conventions and habitat variables are as described in Figure 3.4, Table 3.2, and the text.

Table 3.1. Habitat characteristics recorded for each habitat unit for stream (S), reach (R), and unit (U) scales of analysis. CO=continuous variable, CA=categorical variable.

Habitat Variable	Variable Code	Variable Type	Scales Included	Method of Determination
Unit Area	UArea	CO	All	Calculated from unit length*width
Average Depth	XDep	CO	All	Average of 6 depth measurements within unit
Age 0 Density	YOYDens	CO	All	Calculated from # fish/UArea
Habitat Diversity	HDiv	CA	All	Diverse/Uniform
Dominant Substrate	DomSub	CA	All	Bedrock+Boulder/Cobble/Gravel/Pea gravel/ Sand+Silt+Organic
Unit Type	Type	CA	All	see Figure 3.2
Terrestrial Predator Access	TePred	CA	S,R	Yes/Limited/No
Aquatic Predator Access	AqPred	CA	S,R	Yes/Limited/No
Depth Coefficient of Variation	COVDep	CO	S,U	Calculated from 6 depth measurements
Unit Location	Loc	CA	S	Main/Side Channel
Unit Source	Source	CA	S	Boulder/Large Woody Debris/Scour
Canopy Cover	Canopy	CA	S	Open/Partial/Closed
Sculpins	Sculp	CA	S	Present/Absent

Table 3.2. Characteristics of study streams in the North Fork Coeur d' Alene River subbasin. Valley width: N=narrow, W=wide; Aspect: S=south, N=north, E=east, W=west; SD=standard deviation; # side channels is the number of transects that had a side channel. Age 0 density is at the stream scale and uses reach length required to located requisite number of occupied habitat units.

Stream	Valley Width	Aspect	Conductivity (μmhos)	Elevation (m)	Sinuosity	Mean % Slope (SD)	Mean Valley Width (m; SD)	Mean Wetted Width (m; SD)	# Side Channels	Age 0 Density (#/m)
Cabin	N	SSW	41.0	884	1.2	3.1 (0.7)	42.8 (5.4)	3.03 (0.43)	4/5	0.33
Flat	N	ESE	52.0	914	1.1	3.0 (0.9)	32.0 (12.3)	5.33 (1.10)	1/5	0.24
Yellowdog	N	NE	14.0	808	1.3	2.4 (0.5)	17.1 (1.3)	5.10 (0.76)	0/5	0.21
Clinton	W	SSW	36.0	927	1.8	1.7 (0.0)	144.2 (35.4)	2.59 (0.82)	2/5	0.18
Iron	W	WSW	62.5	930	1.6	1.4 (0.7)	168.0 (31.8)	4.01 (1.83)	1/5	0.42
Halsey		NNW	78.0	939	1.2	2.3 (2.1)	51.7 (13.5)	2.95 (0.63)	3/5	0.29

Table 3.3. Summary and statistical significance of differences in habitat unit and age 0 westslope cutthroat trout characteristics in narrow versus wide stream reaches. (VW=valley width, YR=year, COV=coefficient of variation, NS= not significant at $p<0.10$; standard deviation in parentheses). Significant valley width and interaction p-values in bold. Additional data detail given in Appendix 3.2, Table 3.8.

				Independent Variable p Value			
Variable	**Narrow**	**Wide**	**r^2**	**Model**	**VW**	**YR**	**VW*YR**
N	201	149					
Unit Area (m^2)	1.3 (0.5)	3.6 (1.4)	0.080	<0.0001	**<0.0001**	<0.003	**<0.008**
Unit Average Depth (cm)	10.3 (2.7)	14.2 (1.5)	0.114	<0.0001	**<0.0001**	<0.002	**<0.009**
Unit COV Depth	0.31 (0.01)	0.28 (0.00)	0.052	<0.0004	NS	<0.0001	NS
Age 0 Average Length (mm)	42.1 (4.3)	42.3 (1.3)	0.664	<0.0001	NS	<0.0001	<0.06
Age 0 COV Length	0.13 (0.03)	0.10 (0.02)	0.160	<0.0001	**<0.02**	<0.007	**<0.0002**
Age 0 Density (# age 0/m^2)	2.14 (1.87)	1.50 (1.06)	0.058	<0.002	**<0.0002**	<0.06	NS
# Age 0/Unit	1.5 (0.2)	2.3 (0.6)	0.072	<0.0001	**<0.0006**	<0.03	**<0.0001**

Table 3.4. Summary and analysis of variance statistics of continuous habitat variables occupied by large, medium, and small age 0 westslope cutthroat trout. (NS=not significant at $p<0.10$; standard deviation in parentheses). Significant size and interaction p-values in bold. Additional data detail is given in Appendix 3.2, Table 3.11.

					Independent Variable p Value			
Dependent Variable	**Large**	**Medium**	**Small**	**r^2**	**Model**	**Size**	**Stream**	**Size* Stream**
N	133	142	44					
Fish Length (mm)	54.6 (2.2)	39.9 (2.0)	28.7 (1.4)					
Unit Area (m^2)	2.2 (4.1)	1.2 (1.1)	0.9 (0.7)	0.106	<0.007	**<0.002**	<0.05	NS
Unit Mean Depth (cm)	13.6 (7.1)	10.6 (6.1)	9.3 (6.9)	0.226	<0.0001	**<0.0001**	<0.0001	NS
Age 0 Density (# fish/m^2)	1.6 (1.7)	1.8 (1.5)	2.3 (2.0)	0.127	<0.0007	**<0.07**	<0.004	**<0.04**
# Age 0/ Unit	1.5 (0.9)	1.2 (0.7)	1.1 (0.4)	0.092	<0.03	**<0.0007**	NS	NS

Table 3.5. Habitat unit continuous and categorical variable characteristics and fish variables associated with habitat unit type. Numerical averages are given for continuous variables, with standard deviation in parentheses. For categorical variables, the most frequently occurring category(s) are given. If all categories are equally frequent, the number of categories is given. If two categories were quite frequent, both codes are given with the most common first. Variable codes are as described in Table 3.1. Unit type codes are as described in Figure 3.2. Categorical variable codes: Source: B=boulder, S=scour, W=wood; TePred and AqPred: Y=Yes, L=Limited, N=No; Canopy: C=closed, P=partial, O=open; HDiv: D=diverse, U=uniform; Sculpins: Y=yes, N=no; DomSub: C=cobble, G=gravel, PG=pea gravel. Additional data detail given in Appendix 3.2, Tables 3.11, 3.13, 3.14, 3.15.

Variable	IP	PIP	LPM	LH	FWR	SWR	CWP
CONTINUOUS							
% of Units	7.8	30.7	4.4	38.1	3.8	15.9	6.4
Mean Depth (cm)	10.7 (7.1)	10.1 (4.8)	21.5 (7.6)	12.7 (6.1)	17.2 (13.0)	7.6 (3.6)	15.9 (8.2)
COV Depth	0.27 (0.14)	0.33 (0.12)	0.29 (0.14)	0.26 (0.10)	0.24 (0.10)	0.31 (0.11)	0.31 (0.09)
Unit Area (m^2)	1.3 (0.9)	1.4 (1.2)	2.2 (2.2)	1.4 (1.3)	0.6 (0.9)	1.2 (0.9)	8.4 (10.2)
CATEGORICAL							
Source	W	B	W	3	W	S	W
TePred	L	L	L	L	YL	L	L
AqPred	N	L	Y	LY	Y	L	L
Canopy	C	P	P	P	P	P	P
HDiv	U	2	2	U	2	2	D
Sculp	Y	Y	Y	Y	Y	Y	Y
DomSub	PG	C	C	C	G	C	C
FISH CHARACTERISTICS							
Mean Length (mm)	45.3 (11.1)	40.1 (9.7)	45.7 (9.9)	49.6 (8.8)	49.3 (6.8)	34.5 (5.3)	47.9 (9.7)
COV Length	--	0.13 (0.09)	0.11 (0.07)	0.10 (0.06)	0.11 (0.10)	0.08 (0.04)	0.08 (0.05)
# Fish/Unit	1.0 (0.0)	1.6 (1.2)	1.8 (1.6)	1.6 (1.1)	1.7 (0.7)	1.6 (1.1)	3.0 (5.2)
Fish Density (#/m^2)	1.6 (1.9)	1.8 (1.6)	1.6 (1.5)	1.9 (1.7)	3.6 (2.0)	2.0 (1.6)	0.8 (0.6)

Table 3.6. Distribution of fish sizes among habitat unit types relative to unit type mean depth. Unit types are ordered by depth from deepest to shallowest. Fish size numbers are percentage of all fish in that size category. Dominant percentages per unit type for large and small fish are indicated in bold. Unit type codes are as described in Figure 3.2. L=large, M=medium, S=small.

	LPM	**FWR**	**CWP**	**LH**	**IP**	**PIP**	**SWR**
Mean Depth (cm)	21.5	17.2	15.9	12.7	10.7	10.1	7.6
Fish Size							
L	**5.3**	**6.0**	**9.8**	**60.9**	0.8	17.3	0.0
M	4.2	1.4	4.9	25.4	1.4	36.6	26.1
S	2.3	0.0	0.0	15.9	0.0	**50.0**	**31.8**

Table 3.7. Differences in habitat unit and age 0 westslope cutthroat trout characteristics between units occupied by heterogeneous (HE) versus homogeneous (HO; mix) age 0 size structures (COV=coefficient of variation, NS=not significant at $p<0.10$, standard deviation in parentheses). Significant mix and interaction p-values in bold. Additional data detail is given in Appendix 3.2, Table 3.16.

Variable	**HE**	**HO**	**r^2**	**Model**	**Mix**	**Stream**	**Year**	**Mix* Stream**	**Mix* Year**	**Stream* Year**	**Mix*Stream *Year**
N	72	70									
Unit Area (m^2)	2.9 (4.8)	2.2 (2.4)	0.216	<0.10	**<0.05**	NS	NS	NS	**<0.02**	NS	NS
Unit X Depth (cm)	12.7 (6.7)	12.5 (5.4)	0.216	<0.09	NS	NS	<0.04	NS	NS	NS	NS
Unit COV Depth	0.31 (0.16)	0.28 (0.10)	0.315	<0.0009	NS	NS	<0.008	NS	NS	NS	<0.09
Age 0 Density (# fish/m^2)	2.2 (1.5)	2.3 (2.0)	0.252	<0.03	NS	<0.07	<0.06	NS	NS	NS	NS

APPENDIX 3.1

A LITERATURE REVIEW OF HABITAT DIVERSITY – SIZE VARIATION RELATIONSHIPS IN AGE 0 SALMONIDS

INTRODUCTION

Numerous processes contribute to size variation in age 0 salmonids. Size differentiation may be generated by genetic differentiation between individuals, as well as by parental characteristics, choice of redd location, spawning timing, and other factors that affect emergence timing and size at emergence (e.g. Mason and Chapman 1965; Beacham et al. 1985; Chandler and Bjornn 1988). Additional biotic and abiotic factors produce size differentiation among individuals identically sized and emerging together. Generating processes include genetic and environmental variation and their interaction, each affecting the growth of an individual (Berven and Gill 1983). Environmental factors are diverse and affect both the generation and distribution of variation. Environmental factors include abiotic characteristics such as temperature, productivity, and availability and suitability of habitat (e.g. Donald et al. 1980; Myrick and Cech 1996; Harvey 1998; Rosenfeld and Boss 2001). Biotic characteristics include food availability, intra- and interspecific competition, and predation (Jobling and Baardvik 1994; Reinhardt 1999; Keeley 2001). Habitat characteristics affecting age 0 size are numerous, since the tradeoffs an organism must make to maximize energy acquisition while minimizing energy expenditure and risk of predation are affected by many aspects of its environment (Chapman 1966; Fausch 1984). Habitat diversity affects size variation directly since diverse habitats provide niches for individuals differing in size and therefore habitat needs, as well as indirectly through competition- and predation-mediated effects on age 0 habitat – size variation relationships (Schoener 1974). Here I review age 0 salmonid relationships with its habitat, processes generating size diversity, the roles of habitat diversity, competition, and predation in contributing to size variation, and conditions under which habitat diversity may not contribute to the generation of size variation.

AGE 0 SALMONID HABITAT USE

Habitat selection by age 0 salmonids is driven primarily by competition for food and therefore space (Mason and Chapman 1965; Chapman 1966), energetic profitability maximizing food delivery while minimizing energetic expenditures (Fausch 1984), and vulnerability to predation (Power 1987; Harvey 1991; Fausch 1993). Juvenile salmonids choose habitat structures relative to the tradeoffs they represent among foraging efficiency, intraspecific competition, and predation risk (Fausch 1993). Moore and Gregory (1988b) found age 0 coastal cutthroat trout (*Oncorhynchus clarki clarki*) abundance to be greatest in habitats with low velocity shallow water, abundant detritus and benthic invertebrates, and open canopies. Fausch (1993) provided rainbow trout parr with structures having overhead cover, velocity refuge, and visual isolation from other individuals. He found that structures with overhead cover alone or all three cover components were chosen more often than units without overhead cover, and that parr chose structures closest to the swiftest velocities available or near natural cover. He concluded that cover may provide different functions under different conditions. In high gradient turbulent waters, velocity refuge may be more important than overhead cover whereas in habitats with more moderate flows, overhead cover providing refuge from terrestrial predators may be most important.

Use of water depth by small fish requires balancing benefits of cover from terrestrial predators, where deeper water provides refuge, and aquatic predators, where shallower water provides refuge (Power 1987; Harvey and Stewart 1991), with size-selective predation that is a function of both prey and predator size structure (Schlosser 1987; Rice et al. 1993). Lonzarich and Quinn (1995) found depth to be more important than structure in determining distribution of coho salmon (*Oncorhynchus kisutch*) in artificial channels, but concluded that both are important to small fish for predator avoidance. Harvey and Stewart (1991) found prey use of depth as cover from predators to be mediated by relative presence of aquatic versus terrestrial predators, size structures of predators and prey, and other physical habitat characteristics such as light and turbulence.

Low light levels may in some situations serve as cover for prey. L'Abee-Lund et al. (1993) found juvenile Arctic char (*Salvelinus alpinus*) to take refuge in the pelagic zone of five Norwegian lakes, using darkness as cover from predators. Helfman (1981) found fish in shade were more able to see approaching objects yet were more difficult for predators to detect, and Shirvell (1990) found steelhead (*Oncorhynchus mykiss*) parr chose habitats that had low light levels. However, Moore and Gregory (1988b) suggest that in heavily shaded stream sections, low light may limit age 0 salmonid ability to locate and capture prey.

Salmonid fry generally have substrate size preferences since substrates provide different levels of food and cover. Cutthroat trout fry in an Oregon stream preferred substrates with mixed sizes or complex surfaces such as gravel and cobble and tended to avoid smooth surfaces such as bedrock or sand/silt (Moore and Gregory 1988b). Griffith (1972) found age 0 westslope cutthroat trout used interstitial spaces in cobble for refuge from predators but otherwise demonstrated no clear preference regarding substrate. Lentz (1998) found age 0 westslope cutthroat trout generally preferred smaller substrates, but were also most abundant in side channels with cobble substrates. Shirvell and Dungey (1983) found choice of substrate size to increase with increasing fish size between age classes but did not find a similar relationship within an age 0 cohort.

Habitat containing or created by organic material such as large woody debris may provide more aquatic and terrestrial food than habitats comprised of or created primarily by boulders or other rocky materials (Nielsen 1992). However, Lentz (1998) found that age 0 cutthroat trout displayed no preference for habitats created by large woody debris versus boulders, using habitats in proportion to their availability. Temperature differences were not found between isolated habitats and those adjacent to the main flow in shaded reaches whereas in open reaches isolated habitats tended to be cooler than those adjacent to the main flow (Moore and Gregory 1988b). Open canopy habitats may be more productive and therefore support or generate larger individuals (Moore and Gregory 1988b).

Habitat area and shape may also correlate with fish characteristics. A larger area may provide a larger range of habitat configurations and food resources, and therefore more potential niches (Angermeier and Schlosser 1989). Habitat length may affect size and number of fish supported since dominant fish in salmonid hierarchical dominance structures are found at the head of pools, with subdominant individuals progressively further downstream (Nielsen 1992). In addition to potentially providing opportunity for more diverse habitats, larger habitats may also provide more territories and more diverse fish sizes (Grant and Kramer 1990). Lentz (1998) found that age 0 cutthroat trout did not use habitats smaller than a threshold size and smaller sized juvenile salmonids were closer to stream banks than larger individuals, particularly at night. They suggested that smaller individuals were more vulnerable to the increased predation threat in lower light and that it was more important for them to seek lower water velocities when they were not able to feed. Griffith (1972) and Moore and Gregory (1988b) also found a direct relationship between juvenile westslope cutthroat trout distance from cover including stream banks and fish size.

DIVERSITY GENERATING PROCESSES

Two mechanisms may contribute to a relationship between fish size variation and habitat complexity: complex habitats may generate size diversity or they may support existing diversity generated by other processes within an area. When small fish are able to move between habitats with different characteristics without risk of predation, harm from physical conditions such as high water velocities, or competitive displacement in high density situations, individuals may move to better conditions as their needs change with size or age. In this scenario diverse habitats may support size variation where that variation is generated through mechanisms such as differential emergence timing within a site or immigration of smaller individuals from upstream. Conversely, individuals may be forced to emigrate as energetic need and therefore territory size increases with body size or by smaller individuals or later emergents that are excluded from habitats already occupied (Mason and Chapman 1965; L'Abee-Lund et al. 1993; Bardonnet and Heland 1994; Huntingford and de Leaniz 1997). Kahler (1999) found that 28 to 60% of tagged juvenile coho salmon, cutthroat trout, and steelhead moved at least several stream habitat units during their first summer in western Washington streams. Moore and Gregory (1988b) found mean age 0 cutthroat trout size to be smaller in isolated pools where emigration was prevented, as well as in backwater habitats, suggesting that in their study streams fish would move when able. In an experimental study, Wilzbach (1985) found cutthroat trout were willing to emigrate if food was limited but were much less willing to if cover was unavailable. With low food abundance, presence of cover was not sufficient to prevent individuals from emigrating.

Conditions providing minimal risk associated with movement between habitats are rarely found in headwater stream environments. Predator and competitor densities may be high and physical conditions may be harsh. Under these conditions, individuals may be more likely to stay in sub-optimal habitat with limited growth rather than risk a worse outcome, and size variation may be generated by habitat complexity through mechanisms such as competition, size-selective predation, and differences in resource availability. Salmonid fry generally do not move for several months once territories are established. Habitat quality is therefore critical to early growth and survival (Moore and Gregory 1988b). Nielsen (1992) found juvenile coho salmon in four habitat types (thalweg, backwater, shifting estuarine, margin cutbank) differed in feeding strategy, food choice, growth, and emergence timing. Early emergents obtained optimal habitats, demonstrating larger size than individuals in other habitats. Distinct phenotypes emerged in response to heterogeneous habitat conditions and density of intraspecific competitors.

ROLE OF NICHE DIVERSITY

The association between habitat diversity and biodiversity has been well recognized and documented (Schoener 1974) and as reviewed by Downes et al. (1998) and Bell et al. (1991). Niche packing theory suggests that complex habitats provide more niches, and therefore support more biodiversity than simpler habitats (Klopfer and Mac Arthur 1960). A more complex area may support more biodiversity by retaining a wider variety of organisms that would otherwise emigrate or die. The evolution of habitat preferences enables ecological segregation and reduction in competition between individuals occupying the same area (Schoener 1983; Shirvell and Dungey 1983; Sale 1991; Piet et al. 1999). In salmonids, habitat preference is largely size driven (Everest and Chapman 1972; Shirvell and Dungey 1983), although species-specific preferences have also been identified (e.g. Bisson et al. 1988). Lateral habitats provide gradients in characteristics important to age 0 fish, and habitat needs and opportunities change with increasing size. An individual habitat may be sufficiently complex to accommodate the needs of a growing age 0 fish throughout its first year, or a complex of habitats within a reach may provide the mix of conditions for that individual but require it to move to maintain optimal growth.

Ontogenetic niche shifts have been documented primarily between age classes but also within age classes. Mason and Chapman (1965) suggested that emigration of larger age 0 coho salmon may be evidence for an ontogenetic niche shift, with habitats adequate for emergents no longer meeting the increasing energetic requirements of larger individuals. Moore and Gregory (1988b) found habitat use by age 0 cutthroat trout changed over their first summer, with fish moving within habitats to deeper, faster water further from the water's edge and cover as they grew. McLaughlin and Grant (1994) found brook trout (*Salvelinus fontinalis*) fry to be longer in faster water, as well as having taller tails, more fusiform bodies, and different food preferences than individuals in slower water. Small changes in body length increase a small fish's ability to swim in faster current, allowing for use of deeper water further away from the stream edge and reducing susceptibility to displacement (Everest and Chapman 1972). Luecke (1986) found cutthroat trout smaller than 60 mm preferred planktonic prey whereas trout greater than 70 mm in length shifted to more benthic prey. The shift was related to prey size from smaller zooplankton to larger benthic invertebrates and feeding behaviors were associated with changes in cutthroat trout mouth morphology and gape width. It is unclear whether cutthroat trout in stream settings make similar shifts in feeding behavior although they likely do shift toward larger prey sizes. Drifting macroinvertebrate prey items largely reflect the benthic population, so a change to larger food items by trout may not necessitate a shift in foraging location or behavior as it appears to do in more lentic settings. Baltz and Moyle (1984) and Baltz et al. (1991) identified an ontogenetic niche shift in rainbow trout (*Oncorhynchus mykiss*) that included changes in depth, focal elevation, and velocity, with older individuals using deeper, faster water, and higher in the water column. L'Abee-Lund et al. (1993) found juvenile Arctic char shifted habitats from epibenthic to pelagic habitats with increasing size as a result of reduced susceptibility to predation and increased food demand.

ROLE OF COMPETITION

Within a habitat intraspecific competition for food may be manifested as competition for space in stream salmonids (Chapman 1966). Salmonids generally establish and maintain territories if the food source is diffuse within a habitat, as in a riffle, or a dominance hierarchy if the food source is focused and dominant individuals are able to control access to the source, as in a pool (Chapman 1966). At extremely high densities, juvenile salmonids may switch to schooling behavior (Grant and Kramer 1990). Age 0 salmonids generally establish territories rather than hierarchies within a habitat (Grant and Kramer 1990). Territory size limits maximum population density of salmonids (Grant and Kramer 1990); however, territory size is flexible and may be smaller in more complex environments. Territory size is also influenced by intruder presence, food availability, depth, and water velocity, and increases with fish body size (Grant and Kramer 1990).

Complex habitats may provide more niches to accommodate individuals of different sizes within a cohort as well as enabling more fish to remain in a complex habitat than in a simpler area of the same size. In sufficiently large or diverse habitats, territories become habitat subunits where dominant individuals control territories and subordinate individuals may either “float” at territory margins within the subunit or emigrate in search of a better situation (Nielsen 1992). Cover in complex habitat provides visual separation and may prevent dominant individuals from controlling food sources, and complex habitats may be more likely to have diffuse sources of food since cover may create complex flow patterns entering or within the area. With the hierarchical arrangement, subdominant and floater individuals are found at the downstream end of habitatts, where food is less plentiful (Nielsen 1992).

Interspecific competition may also mediate an organism’s relationship with its environment, and therefore the effect of habitat diversity on size variation. Multiple salmonid species often co-occur, and although species may be morphologically and behaviorally differentiated from each other (e.g. Griffith 1972; Bisson et al. 1988; Bugert and Bjornn 1991) and may prefer different habitats (e.g. Glova 1987; Dolloff and Reeves 1990), juveniles of more than one species may occur in close proximity and share resources (Glova 1987). Habitat differentiation between salmonid species and co-occurring non-salmonid species has also been documented (e.g. Baltz and Moyle 1984 ;Glova 1987). Although salmonids typically feed from the water column whereas sculpins are bottom-feeders (Brusven and Rose 1981; Johnson et al. 1983), indirect competition between salmonids and sculpins has been suggested (e.g. Glova 1987) since consumption of benthic foods may reduce available drift (Brocksen et al. 1968) and drift availability may be limiting in small streams during low flow summer months (Mason 1976).

ROLE OF PREDATION

Predation accounts for a major portion of mortality for early life stages of fish (Werner and Gilliam 1984). Cannibalism may be more common when few other fish species are present or food supplies are poor (Griffiths 1994), both common characteristics of age 0 westslope cutthroat trout habitat. Incidence of cannibalism is likely related to food stress. As food stress increases, foraging effort, prey encounter rate, and prey susceptibility increase and the prey base broadens, resulting in the greater take of conspecifics (Polis 1981). Westslope cutthroat trout (Lentz 1998) and shorthead sculpin (Horner 1978) are not primarily piscivorous. Griffith (1974) found westslope cutthroat trout and brook trout consumed few fish and that cannibalism and piscivory contributed little to their diet. Only 2.2% of 225 adult westslope cutthroat trout had fish in their stomachs in his study. Dippers (*Cinclus mexicanus*) are likely the most common avian predator of fish present in headwater streams in westslope cutthroat trout range; other potential avian predators include kingfishers and herons. Dippers will take age 0 salmonids but likely account for only a small percentage of age 0 mortality under natural circumstances (Mitchell 1968; Thut 1970; Harvey and Marti 1993).

Predator effects on prey size structure can be indirect (e.g. change in prey habitat use or behavior; Rice et al. 1993) or direct (e.g. mortality; Claessen et al. 2002). Indirect effects of habitat complexity on size variation through size-mediated predation and cannibalism may be less important than intraspecific competition for optimal niches and changing needs during ontogenetic niche shifts (Chapman 1966). It is much less likely that mortality is size selective, especially to the extent that effects of predation on age 0 size structure would dominate other sources of size variation in age 0 salmonids. Paradis et al. (1999) conducted a modeling exercise examining effects of prey and predator size and abundance and timing of interaction, concluding that size-selective mortality is likely to be seen only when predation is heavy (greater than 50% of the prey population) or when it comes early within the period of potential predation (in the first 5 days of their simulation). Size-selective mortality is not generally evidenced since although larger prey are more easily detectable, smaller prey are more susceptible, and the opposing directions of size selectivity counteract each other. However, Rice et al. (1993) suggest that prey size structure is a function of predator size structure since larger predators prefer larger prey.

Effects of predation on the distribution of fishes by size among habitats may be substantial. Although predation is not commonly used to explain distribution of stream-dwelling salmonids relative to competition and energetic demands, Lonzarich and Quinn (1995) found mortality of coho salmon, steelhead, cutthroat trout, and stickleback (*Gasterosteus* sp.) to be lower in experimental units with greater depth or cover. Age 0 cutthroat trout move into slower water with more cover at night, presumably to avoid predation, and are not in areas where predators have access to them (Lentz 1998). Adult salmonids move into lateral habitats favored at night to prey on age 0 individuals (Horner 1978). Fausch (1993) found that rainbow trout parr chose experimental structures offering overhead cover, and therefore protection from terrestrial predators, over structures offering visual isolation or velocity refuge. Schlosser (1987) found that habitat use by small individuals of several species was mediated by the presence of a predator. With predators present, small fish were restricted to shallow riffles, where shallow water served as refugia from the larger predators. Small fish resided in pools only when complex structure was present whereas when predators were absent, small fish preferred pools with or without structural complexity. With predators present, niche overlap between large and small individuals was minimized but niche overlap, and therefore influence of competition, among small individuals was maximized. Without predators, small individuals were able to separate into diverse habitats. Bugert et al. (1991) found that juvenile coho salmon, steelhead, and Dolly Varden (*Salvelinus malma*) selected lower positions within the water column in pools without cover than in pools with cover, suggesting an avian predator induced habitat shift, and Bugert and Bjornn (1991) in a laboratory setting found juvenile steelhead and coho salmon changed habitats in the presence of fish predators. Harvey and Stewart (1991) suggested that predator identity may mediate size-based habitat use with aquatic predators limited to small prey, focusing attention of larger prey on terrestrial predators and therefore deeper waters offering refuge from terrestrial predators. Small prey may be ignored by terrestrial predators and therefore may choose shallow water offering refuge from aquatic predators. Therefore, depth distribution of prey may be dependent on relative predation pressure from aquatic and terrestrial predators and on the size distribution of prey organisms. Harvey (1991) found that in the presence of predators, small fish moved to shallower water but larger prey did not.

Butler (1988) found the presence of smallmouth bass predators to have only a weak effect on bluegill prey foraging, abundance, or use of complex habitats. Prey did prefer complex habitats, however, regardless of predator presence possibly due to higher food abundance for the bluegill prey. He suggests that prey may not respond to predator presence in the field as dramatically as they do in laboratory studies since laboratory studies may maximize prey risk whereas under natural conditions, prey may be able to detect level of risk from predators' behavior or other cues.

FACTORS THAT MAY PRECLUDE A SIZE–HABITAT DIVERSITY RELATIONSHIP

Conditions could occur in which an association between habitat diversity and size variation may not be seen. In reaches or habitats where age 0 fish density is sufficiently low, habitats may be under-occupied such that individual fish may occupy large or diverse habitats (Lonzarich and Quinn 1995). Within a reach, habitat diversity and size variation may correlate in high-density habitats whereas in lower density habitats they may not. If fish are unable to emigrate or densities are extremely high, individuals may not be able to obtain improved conditions with increasing body size. In this case, correlation could occur but over-occupation of habitats, with high densities within habitats, stunting, or occupation of all habitats by larger individuals may result. Insufficient size variation may be present within a reach for a relationship to be seen. Factors at broader spatial scales, such as temperature, may be controlling size diversification (Chapter 2), or sampling may have been conducted before sufficient size diversification has occurred. In an individual habitat, occupants may not match conditions if occupancy is in transition as larger or subdominant individuals immigrate or emigrate. In this case a size habitat relationship may still be seen at the reach scale and within other habitats in the reach.

APPENDIX 3.2

DATA SUMMARIES

Table 3.8. Summary statistics of differences in continuous habitat variables and fish characteristics by stream and valley width. Standard deviations are given in parentheses, COV=coefficient of variation.

Stream	N	Unit Depth (cm)	Unit COV Depth	Unit Area (m^2)	Age 0 Length (mm)	Age 0 COV Length	# Age 0/Unit
Cabin	60	7.6 (3.23)	0.30 (0.11)	0.9 (0.73)	42.0 (9.89)	0.11	1.5 (0.88)
Flat	70	10.4 (4.40)	0.32 (0.11)	1.5 (0.86)	37.9 (8.75)	0.12	1.8 (1.03)
Yellowdog	71	13.0 (4.92)	0.30 (0.12)	1.8 (1.53)	46.5 (9.42)	0.17	1.4 (0.72)
NARROW AVERAGE	**201**	**10.3** **(2.69)**	**0.31** **(0.01)**	**1.3** **(0.47)**	**42.1** **(4.30)**	**0.13** **(0.03)**	**1.5** **(0.21)**
Clinton	70	13.2 (8.47)	0.29 (0.12)	2.6 (3.76)	43.2 (11.44)	0.09	1.9 (1.25)
Iron	79	15.3 (8.70)	0.28 (0.12)	4.6 (7.55)	41.4 (8.38)	0.11	2.7 (2.98)
WIDE AVERAGE	**149**	**14.2** **(1.50)**	**0.28** **(0.003)**	**3.6** **(1.44)**	**42.3** **(1.27)**	**0.10** **(0.02)**	**2.3** **(0.60)**
Halsey	64	11.5 (5.71)	0.28 (0.11)	2.6 (4.98)	45.1 (11.14)	0.10	1.8 (1.44)

Table 3.9. Results of chi square tests between age 0 habitat units in narrow and wide stream reaches, shown as counts with wide valley values corrected for differences in sample size. N=number of expected cells in the chi square test. LWD=large woody debris, BO=bedrock and boulder, SaSiO=sand, silt, and organic material. See Figure 3.2 for unit type abbreviations.

Variable	Narrow	Wide	N	χ^2	p
Source			3	481.5	<0.005
Boulder	152	22			
LWD	30	113			
Scour	16	63			
Type			7	86.0	<0.005
LH	66	89			
PIP	91	31			
IP	2	2			
FWR	6	12			
SWR	18	35			
CWP	15	6			
LPM	6	14			
DomSub			5	128.3	<0.005
BO	53	2			
Cobble	83	98			
Gravel	46	61			
Pea gravel	9	8			
SaSiO	7	29			
Sculp			2	52.9	<0.005
Yes	135	183			
No	63	15			
TePred			3	18.2	<0.005
Yes	32	12			
Limited	147	157			
No	19	29			
AqPred			3	11.0	<0.005
Yes	66	84			
Limited	122	111			
No	10	3			
Hdiv			2	6.4	<0.025
Diverse	91	73			
Uniform	106	124			
Canopy			3	4.0	NS
Open	18	26			
Partial	158	150			
Closed	22	21			

Table 3.10. Unit type occurrences among streams and valley widths. Figures given are percentages of all units occurring per unit type. Unit abbreviations are as given in Figure 3.2.

	IP	**PIP**	**LPM**	**LH**	**FWR**	**SWR**	**CWP**
Cabin	1.7	31.7	1.7	38.3	5.0	10.0	11.7
Flat	0.0	41.4	2.9	32.9	2.9	17.1	2.9
Yellowdog	1.4	63.4	4.2	29.6	1.4	0.0	0.0
NARROW AVERAGE	**1.0**	**46.3**	**3.0**	**33.3**	**3.0**	**9.0**	**4.5**
Clinton	1.4	22.9	5.7	38.6	2.9	10.0	15.7
Iron	0.0	8.6	8.6	45.7	10.0	20.0	7.1
WIDE AVERAGE	**0.7**	**15.7**	**7.1**	**42.1**	**6.4**	**16.4**	**11.4**
Halsey	0.0	13.0	2.9	37.7	1.4	33.3	11.6

Table 3.11. Summary statistics of differences in continuous habitat variables by fish size and stream. SD=standard deviation, COV=coefficient of variation, L=large, M=medium, S=small.

Stream		**N**	**X Length (mm)**	**XDep (cm)**	**UArea (cm^2)**	**YOYDens ($\#/m^2$)**	**# Age 0/ Unit**
Cabin	**L**	22	54.7	8.3	0.9	2.6	1.6
			(3.89)	(2.41)	(0.65)	(1.80)	(0.90)
	M	22	39.4	6.1	0.8	2.8	1.2
			(4.08)	(2.47)	(0.85)	(2.22)	(0.87)
	S	8	29.0	7.7	0.8	2.0	1.0
			(2.33)	(2.71)	(0.44)	(1.68)	(0.00)
Clinton	**L**	28	56.4	16.7	3.1	1.3	1.8
			(4.44)	(8.91)	(4.87)	(1.01)	(1.25)
	M	16	38.4	9.9	1.5	1.0	1.1
			(5.57)	(6.35)	(1.08)	(0.59)	(0.34)
	S	10	30.4	10.3	0.9	1.8	1.2
			(2.40)	(11.56)	(0.59)	(1.02)	(0.63)
Flat	**L**	7	50.5	11.2	1.1	1.1	1.1
			(1.38)	(5.39)	(0.49)	(0.35)	(0.38)
	M	29	40.6	11.0	1.1	1.8	1.5
			(5.78)	(5.23)	(0.83)	(1.49)	(0.83)
	S	14	27.8	6.9	0.7	2.7	1.2
			(4.43)	(2.80)	(0.69)	(1.77)	(0.58)
Halsey	**L**	31	56.5	13.5	3.6	1.6	1.6
			(4.89)	(6.26)	(6.73)	(1.59)	(0.88)
	M	21	37.0	8.9	1.2	1.6	1.3
			(2.68)	(4.03)	(0.68)	(1.21)	(0.56)
	S	5	30.0	7.3	0.4	4.6	1.0
			(1.87)	(4.59)	(0.32)	(3.54)	(0.00)
Iron	**L**	15	54.0	17.2	1.3	1.4	1.3
			(3.33)	(9.72)	(0.81)	(0.92)	(0.72)
	M	27	41.4	14.1	1.0	1.7	1.1
			(4.21)	(8.20)	(0.84)	(1.21)	(0.60)
	S	2	28.5	15.5	1.7	1.5	1.0
			(0.71)	(9.25)	(1.94)	(1.67)	(0.00)
Yellowdog	**L**	30	55.5	13.4	1.7	1.7	1.3
			(3.25)	(4.65)	(1.36)	(2.50)	(0.60)
	M	27	42.5	12.1	1.6	1.6	1.1
			(3.18)	(5.45)	(1.63)	(1.45)	(0.60)
	S	5	26.6	16.0	1.4	1.0	1.0
			(2.97)	(4.01)	(0.95)	(0.62)	(0.00)
LARGE		133	54.6	13.4	2.0	1.6	1.5
			(2.23)	(3.35)	(1.13)	(0.53)	(0.26)
MEDIUM		142	39.9	10.4	1.2	1.8	1.2
			(2.02)	(2.75)	(0.30)	(0.59)	(0.16)
SMALL		44	28.7	10.6	1.0	2.3	1.1
			(1.41)	(4.15)	(0.48)	(1.27)	(0.10)

Table 3.12. Results of chi square tests between age 0 habitat units containing only large or small individuals, shown as counts with habitat units containing small individuals corrected for differences in sample size. *indicates that Yates' correction was applied. N=number of expected cells in the chi square test. BO=bedrock and boulder, SaSiO=sand, silt, and organic material. See Figure 3.2 for unit type abbreviations.

Variable	**Small**	**Large**	**N**	χ^2	**p**
DomSub			5	131.5	<0.005
BO	12	17			
Cobble	67	63			
Gravel	39	37			
Pea gravel	15	4			
SaSiO	1	12			
AqPred			3	208.9	<0.005
Yes	15	66			
Limited	118	63			
No*	0	4			
TePred			3	1679.2	<0.005
Yes	12	19			
Limited	121	73			
No	0	41			
Type			7	479.2	<0.005
LH	21	81			
PIP	67	23			
IP*	0	1			
FWR*	0	8			
SWR*	42	0			
CWP*	0	13			
LPM*	3	7			
HDiv			2	4.0	<0.05
Diverse	67	55			
Uniform	67	78			

Table 3.13. Unit type habitat and age 0 westslope cutthroat trout occupancy characteristics. Unit abbreviations refer to those used in Table 3.1. Standard deviation given in parentheses. COV = coefficient of variation. COV length is calculated for only units containing more than one fish and refers to length variation within unit.

Unit Type	Unit Code	Mean Depth (cm)	COV Depth	Unit Area (m^2)	Total Length (mm)	COV Length	# Age 0/Unit	Age 0 Density ($\#/m^2$)	% Units
Isolated Pool	IP	10.7 (7.10)	0.27 (0.14)	1.3 (0.94)	45.3 (11.1)	--	1.0 (0.00)	1.6 (1.86)	7.8
Partially Isolated Pool	PIP	10.1 (4.76)	0.33 (0.12)	1.4 (1.19)	40.1 (9.7)	0.13 (0.09)	1.6 (1.17)	1.8 (1.58)	30.7
Large Pool Margin	LPM	21.5 (7.61)	0.29 (0.14)	2.2 (2.16)	45.7 (9.9)	0.11 (0.07)	1.8 (1.56)	1.6 (1.54)	4.4
Lateral Habitat	LH	12.7 (6.12)	0.26 (0.10)	1.4 (1.30)	49.6 (8.8)	0.10 (0.06)	1.6 (1.09)	1.9 (1.69)	38.1
Fast Water Riffle/Run	FWR	17.2 (13.01)	0.24 (0.10)	0.6 (0.26)	49.3 (6.8)	0.11 (0.10)	1.7 (0.72)	3.6 (2.01)	3.8
Slow Water Riffle/Run	SWR	7.6 (3.61)	0.31 (0.11)	1.2 (0.90)	34.5 (5.3)	0.08 (0.04)	1.6 (1.12)	2.0 (1.62)	15.9
Channel-Wide Pool	CWP	15.9 (8.21)	0.31 (0.09)	8.4 (10.23)	47.9 (9.7)	0.08 (0.05)	3.0 (5.16)	0.8 (0.64)	6.4

Table 3.14. Habitat unit categorical variable characteristics. Numbers given are percentages of units. One category per variable is not presented but may be obtained by subtraction.

Unit Type	Unit Code	Loc Main	Source B	Source W	TePred N	TePred Y	AqPred N	AqPred Y	Canopy C	Canopy O	HDiv D	Sculp Y
Isolated Pool	IP	100.0	0.0	100.0	33.3	0.0	100.0	0.0	66.7	0.0	33.3	66.7
Partially Isolated Pool	PIP	94.4	75.8	19.4	15.3	8.1	4.0	25.8	18.5	11.3	47.6	77.4
Large Pool Margin	LPM	100.0	16.7	72.2	0.0	38.9	0.0	72.2	11.1	33.3	50.0	94.4
Lateral Habitat	LH	95.4	35.5	36.2	8.6	24.3	2.0	43.4	8.6	9.9	36.8	75.7
Fast Water Riffle/Run	FWR	100.0	26.7	73.3	18.6	43.8	0.0	62.5	0.0	31.3	43.8	68.8
Slow Water Riffle/Run	SWR	100.0	21.9	21.9	6.3	1.6	1.6	6.3	1.6	18.8	46.0	87.5
Channel-Wide Pool	CWP	60.6	12.1	60.6	3.0	18.2	3.0	33.3	3.0	0.0	72.7	90.0

Table 3.15. Habitat unit dominant substrate characteristics. Numbers given are percentages of units.

Unit Type	Unit Code	BBO	C	G	PG	SSIO
Isolated Pool	IP	0.0	0.0	33.3	33.3	33.3
Partially Isolated Pool	PIP	25.0	46.8	16.9	7.3	4.0
Large Pool Margin	LPM	5.6	72.2	16.7	0.0	5.6
Lateral Habitat	LH	13.2	36.8	30.3	3.3	16.5
Fast Water Riffle/Run	FWR	6.3	25.0	43.8	12.5	12.5
Slow Water Riffle/Run	SWR	0.0	59.4	35.9	1.6	3.1
Channel-Wide Pool	CWP	3.0	42.4	39.4	3.0	12.1

Table 3.16. Summary statistics of differences in continuous habitat variables between habitat units occupied by heterogeneous (HE) and homogeneous (HO) size mixtures by stream. Standard deviation given in parentheses. COV=coefficient of variation.

Stream		**N**	**Unit Average Depth (cm)**	**Unit COV Depth**	**Unit Area (m^2)**	**# Age 0/Unit**	**Age 0 Density (#/m^2)**
Cabin	**HE**		11.1	0.25	1.1	3.5	3.5
			(5.82)	(0.12)	(0.57)	(2.27)	(1.85)
	HO		8.7	0.29	1.0	2.6	3.7
			(2.59)	(0.10)	(0.72)	(1.08)	(2.58)
Clinton	**HE**		13.6	0.29	3.9	3.2	1.5
			(7.54)	(0.12)	(4.67)	(1.11)	(0.98)
	HO		14.9	0.26	2.7	2.9	1.4
			(5.15)	(0.12)	(1.80)	(1.07)	(0.85)
Flat	**HE**		12.0	0.33	1.5	2.7	2.8
			(3.75)	(0.07)	(1.02)	(0.93)	(1.79)
	HO		10.4	0.29	1.5	2.5	2.7
			(4.83)	(0.07)	(1.01)	(0.67)	(1.97)
Halsey	**HE**		13.1	0.26	4.1	4.4	1.6
			(4.02)	(0.07)	(3.66)	(2.70)	(0.77)
	HO		12.6	0.30	3.6	2.4	1.4
			(6.40)	(0.10)	(3.84)	(0.70)	(0.83)
Iron	**HE**		13.8	0.30	4.1	4.1	1.9
			(9.85)	(0.13)	(7.96)	(5.64)	(1.27)
	HO		14.5	0.26	1.6	2.8	2.1
			(5.31)	(0.13)	(0.75)	(0.84)	(0.94)
Yellowdog	**HE**		11.4	0.40	2.4	2.3	1.5
			(4.70)	(0.10)	1.85	(0.76)	(0.99)
	HO		15.0	0.27	1.8	2.4	2.7
			(4.07)	(0.10)	1.28	(0.73)	(3.38)
HE average			**12.5**	**0.30**	**2.9**	**3.4**	**2.1**
			(1.16)	**(0.05)**	**(1.37)**	**(0.81)**	**(0.82)**
HO average			**12.7**	**0.3**	**2.0**	**2.6**	**2.3**
			(2.34)	**(0.02)**	**(0.90)**	**(0.45)**	**(0.92)**

Table 3.17. Results of chi square tests between age 0 habitat units occupied by age 0 westslope cutthroat trout of heterogeneous (HE) and homogeneous (HO) size structures, shown as counts with habitat units containing homogeneous size structures corrected for differences in sample size. *indicates that Yates' correction was applied. N=number of expected cells in the chi square test. BO=bedrock and boulder, SaSiO=sand, silt, and organic material. See Figure 3.2 for unit type abbreviations.

Variable	**HE**	**HO**	**N**	χ^2	**p**
DomSub			5	3.2	NS
BO	11	7			
Cobble	33	34			
Gravel	18	21			
Pea gravel	2	3			
SaSiO	8	7			
HDiv			2	0.9	NS
Diverse	33	37			
Uniform	38	34			
Type*			6	5.7	NS
LH	25	33			
PIP	23	17			
FWR*****	5	3			
SWR	11	9			
CWP*****	5	7			
LPM*****	3	2			

CHAPTER 4

OVERWINTER SIZE-SELECTIVE MORTALITY AND LIFE HISTORY DIFFERENCES ACROSS A TEMPERATURE GRADIENT IN AGE 0 WESTSLOPE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI LEWISI*)

ABSTRACT

Size-selective mortality in age 0 fishes has been widely documented and the relationship between larger size and survival during the first year has been well documented. Adaptations increasing growth rate and first year size may develop in populations confined to a limited growth environment; life history characteristics may be relaxed in more moderate environments. Ultimately, within-population size variation may vary across gradients in growth potential due to differential pressure to achieve sufficient size for overwinter survival. I tested for the presence of size-selective overwinter survival and life history differences in age 0 westslope cutthroat trout from two streams in the Coeur d’ Alene subbasin of northern Idaho, U.S.A. that differ in their growth environment. I examined two growth responses, growth maintenance under colder conditions and compensatory growth during temperature conditions conducive to growth, that could increase size in a cold unproductive stream. I also examined whether size at emergence was larger in the colder stream. I hypothesized that the emergence window would be longer in the warmer stream since the summer growth season is longer and later emergents may still reach sufficient size to survive winter. I used the growth record available in sagittal otoliths to test for differences between fish collected pre- and post-winter during 2000-01 and 2001-02. Average growth rate differed significantly between pre- and post-winter fish during 2001-02 but not 2000-01. The direction of change differed between the two streams, favoring faster growth in the warmer stream and slower growth in the colder stream. Fish in the warmer stream emerged earlier and displayed an emergence window 9 days longer than in the colder stream during each year. Fish in the colder stream maintained growth at colder temperatures. Size at emergence was also significantly larger in the colder stream. Overwinter selection for high growth rate and longer emergence windows in the warmer stream suggest the relaxation and diversification of life

history characteristics in more moderate environments. Phenotypic responses contributing to increased growth and pre-winter size of age 0 trout in the cold unproductive stream is evidence for the importance of early growth in juvenile fishes. Because cutthroat trout in naturally cold streams may contain less variation, they may be less resilient to disturbance. Finally, streams at temperature extremes may contain intra-specific variation that is important to conserve.

INTRODUCTION

Overwinter size-selective mortality favoring larger individuals has been well-documented under natural and laboratory conditions (e.g. Post and Prankevicius 1987; West and Larkin 1987; Henderson et al. 1988; Post and Evans 1989; Miranda and Hubbard 1994; Smith and Griffith 1994; Griffiths and Kirkwood 1995; Meekan and Fortier 1996; Kirjasniemi and Valtonen 1997; Meyer and Griffith 1997; Schultz et al. 1998; Sutton and Ney 2001) and as reviewed by Sogard (1997). However, smaller individuals may be favored under some circumstances (Gleason and Bengtson 1996; Connolly and Petersen 2003). For example, Connolly and Petersen (2003) found overwinter survival of age 0 steelhead (*Oncorhynchus mykiss*) favored smaller individuals under conditions of unusually high temperatures coupled with limited food supply, since increased metabolism during food shortage detrimentally affected larger fish more than smaller fish. A lack of consistent size selection may also occur, for example in temporally variable environments (Stearns 1989; Scheiner 1993). Good et al. (2001) found size-selective summer mortality in Atlantic salmon (*Salmo salar*) to favor larger individuals during a drought year and smaller individuals during a flood year. When size selection does not occur, size variation might still be encouraged since size-based niche separation may reduce competition for limited resources (Utter 1981; Healey and Prince 1995; Skulason and Smith 1995). Size-selective mortality can be demonstrated through several approaches, as summarized in Appendix 4.1.

Examination of the extent and spatial distribution of size variation and environmental characteristics associated with growth can shed light on ecological and evolutionary factors shaping a species' life history (Hutchings 1991; Conover and Schultz 1995). Variation within a population may suggest either the absence of strong directional selection or limited resources and intraspecific competition. For example, I found in Chapter 2 that within a stream, age 0 westslope cutthroat trout from warmer downstream sites were larger and more diverse in size than those from upstream cooler sites. In Chapter 3, I showed that distribution of age 0 trout among habitats was size-based, potentially reducing intraspecific competition. In spite of apparent advantages, size variation may be limited by the degree of overwinter size-biased mortality. Emergence timing has been linked to spawning timing, temperature in the redd, and size going into winter (Henderson et al. 1988; Einum and Fleming 2000), with progeny of earlier spawners emerging earlier and larger going into winter. Among-site variation in duration of emergence may then correspond to degree of overwinter size-selective mortality. Fish populations in harsh environments could be expected to have a narrower emergence window.

Size variation among populations may indicate the presence of environmental gradients influencing growth. Absence of size variation among populations, however, may have multiple causes. It may indicate the absence of strong environmental gradients influencing growth. It might also indicate the presence of adaptive mechanisms acting to counteract growth limitations, since diversification in some traits may serve to minimize variation in others more closely tied to fitness (Caswell 1983; Thompson 1991). Adaptation can serve to counteract environmental gradients restricting critical life functions such as growth, even potentially producing countergradient variation, or variation in the opposite direction from that expected (Conover and Schultz 1995). Several adaptations are possible that allow organisms to maintain growth and maximize fitness under size-selective population pressures, and include the well-documented elevation of maximum growth rate relative to populations experiencing more moderate conditions, producing countergradient growth (e.g. Conover 1990; Conover and Present 1990; Mortensen and Damsgard 1993; Schultz et al. 1996; Conover et al. 1997; Nicieza and Metcalfe 1997; Yamahira and Conover 2002). Other adaptations include a shift in tolerance to a lower range of temperatures and greater maternal contribution per offspring through larger egg size. Beacham and Murray (1990) conducted a comparative analysis of Pacific salmon (*Oncorhynchus* sp.) species' relationships to temperature and found maximum juvenile size and growth rate to occur at different temperatures for different species. Yamahira and Conover (2002) found maximum growth rates of a northern latitude silverside (*Menidia* sp.) species to occur at colder temperatures than a more southern closely-related species.

Life history theory suggests that when survival is size selective favoring larger individuals, evolution may be toward greater investment per egg (Roff 1992). Otolith nucleus size and size at emergence reflect yolk quantity and egg size (McKern et al. 1974; Hutchings 1991) and egg size has been closely correlated with fry length after yolk has been fully consumed (Beacham et al. 1985; Beacham and Murray 1990; Ojanguren et al. 1996; Einum and Fleming 2000). Egg size has been shown to reflect environmental variability (Kaplan and Cooper 1984; Ojanguren et al. 1996), including limited food supply (Hutchings 1991). A potentially adaptive mechanism for increasing juvenile body size in growth-limited environments is through greater maternal contribution to the next generation by producing larger eggs, resulting in increased size at emergence and body size through critical early growth stages.

Otolith microstructure has, in many examples, proven to be a useful record of an individual's daily growth (Sogard 1991). Daily increment deposition has been documented for most salmonids (e.g. Wilson and Larkin 1980; Marshall and Parker 1982; Neilson and Geen 1982; Volk et al. 1984; Wright et al. 1991; Paragamian et al. 1992; Meekan et al. 1998; Courtney et al. 2000; Zhang and Beamish 2000 and see summary Table 4.10 in Appendix 4.2) including rainbow trout (*Oncorhynchus mykiss*; Wilson and Larkin 1980; Campana 1983; Mugiya 1987a; Mugiya 1987b), a species closely related to cutthroat trout (Stearley and Smith 1993). Increment width has been found to provide an accurate index of growth (e.g. Pannella 1980; Miller and Storck 1982; Wilson and Larkin 1982; Volk et al. 1984; Campana and Neilson 1985; Bradford and Geen 1987; Thorrold and Williams 1989; Fukuwaka 1996; Fukuwaka 1998; Courtney et al. 2000). Although some (e.g. Marshall and Parker 1982; Mosegaard et al. 1988; Molony and Choat 1990; Wright et al. 1990; Bradford and Geen 1992; Secor and Dean 1992; Francis et al. 1993; Bestgen and Bundy 1998) have found a weak or "uncoupled" body:otolith size relationship, most sources of body to otolith size uncoupling are across short time periods or changing conditions or result from inattention to methodolgical constraints.

From the otolith record of daily increments and growth rates, life history information including hatch and emergence dates, age, growth, and occurrence of environmentally-induced stresses experienced by the individual or population can potentially be elucidated since major life history events such as hatching and emergence are stressful and leave unique signatures on the otolith (Campana and Neilson 1985). For example, otolith increment counts have been used to calculate and compare emergence dates and relative ages among and within sites (Graham and Townsend 1985; Thorrold and Williams 1989; Greenberg and Brothers 1991; Warlen 1992; Betsill and Van Den Avyle 1997; Bulak et al. 1997; Morales-Nin and Aldebert 1997).

The objectives of this study were to explore relationships between growth conditions and overwinter size-selective mortality and life history characteristics that may differ across a growth potential gradient. Because I could not link otolith size and body size of post-winter fish, and otolith size is a product of average increment width (growth rate) and number of increments (fish age), I examined overwinter selection for each of these size-associated characteristics. I selected sites on two streams in northern Idaho, U.S.A. that differ in growth conditions, particularly temperature and conductivity, a surrogate for productivity (see Chapter 2). I used the growth history available in sagittal otoliths of fish collected immediately prior to and following the winters of 2000-01 and 2001-02 to compare age 0 cutthroat trout growth and life history characteristics within and between sites. My specific hypotheses were: 1) overwinter size-selective mortality favoring large size would be more likely to be observed in the cold unproductive stream and in either stream during unusually harsh winters, 2) a wider emergence window would be more likely to be seen in the warm than in the cold stream, and 3) growth and emergence characteristics resulting in larger body size would be expected in the cold stream.

METHODS

Winter Conditions

Climatic data for November through the following May were used to characterize winter conditions for 2000-01 and 2001-02. Mean monthly temperature and total monthly precipitation data were obtained from the National Oceanographic and Atmospheric Administration (NOAA) Weather Service for the Kellogg weather station (COOPID #104831, latitude 47:32, longitude 116:08; NOAA 2003). Variables MNTM (monthly mean temperature), DPNT (departure from normal monthly temperature), TPCP (total monthly precipitation), and DPNP (departure from normal monthly precipitation) were used. Normal values were calculated as the difference between actual and departure values. Monthly stream flow data were obtained from the U.S. Geological Service for the gauge station on the North Fork Coeur d’ Alene River above Shoshone Creek near Prichard, Idaho (Station #12411000, latitude 47:42, longitude 115:58). Normal values were calculated as mean values for the period of record, from 1954 for precipitation and temperature data and from 1951 for flow data.

Sample Collection

The study was conducted on Tom Lavin and Brown creeks (Figure 4.1) in the North Fork Coeur d’ Alene River drainage, northern Idaho. These streams were selected for their differences in temperature and productivity, characteristics potentially affecting growth (Table 4.1). At the collection site, Brown Creek is a relatively large, low elevation, productive (high conductivity), warm stream whereas Tom Lavin Creek at the collection site, is high elevation, small, cold, and unproductive. Both streams have had some timber harvest within their drainages above the collection sites, but aquatic habitat quality is high relative to embeddedness, water quality, availability of instream habitat and woody debris, and streamside vegetation. Brown Creek at the collection site has a road paralleling it along the edge of the valley. Effects of the road on instream conditions are likely to be minimal since the valley is relatively wide at the collection site and substantial vegetation exists between the road and channel. The Tom Lavin Creek study site generally has higher age 0 trout densities than the Brown Creek study site (Chapter 2).

Age 0 westslope cutthroat trout were collected by backpack electrofishing and sacrificed from the upper reach of Tom Lavin Creek and the lower reach of Brown Creek in fall and early spring, 2000-01 and 2001-02. Fish length was measured and otoliths were removed.

Temperature recorders (HOBO H1 TEMP datalogger, Onset Computer Corporation), set to record temperature hourly, were placed in each stream in spring to early summer and removed during the final fish collection in the fall of each year. Temperature sequences obtained were: 2000: Brown Creek, July 7 – September 4, Tom Lavin Creek, July 19 – September 6; 2001: Brown Creek, May 12 – October 13, Tom Lavin Creek, June 3 – October 13. During 2001, date of first emergence was approximated for each site by visual observation and/or sampling with an electrofisher for 30-60 minutes per site weekly until age 0 fish were first located.

Otolith Analysis

Sagittal otoliths were used in all analyses. Because left and right otoliths may differ in size (McKern et al. 1974; Neilson and Geen 1982), the left otolith was used whenever possible to avoid potential bias from otolith selection. Right otoliths were used only when the left was abnormal or lost during collection or preparation. Otoliths for which calcium deposition was vateritic, the emergence mark could not be definitively identified, or any significant abnormality in increment deposition was observed along the desired radius were discarded from the sample. Otoliths were mounted on glass slides with thermoplastic resin, ground using 2000 and 1200 grit sandpaper and 9 and 3 μm lapping paper, flipped, and ground similarly on the second side until the emergence mark and daily increments were clearly visible.

Otoliths were viewed with a light microscope through a blue filter at 400X for otolith radius measurement and emergence mark identification and at 1000X for increment width and growth zone measurement. A consistent radius in the dorsal posterior region from the most dorso-posterior primordium approximately 125^{o} relative to the primary axis through the nucleus was used for all increment measurements to avoid problems with nucleus definition and because otolith growth proceeds from individual primordia outwards (Neilson et al. 1985). All measurements except increment width were made twice by the same reader.

To test for a relationship between otolith size and body size, I measured the distance from the emergence mark (see below) to the otolith edge along the radius defined above, for pre-winter fish, and regressed body size on this post-emergence growth zone. Because the growth zone width is a function of increment number and mean increment width, I tested the relative importance of these variables to body length through linear regression. Methods used for quantifying increment number and increment width are described below.

Daily increments have two phases, an organic/protein (hyaline) phase and a calcium phase, usually described as clear and opaque, respectively (Pannella 1980; Mugiya 1987b), although physical descriptions relating to the identity of each band have in some cases been reversed (Campana and Neilson 1985). The organic and calcareous phases are deposited during periods of slow and fast growth, respectively (Pannella 1980), on both daily and annual cycles. Emergence is a stressful period, during which feeding and therefore growth is disrupted and larval fish switch nutrient source from yolk to exogenous feeding. The appearance of the otolith at emergence therefore reflects these stresses, with a stress check consisting of a wider than average translucent zone (cessation of feeding) bordered by a dark band, followed by a series of narrower than average daily increments indicating reduced growth rate during disruption and conversion to exogenous feeding (West and Larkin 1987; Zhang et al. 1995). This stress check has also been referred to as a first-feeding check (Marshall and Parker 1982; Wright et al. 1991; Zhang et al. 1995). For most otoliths examined in this study, the stress check and abrupt decrease in increment width occurred within three increments of each other. In a small number of otoliths the increment width decrease was transitional, with a moderate decrease after the stress check followed up to 7 increments later by a sharper and more extreme decrease in increment width. In these cases, I measured the emergence mark as the outer, later, of the two marks, consistent with (Meekan et al. 1998), who found that emergence followed yolk sac consumption by several days in Atlantic salmon.

Emergence mark appearance was validated through examination of known-age hatchery and wild-caught westslope cutthroat trout. Hatchery westslope cutthroat trout were obtained 84 days post-swimup and a small number of wild fish 22-25 mm in length were collected in spring, 2000 from the study sites and adjacent streams. Age of wild fish was estimated using growth rate estimates from Chapter 2 (see Appendix 2.1).

Daily increment formation was assumed for westslope cutthroat trout in this study since it has been validated for rainbow trout and most other salmonids, as summarized in Appendix 4.2. Increment counts beyond the emergence mark of hatchery and wild fish otoliths used for emergence mark validation were compared to expected counts as an additional measure for confirming daily increment formation.

Counting all daily increments from a known life history event such as emergence outwards to fish collection is the simplest method for obtaining individual fish age and date of emergence. However, in many cases all increments are not clearly visible and total counts are methodologically challenging to obtain (Campana 1992). To obtain estimated increment counts, I varied the method of Ralston and Williams (1988). They used average increment width to calculate growth rate, related growth rate to otolith size, and then integrated the data to provide an estimate of age at various points on the otolith. I measured the width of a daily increment every 210 μm from the emergence mark to the edge (pre-winter samples) or until individual daily increments could no longer be reliably identified (post-winter samples). and calculated the number of increments occurring between measured increments (210 μm divided by measured increment width). This method produced increment width measurements every five to 20 increments (days), depending on increment width, and 7 to 13 increment width measurements per otolith for most collections, depending on otolith size and collection date. Increment width ranged from 11 to 42 μm across streams and years.

Overwinter selectivity for age and growth rate were examined by reconstructing each individual's growth series forwards from emergence and calculating average increment widths for each individual for periods of varying duration after emergence. Bradford and Geen (1987) found that the correspondence between otolith increment width and somatic growth improved across periods of 30 days or longer than across shorter periods; therefore, I calculated average increment width for 30, 45, and 75-day periods after emergence. Otolith size and potentially body size are a function of organism age as well as growth rate. I examined the effect of fish age on overwinter survival by locating on each otolith a sharp decline in increment width, occurring in the fall of each year. I assumed that this decrease in increment width, indicating a growth rate decline, occurred on the same date for all fish per stream and year. Calculating the number of increments on each otolith before this increment width decline produced the age of each individual, which I compared between pre- and post-winter individuals. To remove outliers, I assumed that post-winter fish represented a subset of pre-winter fish and established bounds on each pre-winter collection by rejecting any increment width decline occurrence if increment width was increasing in other individuals during the same period or if the date occurred before temperatures had begun to decline significantly in the fall. I applied these bounds to post-winter growth declines similarly to identify outliers.

Difference in emergence window duration between Brown and Tom Lavin creeks was tested by obtaining an approximate emergence date for each individual. I reconstructed the growth record of each pre-winter fish backwards from collection date. Summing the total number of increments per otolith produced an estimate of total increment number (fish age). Subtracting this number from the collection day of the year produced an emergence date estimate. I calculated the difference between emergence date and mean sample emergence date, and tested for differences between streams. If Brown Creek has a wider emergence date window, differences from the mean will be larger.

To examine whether fish from Tom Lavin Creek were able to maintain growth at colder temperatures than fish from Brown Creek, I compared dates of fall increment width (growth rate) decline for pre-winter fish. To test whether Tom Lavin fish had higher maximum growth rates than Brown Creek fish during periods conducive to growth, I identified periods during which the two streams had similar average temperatures. Adequate temperature conditions were not available for 2000 for pairs to be identified; therefore only data collected during 2001 were analyzed. I selected periods for which the temperature profile histories prior to the periods of interest had similar behaviors (rising, falling, or stable temperatures) as well, since some investigators have identified the presence of a time lag between change in somatic growth and otolith growth response (e.g. Neilson and Geen 1986; Molony and Choat 1990; Pepin et al. 2001; see Appendix 4.2). Average increment width was calculated for each member of each pair.

Otolith size at emergence between Brown and Tom Lavin creeks was examined by using the same radius as described above for increment width measurements and measuring the distance from the primordium to the emergence mark.

Statistical Analysis

Error rates between readings of emergence mark location (primordium to emergence mark, 40X, all fish), growth zone width (emergence mark to edge, 100X), and otolith radius (primordium to edge, 40X) were estimated using Chang's (1982) percent coefficient of variation (%CV) as described by Campana and Jones (1992). They suggest that although the %CV is a measure of precision and not a substitute for accuracy, it is a useful measure of reproducibility. Although acceptable %CV levels vary with the nature of the structure, species, and reader, a CV of 5% is commonly used as a reference point (Campana 2001).

Emergence date estimated from increment counts when compared to field observations made during 2001 suggest that my method of estimating total increment count by using increment width data extrapolated over the otolith growth zone (emergence mark to edge) overestimated the number of increments and therefore actual age. I estimated the error for Brown Creek to be 17 to 21 days (mean = 19 days) and for Tom Lavin Creek to be 7 to 15 days (mean = 11 days; Table 4.6). Because the error was greater for Brown Creek, compensatory growth analyses comparing Tom Lavin and Brown creeks could have been biased. To test for this bias, I corrected the data by assuming all increment count error occurred at the end of the growth period (outer edge of the otolith), maximizing the potential bias. It is more likely that error occurred throughout the growth period and reflects the greater number of increments on Brown Creek otoliths. I conducted the two compensatory growth analyses using both the corrected and uncorrected data. All other analyses were conducted within stream or used absolute rather than relative emergence date and were not affected by the difference in error between streams.

Emergence marks on the 84-day old hatchery fish were similar in appearance to those of wild fish. Mean increment counts underestimated known age by an average of 8 increments (mean = 76.3 increments) whereas count estimates based on subsampling increment width every 210 μm overestimated the actual count by a mean of 23 days (mean = 106.5 increments). Location of the emergence mark and increment counts outside the emergence mark in the wild fish were consistent with expectations, suggesting that increments were deposited daily.

Normality of the data was confirmed for total fish length, average increment width, age at fall daily growth rate decline, date of fall growth rate decline, otolith size at emergence, and emergence date difference from the mean through examination of box and whisker plots and normal probability plots and calculation of skewness and kurtosis coefficients. Most variables were normal in all respects. Emergence date difference from the mean for Brown Creek during 2000 displayed unacceptably high kurtosis due to an outlier that was excluded from analyses.

Linear regression was used to examine the relationship between pre-winter fish length and number of increments (fish age) and average increment width (growth rate). Two-sample t-tests were conducted on average increment width and age at fall daily growth rate decline between collection dates within stream and year to test for the presence of overwinter selection for growth rate and age, respectively, between pre-winter and post-winter individuals (H_o#1). Analysis of variance (ANOVA) including factors Stream and Year and the interaction term was used to test for differences in duration of emergence between streams (H_o#2). T-tests were conducted on each temperature pair to test for differences in growth rate when temperature was controlled, and ANOVA was used to test for a difference in fall growth rate decline day between Brown and Tom Lavin creeks during 2001-02 (H_o#3). ANOVA including factors Stream, Collection, and Year and all interaction terms was used to examine differences in otolith size from primordium to emergence mark, or nutrient availability from yolk (H_o#3). A significance level of $p<0.05$ was used in all comparisons. Systat (Systat Version 8.0, SPSS, Inc. 1998, Standard Version) was used for all analyses.

RESULTS

Winter weather conditions differed between the two years. Winter temperatures in 2000-01 were colder than normal whereas in 2001-02, early winter temperatures were warmer than normal and late winter temperatures were colder than normal (Table 4.2). Total monthly precipitation was lower than normal during 2000-01 and higher than normal in 2001-02 (Table 4.2).

Of the entire sample from both streams over 2 years, 6.5% of samples were unusable (both otoliths), of which 1.1% were rejected as vateritic and 5.4% were acceptable but lost or ruined in preparation. Of the otoliths for which data were obtained, 16.0% were from right otoliths, of which 4.5% were due to vateritic left otoliths and 11.5% were due to loss or preparation problems. For Brown Creek, data were obtained from 14 (fall) and 28 (spring) otoliths during 2000-01 and from 39 and 36 otoliths during 2001-02, respectively. For Tom Lavin Creek, data were obtained from 18 and 29 otoliths during 2000-01 and 41 and 39 otoliths during 2001-02, respectively.

Percent coefficient of variation for emergence mark location, growth zone, and otolith radius was 1.13, 2.45, and 1.03%, respectively. Growth zone error rates were higher since data were recorded at 100X with greater accuracy, such that the same degree of observer visual error represented a greater length error on the otolith.

Size variation was greater in Brown Creek during both years. Average total length (mm, SD) of post-winter collections during 2001 and 2002 were: Brown Creek, 63.2 (7.8) and 65.2 (9.3), respectively and Tom Lavin Creek, 50.2 (5.8) and 50.7 (6.1), respectively. Although sample fish in pre-winter collections were larger in Brown Creek than in Tom Lavin Creek (Chapter 2), average body lengths were not directly comparable since collections were made on different dates across streams and years (Table 4.3).

The regression of total length on otolith growth zone was statistically significant ($p<0.0001$) for each stream when pooled over years as well as within year (Figure 4.2). Coefficients of determination (r^2) for the pooled data for Brown and Tom Lavin creeks were 0.798 and 0.652, respectively. Converting the data to the natural log scale did not improve the relationship (r^2= 0.814, 0.642, respectively). The slope of the relationship was higher for Brown Creek (0.19 mm/μm versus 0.11 mm/μm; Figure 4.2). Regression of total length on average increment width and number of increments was statistically significant for both streams in both years and was a function of both variables (Table 4.3). The r^2 values ranged from 0.392 to 0.799 for the four regressions (2 years X 2 streams). The contributions of increment number and increment width to predicting total length was relatively constant over the 2 years but differed between streams. Average 30-day increment width contributed more to total length for Tom Lavin Creek than it did for Brown Creek whereas increment number contributed less to total length for Tom Lavin Creek than it did for Brown Creek (Table 4.3).

Overwinter Size selection

Average growth rate was significantly different between fall and spring collections during 2001-02 but not during 2000-01 (Table 4.4, Figure 4.3). However, the direction of selective mortality was in opposite directions in the two streams, with higher growth rate averages favored in spring in Brown Creek and lower growth rate averages favored in Tom Lavin Creek. Growth rate relationships did not change significantly among averages over 30, 45, and 75 day periods after emergence with the exception of Tom Lavin Creek during 2001-02 (Table 4.4). For this period, the 30-day post emergence increment width averages were significantly different between pre- and post-winter fish, but the 45-day post emergence averages were not significantly different.

I found no evidence of overwinter selection for emergence timing (Table 4.5) for either stream (Figures 4.4, 4.5). The comparison for Brown Creek, however, was possible only during 2001-02. Brown Creek and Tom Lavin Creek average age at fall growth rate decline were 83 and 48 days, respectively, during 2001-02.

Emergence Duration

Timing and duration of emergence varied substantially between streams and years, with duration of emergence longer and earlier in Brown Creek than in Tom Lavin Creek in both years (Table 4.6). In a combined ANOVA, the difference in emergence duration was not significant for 2000 since the long emergence duration in Brown Creek was due to one early-emerging outlier. I did not discard this point from analyses since total length of this individual at collection (58 mm) compared to the sample average (45.4 mm) suggested that its early emergence date was legitimate. Emergence duration during 2001 was significantly different between streams.

Growth and Emergence Characteristics

During 2000 and 2001, daily average water temperatures in Brown Creek were 1.7 and 2.6 ^{o}C warmer, respectively than Tom Lavin Creek (Figure 4.6). The summer high temperature periods in 2000 and 2001 were July 29 to August 11 and August 9 to August 18, respectively.

Average growth rates of Brown and Tom Lavin creeks during paired 5-day periods in 2001 for which temperature averages were equal were nearly identical for the two periods examined (Table 4.7, Figures 4.6, 4.7). Correction of Brown Creek data for differences in emergence date error between Brown and Tom Lavin creeks did not affect analyses. All results presented use uncorrected data.

Fall growth rate decline occurred one day later in Tom Lavin Creek than in Brown Creek during 2001 (Table 4.8, Figure 4.8). Tom Lavin Creek was 0.8 ^{o}C colder (14-day average) at this time than Brown Creek, and averaged 2.6 ^{o}C colder during 2001 for the period for which I recorded stream temperatures. Using Brown Creek data maximally corrected for difference in emergence date error shifted the 2001 date of fall growth rate decline to October 2 for this stream and produced a significant t-test of difference in fall growth rate decline. However, the temperature at which the decline occurred was not affected by the correction (uncorrected: 9.44 ^{o}C; corrected: 9.35 ^{o}C). All 2001 results presented use uncorrected data. Although I was not able to obtain data from Brown Creek during 2000, the fall decline date for Tom Lavin Creek during 2000 was 5 days earlier than in 2001, consistent with differences between temperature profiles for the 2 years.

Otolith size at emergence was significantly different between streams and collection periods (fall versus spring) but not years (Table 4.9, Figure 4.9). Otoliths were larger from Tom Lavin Creek and from pre-winter collections. However, the ANOVA interaction term between stream and year was also significant; most of the difference between streams was seen during the 2000-01 collection.

DISCUSSION

Overwinter selection for early growth rate was evidenced in both streams in 2001-02 but not in 2000-01, suggesting temporally variable overwinter size selectivity. This is in agreement with the finding of Good et al. (2001) that size selection may vary with climatic conditions among years and suggests that size variation may have adaptive value. Winter climatic and hydrologic conditions differed between the two years, with 2000-01 colder with less precipitation than normal and 2001-02 warmer with more precipitation than normal. Variability in environmental conditions appears to maintain variation within a population, when size selection does not consistently favor one size (Stearns 1989; Scheiner 1993). Within-population size variation has value in that it allows a population to respond to unpredictable climatic conditions favoring large size in some cases and small size in others.

I predicted that overwinter selection for large size (faster growth rates) would be more likely to be seen in Tom Lavin Creek and during harsher winters. My findings of overwinter conditions favoring fast growth rates in Brown Creek and slow growth rates in Tom Lavin Creek is inconsistent with that hypothesis. In general, large size has been found to be advantageous for surviving early winter cold temperatures, since larger body size is associated with greater fat stores and tolerance of cold temperatures. The mechanism of overwinter selection in my study appears to be different, with late winter duration and flow conditions more important than early winter conditions. Colder temperatures occurred in 2000-01, the year I did not find size selection. However, 2001-02 had colder early spring conditions and deeper than average snowpack. These conditions produced a longer colder than average spring with an extended period of higher than average flows. My study site on Brown Creek was located at its downstream end where it is relatively large for a stream supporting age 0 cutthroat trout (Dunnigan 1997). Selection for large size in Brown Creek may have been the result of associated greater ability to withstand prolonged harsh late winter temperature and flow conditions rather than early winter cold temperatures in this stream.

In Tom Lavin Creek, the possibility of selection for small size and adaptation for increasing size in a growth-limited environment seems contradictory. Late winter conditions in Tom Lavin Creek during 2001-02 would have been similar to those in Brown Creek although delayed. The same mechanism of size selection may have been acting in this stream, but favoring small size. Although production of an optimal size for prevailing environmental conditions through egg size and emergence time seems likely, stochastic environmental factors after emergence generate variation that cannot be anticipated evolutionarily through maternal control (Weeks 1993). In harsh environments there may be a winter habitat availability advantage for smaller fish. Smaller individuals may be able to take advantage of smaller and potentially deeper interstitial habitats than larger individuals and may therefore be more able to withstand winter conditions, particularly if habitat is limited (Shirvell and Dungey 1983). Werner (1994) found smaller size classes of two frog species to be less susceptible to and more tolerant of intra- and interspecific competition per unit biomass than were larger size classes. Intraspecific competition in high density habitats with limited resources may represent another example of an advantage to being small.

If overwinter size selectivity does not consistently favor any one size, selection for early emergence as a mechanism for maximizing first-year growth would not be expected. I found no significant difference in emergence timing (age) between pre- and post-winter fish in either stream during either year. Although increased age contributes to absolute growth, mechanisms other than fall body size appear to be controlling emergence. Other benefits to early emergence have also been documented, for example, early emergents have early access to territories and higher quality habitats (Huntingford and de Leaniz 1997). Selection for emergence timing for first-summer benefits would have already occurred by fall, however, and would not have been reflected in my data. Benefits may also accrue to late emergents that may offset the advantage in size gained by early emergents. Possibilities include the respective temperature and flow regimes experienced by early versus late emergents and the importance of emergence timing coincidental with food item production (Betsill and Van Den Avyle 1997). Early size disadvantages of later emergence may be balanced by later growth compensation, as well, including the types of growth characteristics I examined between populations.

The emergence window was longer in lower elevation, warmer, more productive Brown Creek than in the higher elevation, colder, less productive Tom Lavin Creek, as predicted. The difference was not statistically significant during 2000, most likely due to limited sample size and the pattern was clear in 2001-02. Life history characteristics may relax in more moderate sites, such that multiple strategies for growth succeed, greater variation is evidenced, and intraspecific competition is reduced. In a harsh environment all individuals may be required to follow the same restricted scenario in order to accomplish the minimum required body size for overwinter survival and competitive pressures. Limited variation for a given life history trait can be an indicator of intense selection pressure (Chambers 1993). Selection pressure for a specific emergence period may therefore be more acute in Tom Lavin Creek than in Brown Creek. Since life history traits closely linked to fitness tend to have less variation (Stearns 1983), emergence timing may be more critical in Tom Lavin Creek than in Brown Creek. Finally, degree of plasticity for a given trait may relate to the degree of compromise among multiple traits, responsive to multiple selection pressures in a given environment (Berven and Gill 1983). My study streams may have very different selection pressures such that the ultimate balance in each produces different levels of plasticity for emergence timing.

My data suggest that fish in Tom Lavin Creek may have developed compensatory growth responses to increase body size in a harsher environment. Fish in that stream appeared to maintain growth at lower temperatures, compensate during periods conducive to growth, and have larger otoliths at emergence, presumably linked to larger egg size and body size at emergence. Both temperature responses to limited growth environments have been demonstrated in salmonids before (e.g. Beacham and Murray 1990; Mortensen and Damsgard 1993; Nicieza and Metcalfe 1997). Because my study streams differ in temperature but also productivity and density, I am not able to conclude definitively that compensatory responses are in response to temperature. And, because growth rate slows with increasing body size (Ricker 1979), larger body size in Brown Creek during compensatory growth comparisons may have confounded my results. However, Brown Creek appears to have maintained a higher growth rate that Tom Lavin Creek (Chapter 2, Appendix 2.1), suggesting that reduced growth rate as a result of larger body size in Brown Creek is not influencing this analysis but also providing conflicting evidence regarding the ability of Tom Lavin Creek fish to maintain compensatory growth rates during periods conducive to growth. I Increased size at emergence in response to growth pressure in an environment limiting growth has not been well documented. The balance between egg size and number should maximize parental fitness in a given environment (Stearns 1992); different environments might therefore be expected to display different balances. My results suggest that locally adaptive mechanisms may have developed at the scale of individual tributaries, emphasizing the importance of intraspecific diversification in maximizing early growth opportunity by age 0 salmonids.

Differences in life history and growth characteristics I observed between Tom Lavin and Brown creeks suggest that life history type composition in stream systems may be associated with productivity gradients, consistent with Gross (1987) for anadromous salmonids. Both migratory and resident life histories reside in the Coeur d’ Alene subbasin. The spatial origins of these life history types and causal processes responsible for their generation are not well understood. Tom Lavin Creek appears to contain a mixture of migratory and resident fish (B. Rieman, unpublished data), based on otolith microchemistry analysis. Although large fish that are most likely migratory have been observed in Brown Creek (K. McGrath, personal observation), little is known of the life history composition in this stream. Large body size has been associated with larger egg size as well as differences in spawning timing and therefore emergence timing, consistent with characteristics I observed in Tom Lavin fish.

If local adaptation has occurred at the scale of Tom Lavin Creek it has important management and conservation implications. Local adaptation is an important factor contributing to diversity within salmonid species, and therefore their stability and persistence (Taylor 1991). If cutthroat trout respond to their environment through adaptation at this scale, management and conservation strategies for this subspecies should also be targeted at these scales, or at least at scales consistent with the environmental gradients influencing the differences that emerge. Naturally cold streams may represent a fundamentally different environment and template for adaptation than naturally warm streams. Management actions that alter stream productivity by affecting water temperature or nutrient contribution or that target common environmental conditions across streams may contribute to loss of phenotypic variation. Maintaining natural environmental differences among streams will be important to conserve diversity generated at this scale.

Management and conservation actions may need to focus on maintaining natural patterns of habitat diversity and population density at larger scales as well, since species operate at multiple scales for different processes (Rabeni and Sowa 1996; Labbe and Fausch 2000) and in response to gradients occurring different scales (Morris 1987; O'Neill et al. 1988; Carlile et al. 1989; Lewis et al. 1996; Rabeni and Sowa 1996; Cooper et al. 1998). In Chapter 2, I found that although the stream scale contained significant variation in body size as well as size variation, larger scales contained even more variation. Westslope cutthroat trout across its range experiences wider gradients of temperature and productivity than those occurring within the Coeur d’ Alene subbasin. Adaptive mechanisms may be expected to be sharper and more defined across wider gradients and broader spatial scales and may be more likely to be genetically-based. Other important variation-generating gradients and occurrence of critical resources may occur at these broader scales, as well. Several areas for future research are apparent from the results of my study, and include 1) better understanding of relationships between genetic and life history structuring within westslope cutthroat trout and between this subspecies and other salmonid species with apparently different relationships to their environment, 2) mechanisms guiding development of local adaptation, including relationships between phenotypic plasticity within the individual and genetic structuring of adaptive response among populations, 3) better understanding of phenotypic variation, its production, and values, and relationships to temporal and spatial variability, and 4) interrelationships among life history characteristics, linked by shared response to environmental gradients. Causes, consequences, and evolutionary potential of phenotypic plasticity are important questions in the ecology and conservation of organisms in variable environments (Schlichting 1989). Better understanding of historic and current genetic structuring may help to guide management and potentially restoration of westslope cutthroat trout habitats. Understanding of adaptive mechanisms driving its development will contribute to understanding speciation processes, since intraspecific phenotypic diversification in response to environmental gradients is likely the first step toward speciation (Skulason and Smith 1995). Conservation of intraspecific diversity depends on understanding relationships between that diversity and the suite of environmental gradients, and their spatial and temporal patterns, responsible for generating that diversity (Healey and Prince 1995).

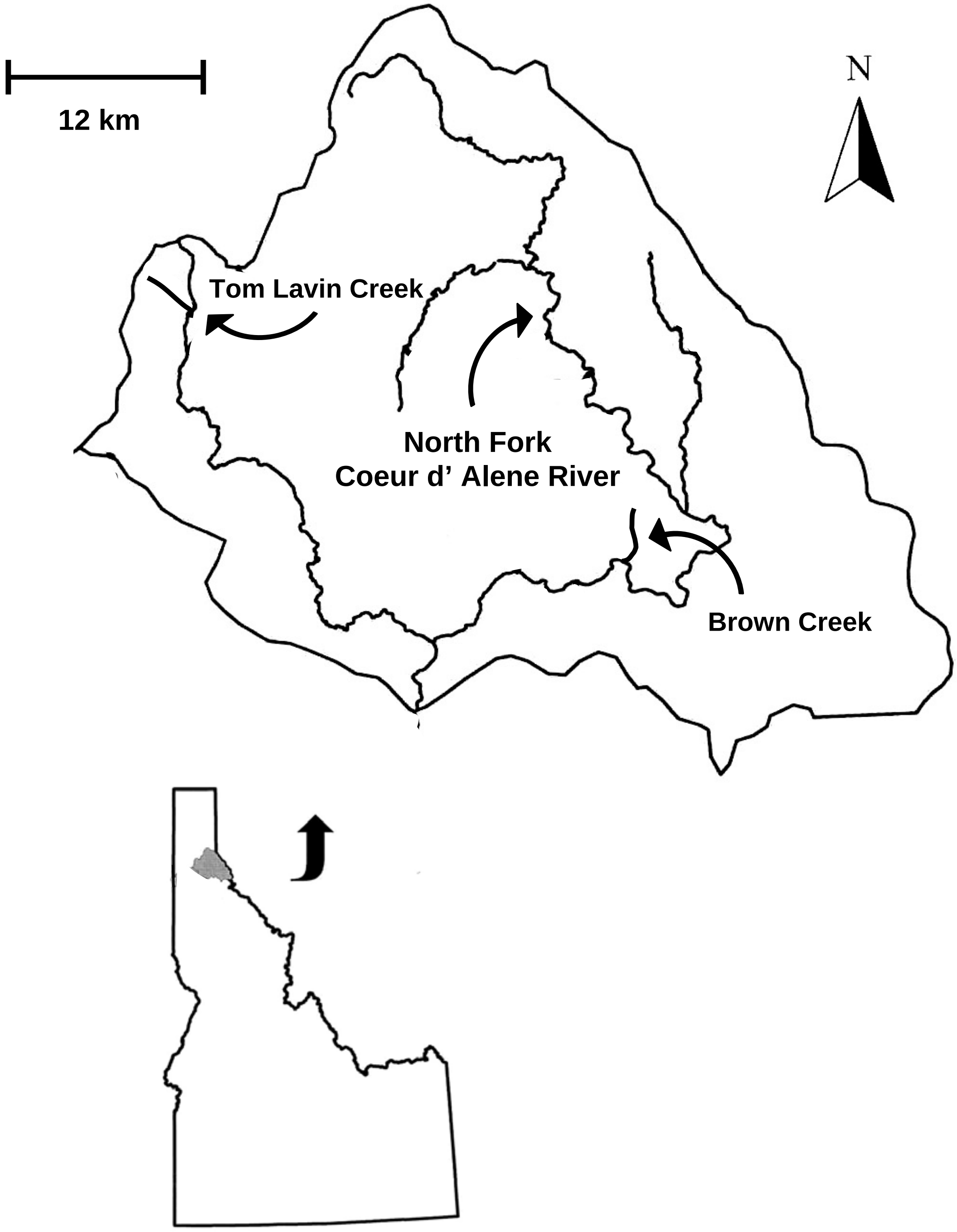


Figure 4.1. Study area in the North Fork Coeur d’ Alene River subbasin, northern Idaho.

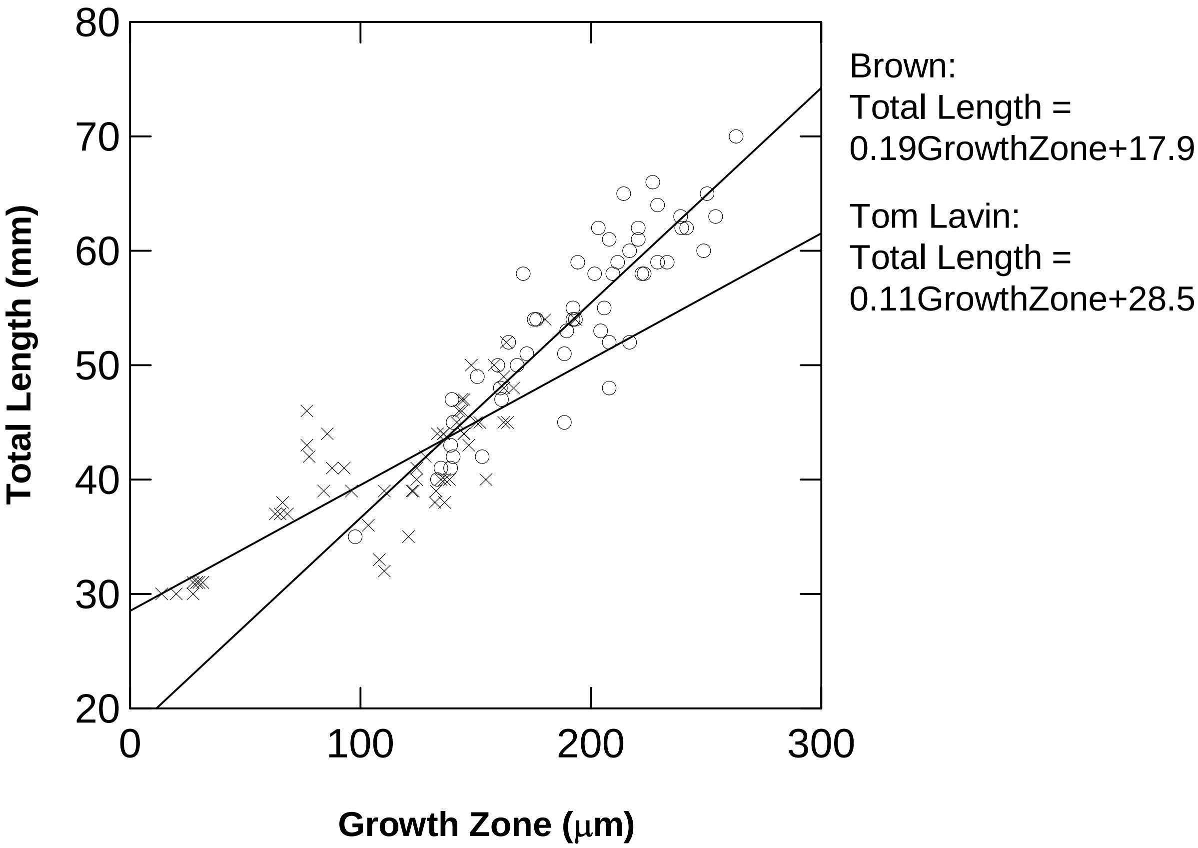


Figure 4.2. Relationship between otolith growth zone (emergence mark to otolith edge for pre-winter fish) and body total length. Regression formulas given per stream (Totlen=total length, GZ=growth zone). Data points represented by (o) and (x) are Brown and Tom Lavin creeks, respectively.

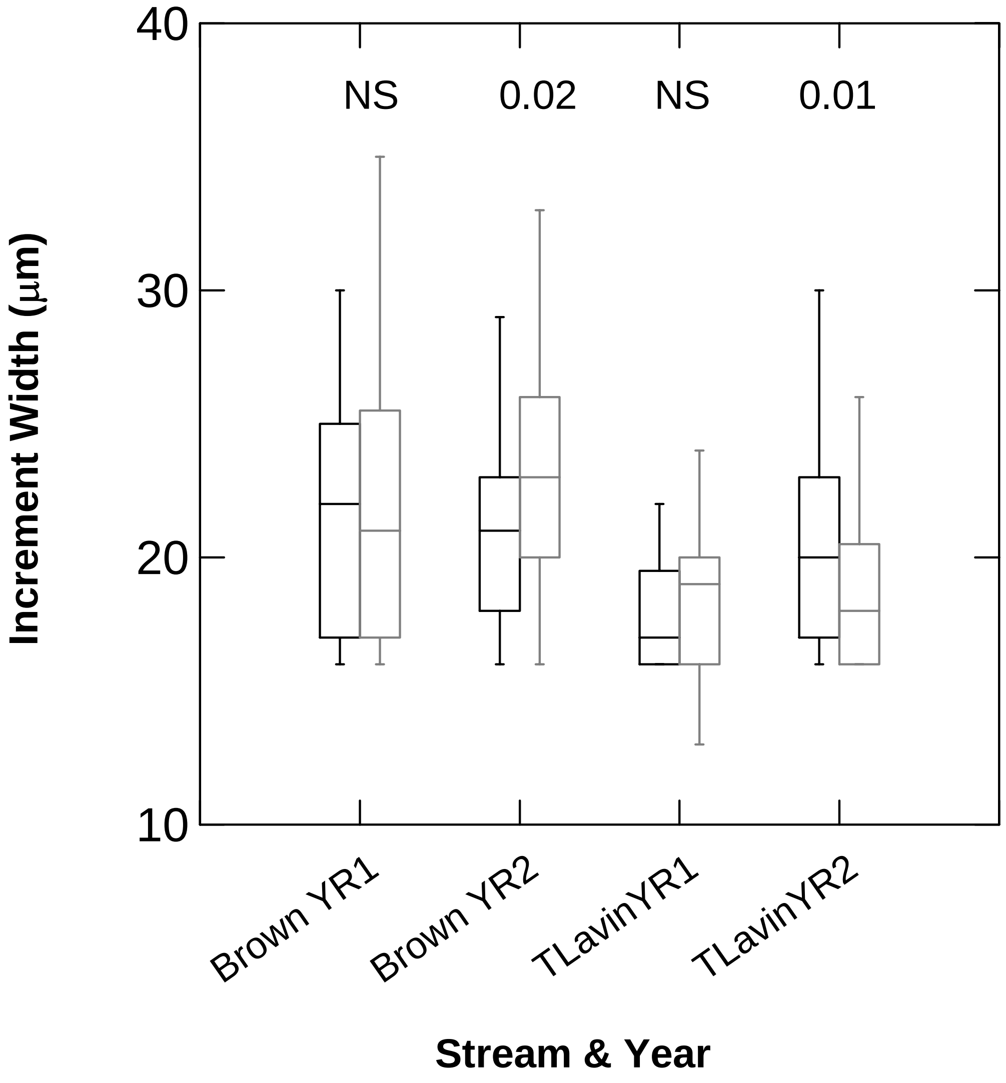


Figure 4.3. Boxplot of average otolith increment width during the first 30 days after emergence for pre-winter (in black) and post-winter (in gray) samples. Boxes represent the interquartile range, the line across the box represents the median value, and vertical lines extending from the box show highest and lowest values, excluding outliers. Outliers (asterisks) represent values that are 1.5 to 3.0 times the interquartile range. T-test significance levels given above each test pair.

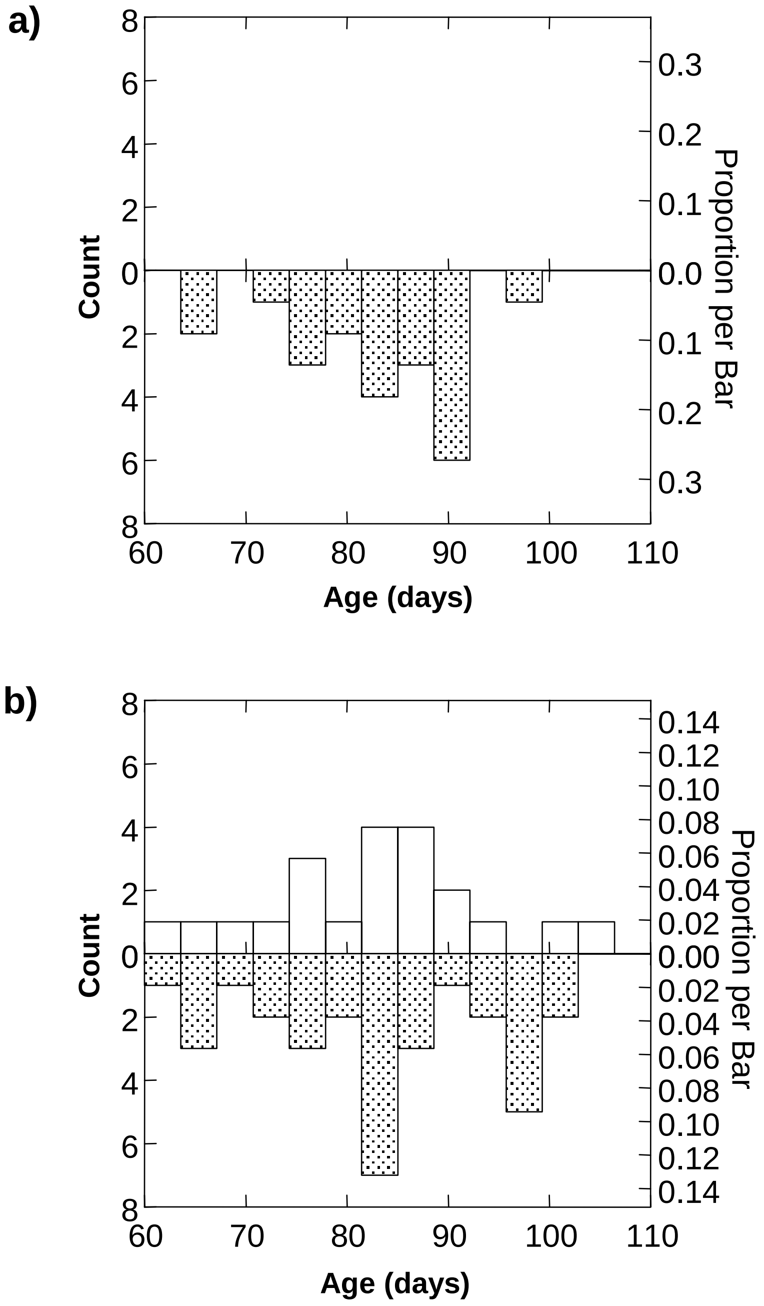


Figure 4.4. Age at fall growth rate decline, Brown Creek, from pre-winter (open bars) and post-winter (stippled bars) samples during a) 2000-01, b) 2001-02.

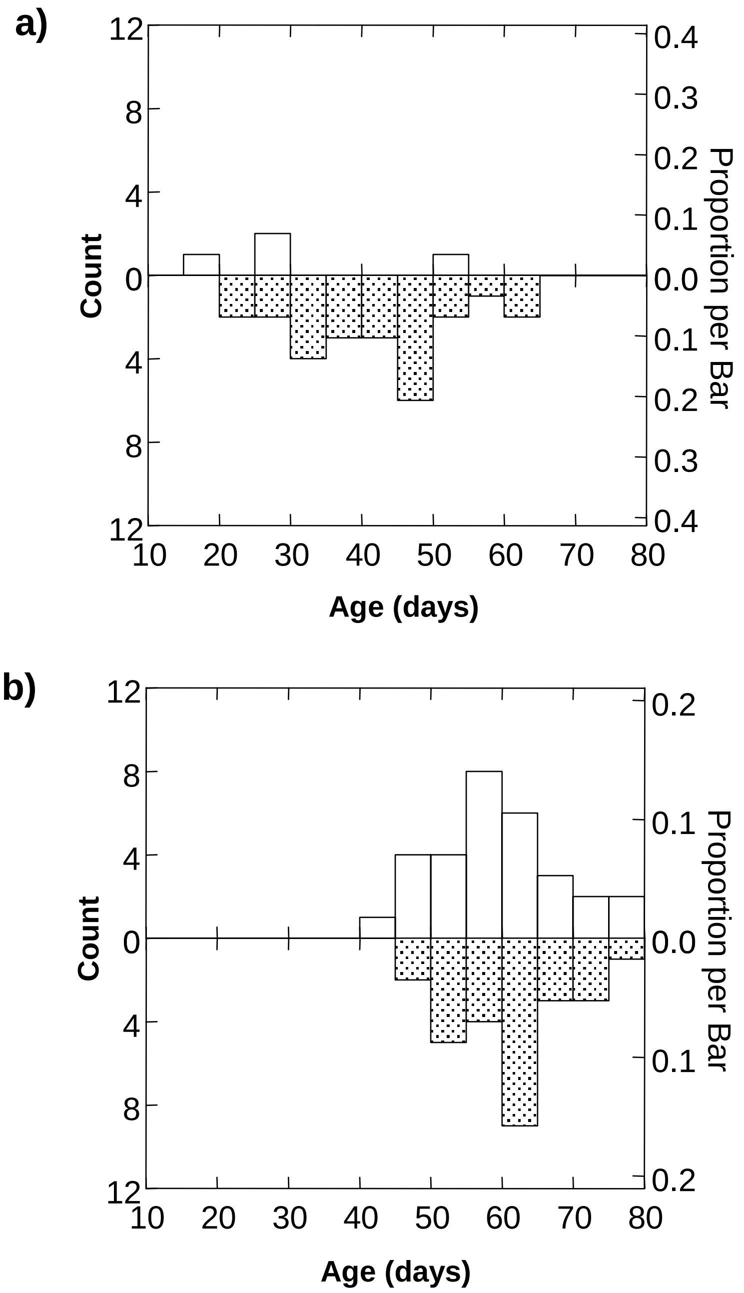


Figure 4.5. Age at fall growth rate decline, Tom Lavin Creek, from pre-winter (open bars) and post-winter (stippled bars) samples during a) 2000-01, b) 2001-02.

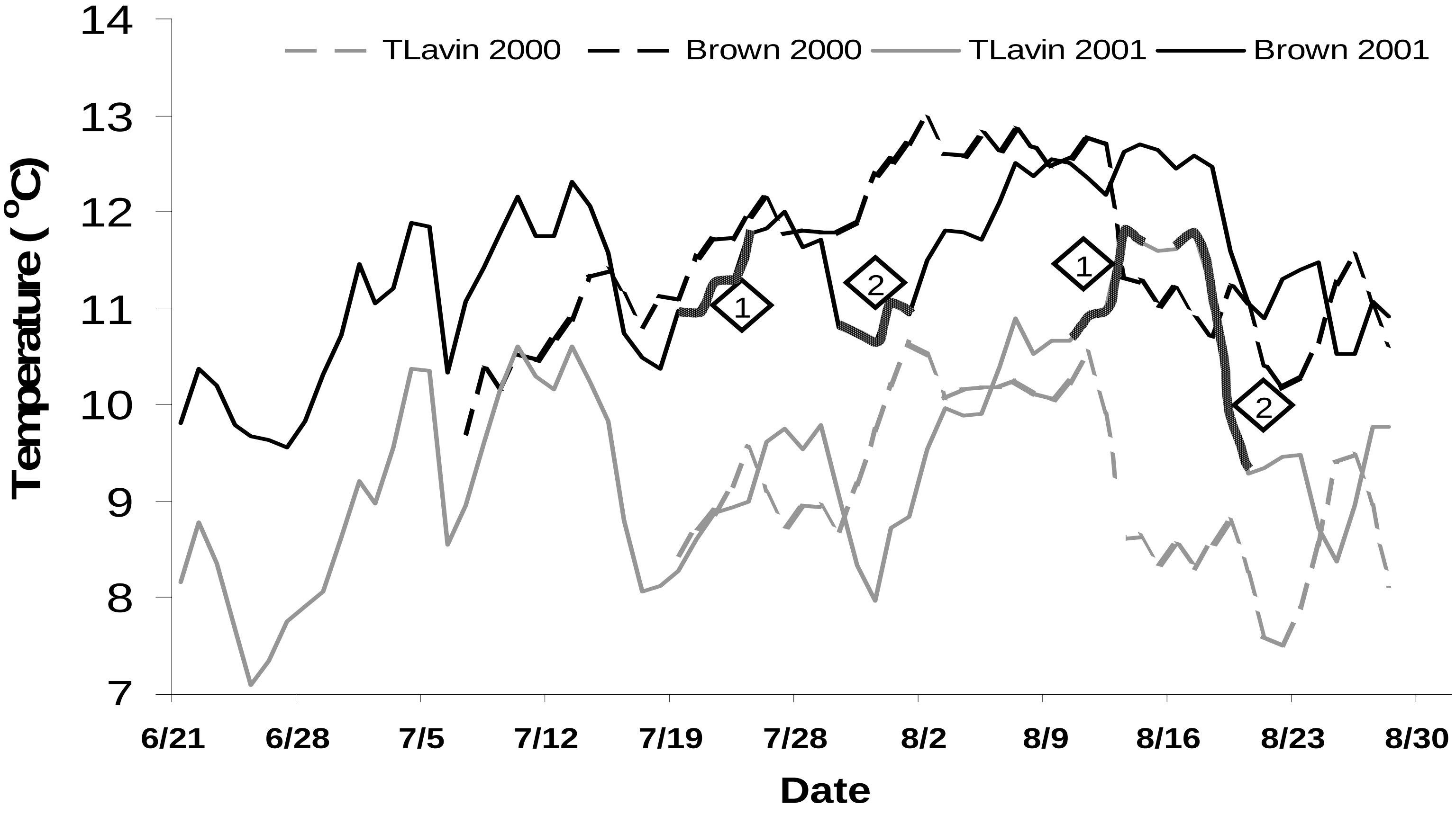


Figure 4.6. Temperature profile for Brown and Tom Lavin (TLavin) creeks, 2000-01. Numbered diamonds indicate paired periods for which average temperature was approximately equal for the two creeks and for which compensatory growth increment width averages were obtained, and correspond with Table 4.5 and Figure 4.7.

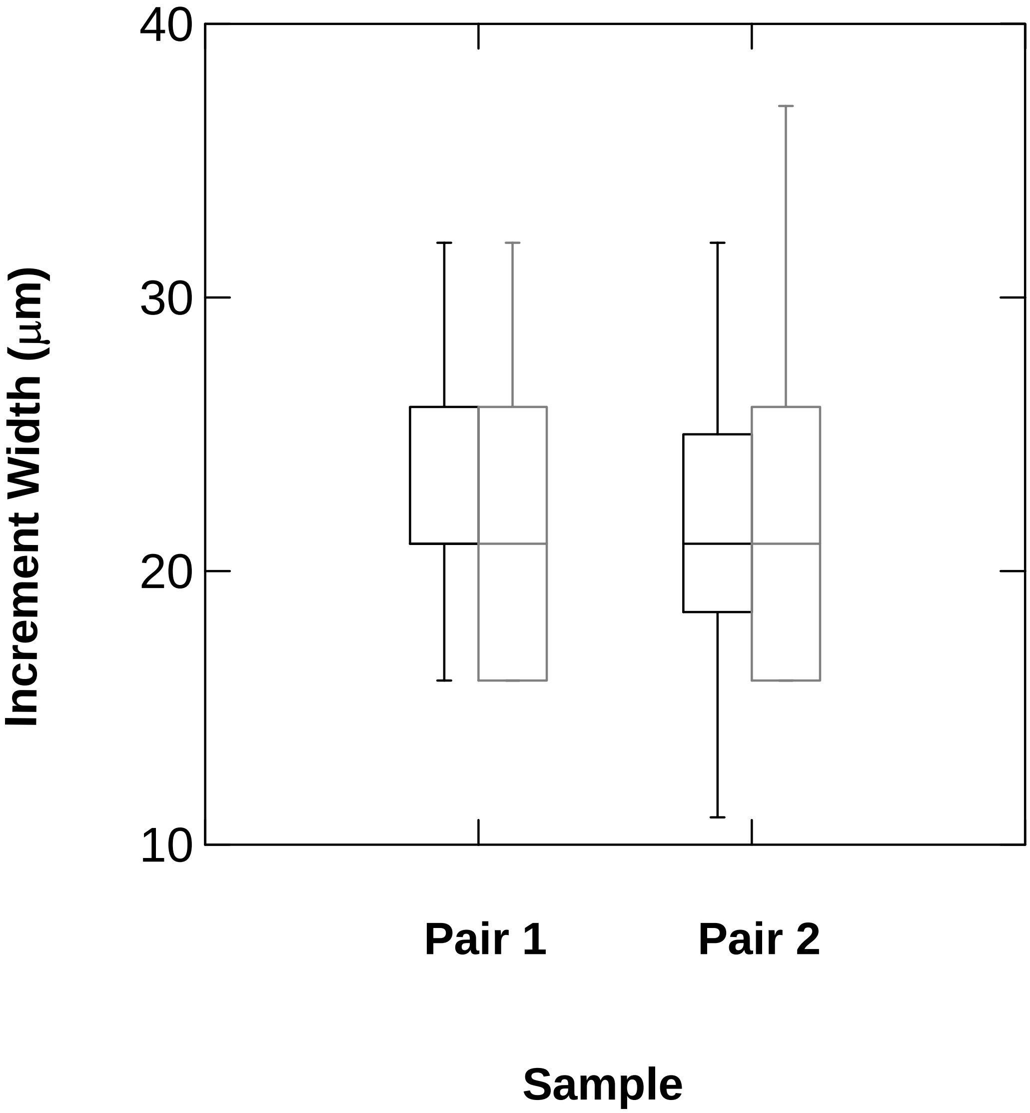


Figure 4.7. Boxplot of average 5-day increment width during 2001when controlled for temperature, for Brown Creek (in black) and Tom Lavin Creek (in gray) by comparison pair. Boxplots are as defined in Figure 4.3.

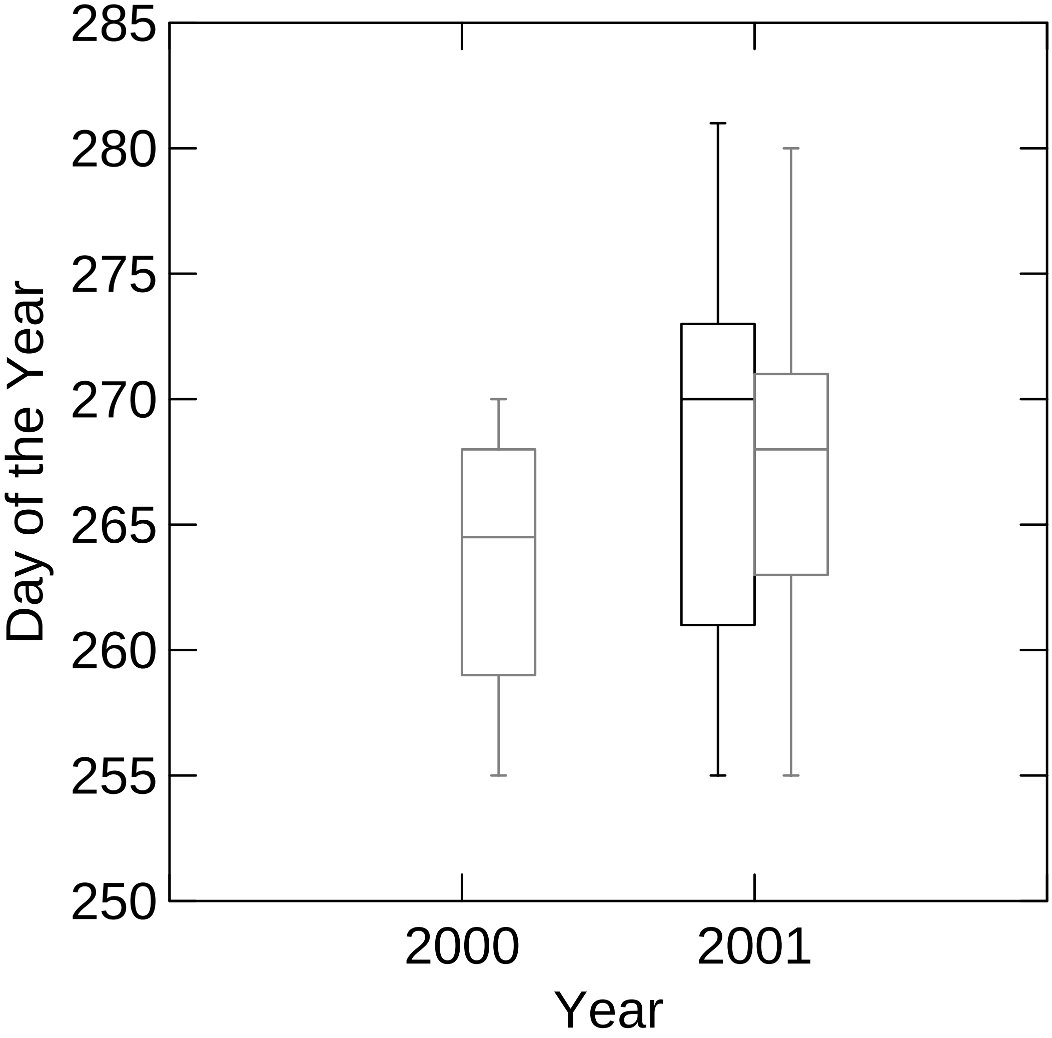


Figure 4.8. Boxplot of fall growth decline day of the year for Brown Creek (in black) and Tom Lavin Creek (in gray). Boxplots are as defined in Figure 4.3.

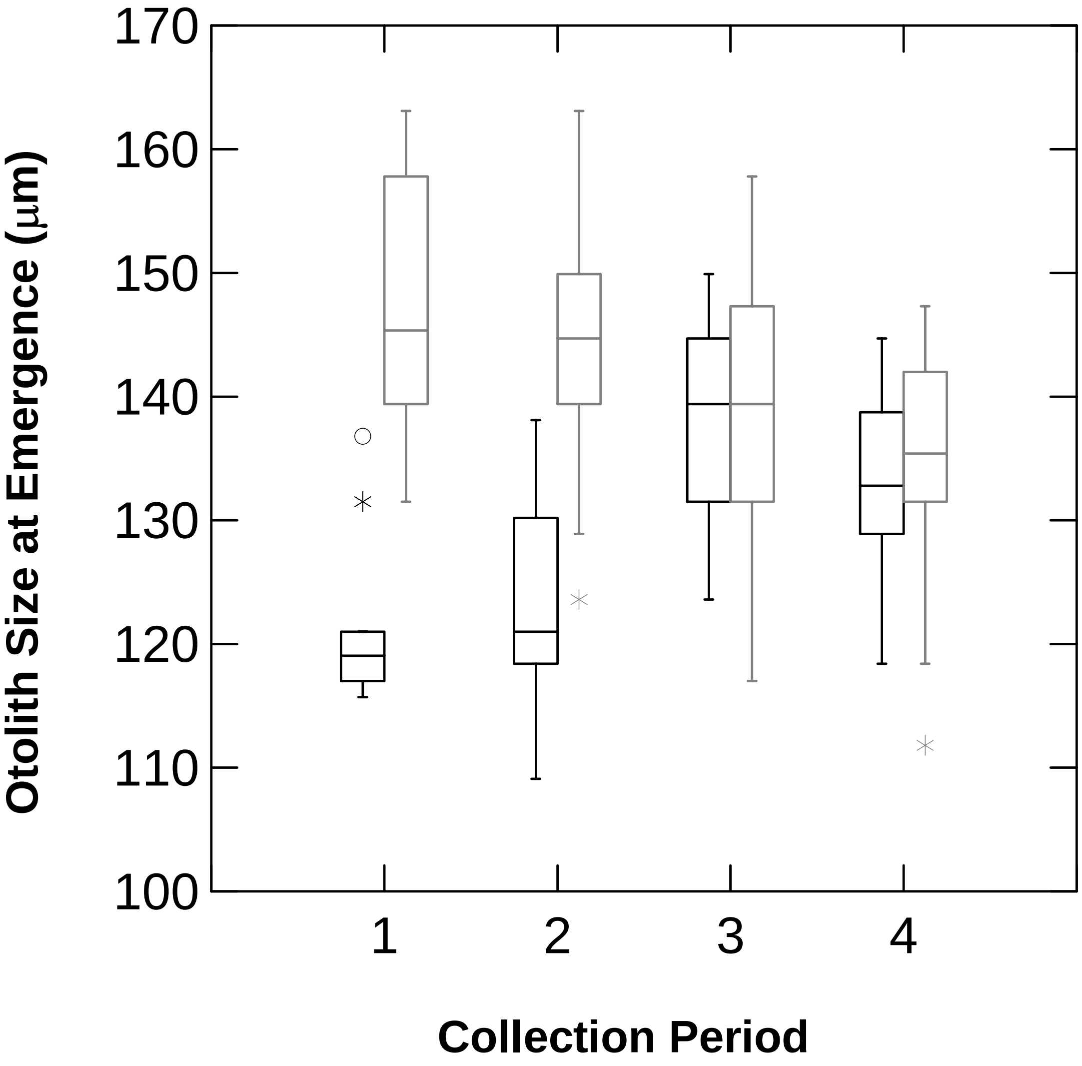


Figure 4.9. Boxplot of otolith size at emergence for Brown Creek (in black) and Tom Lavin Creek (in gray) by collection periods (1=fall 2000, 2=spring 2001, 3=fall 2001, 4=spring2002). Boxplots are as defined in Figure 4.3.

Table 4.1. Environmental characteristics of collection sites on Brown and Tom Lavin creeks, Coeur d'Alene subbasin, northern Idaho. (S=south, W=west, E=east).

Stream	**Aspect**	**Average Conductivity (μmhos)**	**Elevation (m)**	**Headwater Distance (m)**	**Valley Width (m)**
Brown	SW	71.5	732	5295	65
Tom Lavin	SSE	13.0	1109	2342	19

Table 4.2. Monthly average temperature and total precipitation (PPT) for the winters of 2000-01 and 2001-02. Precipitation sum is cumulative total precipitation for months for which normal value data were available (excludes December, February). See text for definition of normal values.

Climatic Variable	**Year**	**November**	**December**	**January**	**February**	**March**	**April**	**May**	**Sum**	**Mean**
Mean Temperature (oC)	00-01	-1.2	-2.6	-1.5	-1.4	4.1	6.6	12.7		2.4
	01-02	4.4	-1.3	-0.2	-0.6	1.1	7.0	11.1		3.1
	Normal	2.2	-2.0	-3.4	0.5	3.6	7.8	12.2		3.0
Total PPT (cm)	00-01	4.10	7.85	7.13	5.05	3.38	7.48	5.40	40.38	5.77
	01-02	10.70	11.25	18.48	7.98	10.33	4.85	8.18	71.76	10.25
	Normal	9.38	NA	9.73	NA	10.33	6.43	6.15	42.00	6.00
Monthly Stream Flow (m^3/sec)	00-01	28.2	23.4	23.4	24.5	80.4	238.2	367.5	785.6	112.2
	01-02	75.9	78.3	295.8	180.9	222.9	888.6	1033.8	2776.2	396.6
	Normal	99.9	153.6	150.9	209.1	271.8	630.0	638.1	2153.4	307.6

Table 4.3. Regression of total body length (mm) on 30-day average increment width (μm) and total number of increments. Only pre-winter fish were used in the analysis.

Stream	Year	Total Length (mm; SD)	Model p	r^2	Increment Number Coefficient	Increment Number p	Mean Increment Width Coefficient	Mean Increment Width p	N
Brown	2000-01	45.4 (6.0)	0.03	0.496	0.45	0.02	0.87	0.02	14
	2001-02	57.4 (5.8)	0.0001	0.392	0.37	0.0001	0.60	0.02	39
Tom Lavin	2000-01	30.6 (0.5)	0.002	0.799	0.28	0.002	1.23	0.004	11
	2001-02	43.1 (5.2)	0.0001	0.543	0.33	0.0001	1.01	0.0001	41

Table 4.4. Results of t-tests on selection for overwinter growth rate average.

			Duration of Test Period (days)								
			X30			X45			X75		
Stream	**Year**	**Collection**	**N**	**X (μm;SD)**	**p**	**N**	**X (μm;SD)**	**p**	**N**	**X (μm;SD)**	**p**
Brown	2000-01	Fall	14	22.1 (4.8)	NS	14	23.1 (4.1)	NS			
		Spring	28	21.5 (5.4)		28	22.6 (4.9)				
	2001-02	Fall	39	20.9 (3.4)	0.02	39	21.2 (3.5)	0.004	39	21.3 (2.8)	0.001
		Spring	36	23.1 (4.1)		36	23.8 (4.0)		36	23.8 (3.5)	
Tom Lavin	2000-01	Fall	11	18.1 (2.2)	NS	6	16.8 (1.3)	NS			
		Spring	29	18.5 (2.7)		29	18.0 (2.4)				
	2001-02	Fall	41	20.5 (3.4)	0.01	41	20.0 (2.9)	NS			
		Spring	39	18.6 (3.0)		39	19.2 (2.9)				

Table 4.5. Age at fall growth rate decline. All t-tests comparing collection periods within stream and year were non-significant at $p<0.05$.

Stream	Collection	Year	N	Age (days; SD)	Range (days)
Brown	Fall	2000-01	0	--	--
	Spring		22	82.7 (8.5)	64-96
	Fall	2001-02	21	82.8 (10.7)	61-105
	Spring		32	83.4 (11.1)	63-100
Tom Lavin	Fall	2000-01	4	32.0 (14.1)	19-52
	Spring		25	40.9 (11.5)	20-63
	Fall	2001-02	30	58.6 (8.9)	42-76
	Spring		27	60.3 (8.2)	45-76

Table 4.6. Emergence date statistics for Brown and Tom Lavin creeks based on otolith daily increment count estimation. Mean emergence difference is the difference of individual emergence dates from the sample mean. ANOVA of emergence difference within year (p) was not significant for 2000 and was significant for 2001, at p<0.5.

Stream	Year	N	Estimated Emergence Date Range	Emergence Duration (days)	Mean Emergence Difference (days; SD)	p	Median Estimated Emergence Date	Approximate Date of First Emergence
Brown	2000	14	May 30-July 2	33	7.3 (5.8)	NS	June 28	-
Tom Lavin		18	August 2-August 26	24	7.4 (3.3)		August 10	-
Brown	2001	39	June 7-July 15	38	9.0 (5.9)	0.03	June 30	June 24-28
Tom Lavin		41	July 13-August 11	29	6.2 (3.8)		July 26	July 20-28

Table 4.7. Increment width averages for data pairs over 5-day periods in 2001 for which temperature averages were equal, and t-test results between pairs. See temperature plot (Figure 4.6) for stream temperature profiles for selected pair periods. Temperature history describes stream temperature behavior during the test period relative to the 8-day period immediately preceding. (p value: NS=not significant).

Pair	**Stream**	**Start Date**	**Mean Temperature (^{o}C)**	**Temperature History**	**N**	**Increment Width (μm; SD)**	**p**
1	Brown	July 28	10.8	Falling	39	21.3 (4.3)	NS
	Tom Lavin	August 16	10.8	Falling	41	21.3 (4.8)	
2	Brown	July 19	11.2	Rising	39	20.5 (4.3)	NS
	Tom Lavin	August 10	11.2	Rising	41	21.8 (5.3)	

Table 4.8. Mean day of the year and temperature of fall growth decline for Brown and Tom Lavin creeks. ANOVA analysis of mean growth rate decline day for 2001 was non-significant at $p<0.05$.

Year	Stream	N	Mean Growth Rate Decline Day (SD)	p	Mean Growth Rate Decline Date	14-day Average Temperature (^{o}C)	Mean Pre-Decline Increment Width (μm; SD)
2000	Brown	--	--	-	--	--	--
	Tom Lavin	4	263.5 (6.4)		September 20	--	21.0 (4.3)
2001	Brown	21	267.3 (7.7)	NS	September 24	9.44	19.3 (3.5)
	Tom Lavin	30	267.8 (6.6)		September 25	8.22	18.3 (2.6)

Table 4.9. Average otolith size at emergence between streams and years. (ANOVA factors significant at *** = p<0.0001, *=p<0.05, NS=not significant).

Stream* **	**Collection***	**Year^{NS}**	**N**	**Mean (μm; SD)**	**Range (μm)**
Brown	Fall	2000-01	14	121.6 (6.67)	115.7-136.8
	Spring		28	123.5 (7.63)	109.1-138.1
Tom Lavin	Fall		18	148.7 (9.66)	131.5-163.1
	Spring		29	143.6 (9.19)	123.6-163.1
Brown	Fall	2001-02	39	137.9 (6.92)	123.6-149.9
	Spring		36	133.3 (6.93)	118.4-133.3
Tom Lavin	Fall		41	138.9 (11.02)	117.0-157.8
	Spring		39	135.7 (8.41)	111.8-147.3

APPENDIX 4.1

APPROACHES TO DEMONSTRATING SIZE-SELECTIVE MORTALITY

Several approaches have been used to demonstrate size-selective mortality in fish populations over specific time periods. They generally involve either monitoring the fate of specific individuals over time or inferring population changes over time through changes in population parameters linked to body size. These methods, their strengths and weaknesses, and authors' findings, are reviewed briefly below.

USE OF MARKED OR CAPTIVE FISH

Field Studies of Marked Fish

Use of marked fish recaptured one or more times over the period of interest may provide the best evidence for size-selective mortality since loss of individuals of specific sizes can be documented. However, since recapture rates in stream fish populations are often low, considerable effort is required to obtain large sample sizes and avoid the dangers of drawing inference from small sample sizes. Tagging and sampling methods can be size selective, confounding results.

This method has been successfully used to demonstrate size-selective mortality. For example, Hunt (1969) analyzed recapture data from marked hatchery brook trout (*Salvelinus fontinalis*) released into a Wisconsin stream between 1954 and 1964, and found overwinter survival was higher during years when released fish were larger. Boss and Richardson (2002) used mark recapture methods to examine overwinter survival of cutthroat trout fed versus unfed during the previous summer, and found no difference in survival between larger (fed) and smaller (unfed) individuals. Garvey et al. (1998) used mark recapture to examine overwinter survival age 0 largemouth bass (*Micropterus salmoides*) in ponds and reservoirs under varying scenarios of predation threat and food availability and found both factors affected size-selective mortality. When fish were fed and predators were absent, size-selective mortality was not seen, whereas when food was restricted and predators were present size-selective mortality directed at smaller individuals was seen. Bradford et al. (2001) did not find overwinter size-selective mortality of juvenile chinook salmon

(*Oncorhynchus tshawytscha*) in an upper tributary to the Yukon River. They attributed overwinter survival at this high-latitude site to the availability of habitat influenced by groundwater and therefore with limited formation of aufeis. Quinn and Peterson (1996) found that overwinter survival rate of larger juvenile coho salmon (*Oncorhynchus kisutch*) was higher in one of two years studied and survival was linked to availability of overwintering habitats containing woody debris.

Field Studies of Caged Fish

Confinement of fish in a natural environment has the advantages of being able to follow individuals, similar to mark recapture methods, while examining fish response under conditions more natural than a laboratory or hatchery setting. However, confinement may interfere with behavior, food availability, or water flow (e.g. Smith and Griffith 1994). They and Meyer and Griffith (1997) studied overwinter survival of caged rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. Smith and Griffith (1994) found survival favored larger individuals and was higher when cobble substrate providing cover was available. The smallest test fish (<100 mm) did not survive winter under any scenario. Meyer and Griffith (1997) examined effects of water temperature on overwinter survival and found survival to favor larger rainbow trout at the colder site and no size-selective mortality at the warmer site, and brook trout survival favoring larger individuals at both sites. Post and Evans (1989) used lake enclosures to examine overwinter size-selective mortality of age 0 yellow perch (*Perca flavescens*) and found survival and growth of smaller individuals to be lower than that of larger individuals.

Laboratory & Hatchery Studies of Captive Fish

Laboratory studies are able to control most sources of variability, such that results can be more conclusive than many field studies. However, inconsistencies between field and laboratory studies have been demonstrated (Post and Evans 1989). Laboratory studies may not include all sources of overwinter stress experienced by fish under natural conditions or may add additional stresses confounding results (Schultz et al. 1998).

Post and Evans (1989) studied overwinter size-selective mortality of yellow perch using laboratory, caged field, and mark recapture methods. In laboratory studies, they found that although all test fish lost weight, starved and smaller fish lost more weight. Starved small fish suffered 46% mortality compared to 1% mortality in starved large fish. In hatchery ponds and outdoor raceways with age 0 largemouth bass, Garvey et al. (1998)

found some cannibalism and size-selective mortality directed at smaller individuals within year class in ponds with larger size variation, but no size-selective mortality in raceways or ponds with relatively narrow size ranges even during food denial with all fish losing weight. Pratt and Fox (2002) found no overwinter size-selective mortality of age 0 walleye (*Stizostedion vitreum*) in outdoor hatchery ponds. Counter to the most common finding in published studies, smaller fish in their study gained weight overwinter whereas larger fish lost weight. In the presence of predators, however, smaller fish lost weight. In laboratory tanks, Schultz et al. (1998) found overwinter size-selective mortality of Atlantic silverside (*Menidia menidia*) to favor larger individuals when food was withheld but not when food was provided and survival to be higher in stocks from higher latitudes with greater tolerance of winter stresses than stocks from lower latitudes. In laboratory tanks, (Kirjasniemi and Valtonen 1997) found size-selective mortality to favor larger individuals in age 0 roach (*Rutilus rutilus*) from two lakes in central Finland, but did not find a consistent size limit for survival. Approximately the same proportion of individuals survived from each stock, suggesting that competition may be one mechanism involved in the selection favoring larger individuals.

INFERENCES FROM POPULATION PARAMETERS

Use of Otoliths to Backcalculate Body Length

The age and growth record potentially stored in the otolith has been used to demonstrate changes in a population over time, including size-selective mortality. Use of otoliths presents significant methodology challenges including preparation and interpretation. Backcalculating body length from otolith increment width requires that increment deposition frequency is regular and correctly defined and that the relationship between otolith and somatic growth is accurately described. Use of the otolith growth record often requires that all individuals in a population or at one time period establish the same otolith to body length relationship. This assumption has not consistently been found. See Appendix 4.2 for additional discussion.

Nevertheless, information obtained from otoliths has been used to successfully demonstrate size-selective mortality. Gleason and Bengtson (1996) used otolith microstructure and the biological intercept back-calculation method (Campana 1990), collecting inland silversides (*Menidia beryllina*) weekly or biweekly for 3 years and identifying the period of most intense size-selective mortality. Post and Prankevicius (1987) found that in a slow-growing population, larger, faster-growing age 0 yellow perch had higher survival rates than slower-growing smaller individuals. In a faster-growing population, survival was not size selective. They attributed survival of larger individuals to size-selective predation. Good et al. (2001) investigated size-selective mortality in Atlantic salmon fry during two summers that differed in weather conditions and found size-selective mortality to be directed at smaller individuals during a summer of drought and at larger individuals during a summer with flood conditions. West and Larkin (1987) documented size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) directed at smaller individuals at emergence. Meekan and Fortier (1996) compared growth rates of pre- and post-winter populations of larval Atlantic cod (*Gadus mordua*) using otolith increment widths. Because they established a linear relationship between increment width and somatic growth, they were able to conclude that overwinter survival was size selective as well as growth rate selective.

Comparison of Pre- and Post- Length Frequencies

Comparison of length frequency distributions across time have been used to examine size-selective mortality. This method is relatively simple and requires less intensive field efforts than most other methods. However, Ricker (1967) demonstrated that size-selective mortality would not alter the shape of a length frequency distribution if the relationship between size and survival was linear, and that the effect of size-selective mortality on mean length would also be small. Therefore, conclusively showing size-selective mortality by comparing length frequency distributions over time may be very difficult. In addition, this method is not able to show size-selective mortality if size-dependent growth occurs during the period of interest (Post and Evans 1989).

Post and Evans (1989) examined overwinter size-selective mortality of yellow perch in four lakes by comparing length frequency distributions of caged fish between fall and the following spring while controlling for differences in winter duration and mean fall body size in their model. They found size-selective mortality favoring larger individuals in most lakes studied. Henderson et al. (1988) collected sand smelt (*Atherina boyeri*) monthly and used length frequencies and abundances to estimate mortality and change in length. They demonstrated an increase in mean fish length without an increase in maximum length, evidence that size-selective mortality favoring larger individuals had occurred. Similarly, Griffiths and Kirkwood (1995) sampled roach and perch (*Perca fluviatilis*) monthly in a British reservoir demonstrated a lack of growth in roach during winter months, concluding that changes in average length were due to size-selective mortality. Miranda and Hubbard (1994) sampled largemouth bass in a Mississippi reservoir monthly from June through the following March. They demonstrated that changes in the shape of the length frequency distribution were best explained by size-selective mortality favoring larger individuals. They documented the development of a bimodal length frequency distribution, and then disappearance of most of the smaller mode during late autumn and early winter coincident with declining fat reserves and water temperatures. Toneys and Coble (1979) also documented greater overwinter mortality of the smaller length mode.

Differences in Size Structure among Cohorts

Hunt (1969) examined overwinter survival of marked hatchery brook trout in a Wisconsin stream and found overwinter survival was higher in cohorts that were larger at release. Other factors in addition to fish size could be responsible for the survival pattern observed, including fish density and winter duration and intensity. Post and Evans (1989) compared overwinter mortality of two cohorts of age 0 yellow perch differing in size and found the smaller cohort suffered 34% higher mortality than the larger cohort.

APPENDIX 4.2

METHODS FOR THE EXAMINATION AND INTERPRETATION OF FISH OTOLITH MICROSTRUCTURE

INTRODUCTION

The microstructure of fish otoliths contains unique and valuable life history information including hatch and emergence dates, age, daily growth, and occurrence of environmentally-induced stresses experienced by the individual or population. Visible otolith microstructure, in particular daily increment counts and widths provide information regarding fish age and growth rate, respectively (Pannella 1980). However, the processes involved in extracting that information are fraught with numerous challenges, potential errors, and biases that must be addressed during otolith preparation and interpretation. Steps in otolith preparation during which serious mistakes could be made include otolith selection, mounting, grinding, viewing, and interpretation (data extraction), which includes increment counting and otolith and increment measurement (Campana 1992; Panfili and Ximenes 1992; Pepin et al. 2001). Analysis and interpretation of otolith microstructure data can also produce erroneous results (Campana and Jones 1992).

Techniques for the use of otolith microstructure have advanced considerably since the mid-1980s, when otoliths were first used in fisheries science, and many of the potential problems with otoliths have been identified and addressed. However, the researcher must be aware of potential problems to avoid incorporation of bias and error into otolith data. Pannella (1980) provides an early review of otolith microstructure and methods for its interpretation. A more comprehensive and detailed review addressing otolith microstructure is provided by Stevenson and Campana (1992), including measurement and interpretation of otolith microstructure (Chapter 4), analysis of otolith microstructure data (Chapter 5), validation (Chapter 6), and sources of error in otolith microstructure examination (Chapter 7). Campana (2001) also reviews age validation methods and sources of error and Jones (1985) reviews use of otolith microstructure for aging of larval fish. This literature review focuses on methods and methodological issues most relevant to the use of age 0 salmonid otoliths for study of overwinter size-selective mortality.

OTOLITH PREPARATION

Sagittal otoliths to be used for microstructure examination must be selected carefully. A low percentage of otoliths are composed partially of crystalline structures (vaterite, calcite) other than the most common form, aragonite (Neilson 1992). Anomalous structures may contain daily increments (Campana 1983), but increment width may not consistently reflect somatic growth (Neilson 1992). Although most authors have found left and right sagittal otoliths to be similarly sized and equally valid for use and have therefore chosen left and right otoliths randomly (West and Larkin 1987) or with respect to other issues (e.g. crystalline form as discussed above), Neilson and Geen (1982) found left otoliths to be significantly larger than right otoliths in chinook salmon and Neilson et al. (1985) found left otolith nuclei to be larger than right otolith nuclei. Both studies used only left otoliths. Care should be taken to avoid introducing bias during otolith selection and preparation since for example, smaller otoliths may be more susceptible to breakage or loss during preparation (Neilson 1992).

Grinding of both sides of age 0 salmonid otoliths for daily increment interpretation will produce the best image (Campana 1992). Grinding includes removal of one side of the otolith using progressively finer sandpaper, from 1200/2000 grit to 3um, flipping the otolith, and repeating the process on the other side. The first side has been sufficiently ground when daily increments can be seen just below the surface, but are not yet on the surface (S. Campana personal communication). Both over- and undergrinding can produce errors. Overgrinding may result in loss of increments at the otolith core or edge or both, whereas undergrinding may result in insufficient increment resolution and undercounting, or, seeing the increment more than once and overcounting (Wilson and Larkin 1980; Campana 1992; Neilson 1992). Inconsistent selection of the grinding plane can also bias increment width or count estimates (Panfili and Ximenes 1992).

Light microscopy and scanning electron microscopy (SEM) are the two most common options for viewing prepared otoliths (Neilson 1992). The two methods share many of the same methodological strengths and weaknesses as well as having unique advantages and disadvantages. SEM requires more preparation time but can avoid some of the problems associated with light microscopy, such as discrimination between daily and subdaily increments and limited ability to resolve narrow increments. The theoretical resolution limit with light microscopy is 0.27 μm, and in practice it is likely to be closer to 1.0 μm due to resolution problems. Increments narrower than 1.0 μm often can not be seen, and counts may be inaccurate during slow growth periods (Campana 1992) . Resolution of fine increments is not generally a limiting problem of light microscopy, however, since it is only a problem in very slow growing fish (Jones 1992).

Viewing increments at widths of 1-2 μm is most effective at 400X and increments smaller than 1-2 μm at 1000-1250X (Campana 1992). Discerning between daily and subdaily increments is easier at this magnification than at higher magnification (Campana 1992; Volk et al. 1995). Insufficient magnification can make counting increments difficult since the human eye tends to wander randomly when viewing too many similar objects (Campana 1992). Ideally, magnification should be adjusted to include approximately 20 increments in the field of view (Campana 1992). Use of a blue or green light source or filter provide the best increment resolution including slow growth bands and can improve resolution by 15-20% (Campana 1992). Effective use of lighting and focus capabilities of the microscope can also dramatically improve resolution (Campana 1992).

USING INCREMENT COUNTS TO ESTIMATE AGE

Mechanisms of Daily Increment Formation

Daily increment formation appears to be controlled by an endogenous circadian rhythm entrained by photoperiod some time before hatching (Campana 1983; Campana and Neilson 1985; Mugiya 1987a; Wright et al. 1991). First increment deposition date is species specific, varying from before hatching to time of first feeding in some salmonids (Campana and Neilson 1985). Other increment frequencies triggered by “masking” factors such as temperature (Brothers 1978; Campana 1983; Campana and Neilson 1985) or feeding periodicity (Neilson and Geen 1982; Campana and Neilson 1985) may be overlain on top of daily increments, making identification and numeration of daily increments more difficult. Daily deposition of increments may cease below some minimum temperature. For example, Marshall and Parker (1982) found increment deposition in juvenile sockeye salmon to cease below 5^{o}C. However, Neilson and Geen (1982) found continued increment deposition below 4^{o}C in chinook salmon. Increment deposition may not be daily under other extreme conditions such as prolonged starvation (Jones 1985). Failure to document daily increment formation may be explained by: 1) resolution limits of light microscopy in regions of slow growth (undercount), 2) constant temperature conditions reducing increment contrast and therefore detectability (undercount), 3) inadequate otolith preparation resulting in insufficient removal of overlying material obscuring increments (undercount), or 4) failure to distinguish between daily and subdaily increments (overcount; Campana and Neilson 1985). Daily increments have two phases, an organic/protein (clear or hyaline) phase and a calcium (opaque) phase (Pannella 1980; Mugiya 1987b). The clear phase is deposited during periods of slow growth, whereas the opaque phase is deposited during periods of fast growth (Pannella 1980), on both daily and annual cycles. In rainbow trout, both phases deposit daily in varying amounts diurnally and antiphasically, with the protein phase peak at night at 2200 and the calcium phase peak at 1600 and trough at 2200 (Mugiya 1987b).

Documentation of Daily Increments in Fishes

Daily otolith increment deposition has been documented for many salmonid species, including all Pacific salmon species, as well as for many other freshwater and marine species. Daily increment deposition appears to be almost universal in young fish under normal environmental conditions and hatchery conditions simulating natural conditions (Campana 1983; Jones 1985). A summary of studies documenting daily increment deposition for salmonids is presented in Table 4.10. Exceptions have been documented. For example, Volk et al. (1995) documented increment counts both underestimating and overestimating daily age of pink salmon (*Oncorhynchus gorbuscha*). They suggested that increment counts exceeding known age may result from confusion of daily and subdaily increments, since increment counts of slow growing individuals had near daily increment deposition whereas faster growing individuals had more increments. During very slow growth, increment deposition may cease or become intermittent, and light microscopy may fail to distinguish between closely spaced increments. In addition, their study was conducted at a high latitude with an unusual photoperiod of 20+ hours of daylight and no complete darkness, potentially disrupting increment deposition.

Validation of Daily and First Increment Deposition

Validation of microstructure and its interpretation, such as daily increment formation, hatch and emergence/first feeding checks, and date of first increment formation may be essential, depending on the questions being addressed using information stored in otoliths. Methods to validate daily increment deposition generally involve marking otoliths using chemicals such as tetracycline or cyclein, which are taken up by the organism and incorporated into the otolith, and which produce fluorescence under ultraviolet light (e.g. Paragamian et al. 1992), or by exposing the organism to a stress such as temperature change sufficient to produce an identifiable stress check in the otolith. Under laboratory or captive field conditions, the number of increments deposited can then be compared with the known days since treatment. A regression line of the two variables should produce should be 45^o and pass through the origin. Hatch and emergence dates should be validated if used to begin daily increment counts in life history studies (Neilson 1992). He and Geffen (1992) suggest that extending validation from laboratory settings to field settings or from one life history stage to another may be invalid since microstructure formation is responsive to the environmental conditions of the organism during formation. Daily otolith increment formation has been relatively well validated. Past researchers may have tended to assume stress checks to be associated with hatch or emergence rather than validating their source, but numerous studies have since validated these checks for a variety of species. Geffen (1992) reviews validation of increment deposition rate, time of initial increment formation, the otolith to somatic growth relationship, and physiological mechanisms of increment deposition.

Counting Increments

The radius selected for increment counting must be selected carefully. Shorter radii are more likely to contain an incomplete complement of increments whereas longer radii are more likely to contain troublesome subdaily increments (Campana 1992). Both conditions potentially introduce avoidable error into increment counts (Campana 1992). A midlength radius should be selected that contains clearly resolved increments and does not contain stress checks or structural anomalies that would interfere with increment deposition or counting (Pannella 1980; Campana 1992). The posterior dorsal quadrant of the otolith was used by Marshall and Parker (1982) to count daily increments of sockeye salmon.

Early studies reported that increment deposition began at emergence (or yolk sac absorption; e.g. Wilson and Larkin 1980; 1982). First increment deposition has been documented at hatch for chum salmon (*Oncorhynchus keta*; Volk et al. 1984), and at least 12 days prior to hatch in sockeye salmon (Marshall and Parker 1982). Clear hatch and emergence checks have been documented in salmonids, including Atlantic salmon (Meekan et al. 1998). Increments within the hatch check occur but frequency of deposition has not been determined, and the conformity of primordia with regard to date of first increment formation, and therefore consistency of increment counts among primordia, has also not be studied. Primordia increase in size by the addition of concentric layers to the outside of theh otolith Neilson et al. (1985). They considered the first growth increment to be deposited after fusion of all primordia. Primordia become encapsulated by calcium carbonate and other materials soon after formation (Brothers 1984). He suggested that a core of opaque material surrounds the primordia, rather than the immediate initiation of layering of opaque and clear layers that occurs with daily increment deposition. Salmonids are characterized by multiple, separated primordia, each with its own core (Brothers 1984). Most studies initiate increment counts at the hatch or emergence check (e.g. Campana 1992).

Challenges to using increment counts for age estimation or dating significant life history events such as emergence include difficulties counting through annuli, beyond the first 100-200 days of life (after which increments become more difficult to discern), and through stress checks, identification of the date of first increment formation, and discrimination between daily and subdaily increments (Brothers et al. 1976; Miller and Storck 1982; Campana and Neilson 1985). Daily increments can be easily confused with other visible structures, including double images of daily increments, subdaily increments, stress checks, scratches and other visual artifacts (Pannella 1980; Campana 1992). In addition, in sufficient grinding may produce one broad dark band that consists of several daily increments (Campana 1992). Frequent fine focus adjustment, following of increments around the otolith, and examination at different magnifications will help to differentiate between daily and subdaily increments or other visual structures and avoid over or under counting (Marshall and Parker 1982; Campana 1992). Daily increments are generally regularly spaced whereas subdaily increments may be much more irregularly spaced and appear fainter than daily increments (Miller and Storck 1982). Subdaily increments have been documented in salmonids (Marshall and Parker 1982; Neilson and Geen 1982; Campana 1983). Understanding common growth patterns, from relatively slow growth around the hatch check or associated with decreasing temperatures in the fall, to faster growth during warmer, more productive periods, can help to interpret otolith microstructure (Campana 1992). He also recommends using identifiable interruptions such as checks, cracks, or other irregularities to break counting into segments of 10-15 increments, since the human eye tends to wander when viewing larger numbers of similar objects.

Increments are rarely clearly visible and discernible from primordia to the edge. Minor interpolation of insufficiently visible increments can be acceptable if limited to approximately 5% of increments counted and occurring through regions of constant growth (Campana 1992). Therefore, interpolation is acceptable toward the edge of the otolith but not near the nucleus where growth is variable (Campana 1992). Interpolation of increments at the otolith edge may be more accurate than a visual count since these increments may not be visible or their appearance may be distorted (Campana and Neilson 1985).

Error in age estimation using increment counts can be associated with the visual record in the otolith, otolith preparation or interpretation. Increment counts per otolith should be conducted at least twice, preferably at least once each from the nucleus outward and from the edge inward (Campana 1992). The average of the two counts per individual was used by Marshall and Parker (1982). Otolith interpretation is a subjective process that can be improved through reader experience, confirmation by other readers, or validation studies. Oldest and youngest age groups are the most difficult to age accurately (Campana 2001). The ability of the otolith to deliver a visual record of age is generally biased, but can be biased in either direction (over or underestimated age) whereas otolith preparation and interpretation can be biased or random (Campana 2001). Average percent error (APE) and coefficient of variation (CV) can be used to quantify aging precision (Campana 2001). CV is most commonly used in otolith microstructure studies reviewed (84%) by (Campana 2001). A CV of <5% is considered acceptable (Campana 2001). Procedures for reducing and estimating error in age estimation and converting increment counts to age estimates are summarized by Campana and Jones (1992).

USING OTOLITH SIZE TO PREDICT BODY SIZE AND GROWTH

Measuring Otoliths And Otolith Increments

Because otoliths grow asymmetrically and growth relationships between body length and otolith metrics may vary, one axis or radius of measurement must be used for all repeat measurements as well as among individuals (Campana 1992). If single or groups of increments are to be measured, the axis of measurement must contain a linear, complete, and clear record of all increments (Campana 1992). Since radii do not intersect all increments at 90^o, each increment or small group of increments should be measured on approximately the same radius and perpendicular to the particular increment(s; Campana 1992). Pepin et al. (2001) found increment width measurement to be less precise with narrower increments typically occurring in younger individuals and especially early within the first growing season, concluding that increment measurement error will account for a larger percentage of total error in smaller individuals and that measurement must therefore be more precise. Meekan et al. (1998) concluded that otolith and body length measurements must be reliable and consistent since measurement error could easily generate poor otolith to somatic growth relationships capable of obscuring meaningful ecological processes such as size-selective mortality.

Otolith shape is irregular and changes with otolith growth, making consistent otolith measurement challenging. Two common otolith metrics are total otolith length as the longest diameter of the otolith through the nucleus and the diameter perpendicular to the maximum length also passing through the center of the nucleus (e.g. Marshall and Parker 1982; Gleason and Bengtson 1996). Neilson and Geen (1982) and others have defined total otolith length as the maximum distance from the rostral tip of the emergence check to the posterior edge of the otolith (total otolith length minus the rostrum). West and Larkin (1987) explored otolith shape relationships to body length by measuring 5 otolith dimensions, otolith area, and 3 radii. They found area to be the best of all measurements at predicting body size, but total otolith length was easier to measure and more precise. Their definition of total length was the axis through the nucleus and the rostral trip of the emergence check. All correlation coefficients were relatively low. Meekan et al. (1998) found that otolith size and body size correspond poorly at emergence and a progressively stronger relationship develops post-emergence. Therefore, otolith metrics from the emergence check through the active growth zone will most accurately predict somatic growth. Radii in the posterior dorsal quadrant are commonly measured (e.g. Wilson and Larkin 1982; Volk et al. 1984). Mosegaard et al. (1988) divided the otolith of Arctic char (*Salvelinus alpinus*) into eight equal angular intervals and found otolith growth in all but the interval containing the sulcal groove to be closely correlated. They measured all otolith radii from the most anterior primordium.

Using the nucleus as one point in measurement can introduce error since defining the center or extent of the nucleus is subjective (Neilson et al. 1985). Progeny from a single salmonid female can differ in number of primordia and in nucleus size, and variable numbers of primordia have been documented for all five Pacific salmon species (*Oncorhynchus* sp.; Neilson et al. 1985). They defined the nucleus as the area enclosed in an increment that included all primordia except one anterior-ventral primordium associated with the rostrum. Varying nucleus size introduces error into the otolith to body length relationship suggesting that otolith measurements independent of nucleus size may most reliable (Neilson et al. 1985).

Establishing an Otolith to Body Length Relationship

Most growth back calculation procedures assume and are based on some proportionality between fish length and some measure of otolith size, and depend on the effectiveness of relating otolith and body size (Carlander 1981). Back calculation of length and growth requires accurate estimation of fish age or time passage from otolith daily increment counts (Jones 1985). Otolith and somatic growth have been successfully linked.

For example, Volk et al. (1984) found a direct relationship between mean daily otolith increment width and growth rate of juvenile chum salmon, Miller and Storck (1982) found a direct relationship between otolith and body size in age 0 largemouth bass, and Courtney et al. (2000) found a significant relationship between otolith size and body size in juvenile pink salmon. Otolith measurements used by Courtney et al. (2000) included otolith area, the major axis, and the minor axis. They obtained an r^2 of only 0.48, citing problems with backcalculation methods discussed below and as reviewed by Campana and Jones (1992) and Neilson (1992). Fukuwaka (1998) established a nonlinear relationship between otolith and body size of juvenile chum and sockeye salmon.

The nature of the otolith to fish growth relationship between must be well established (Jones 1992) and can be curvilinear (isometric), common in many species during the larval stage, or linear, more usual for juveniles and adults (Campana and Neilson 1985; Pepin et al. 2001). Many studies have assumed a linear relationship. Campana (1990) suggested a method to address growth rate nonlinearity by daily weighting of growth rate changes, transforming the nonlinear relationship to a linear one. Fukuwaka (1996) found the otolith to body length relationship of juvenile chum salmon to be allometric but non-linear. He tested one linear and two curvilinear models and found one of the curvilinear models incorporating body length and otolith length at hatch to have the best fit. Pepin et al. (2001) also found a curvilinear relationship in larval radiated shanny (*Ulvaria subbifurcata*). Individuals with poor growth may have an atypical otolith to somatic growth relationship necessitating the use of more than one model within a single population (Marshall and Parker 1982; Jones 1992). Growth data for early life stages can be fit to a greater variety of curves including exponential, logistic and Gompertz models than later stages, as reviewed by Jones (1992). She suggests avoidance of models having an upper asymptote in early stages since growth does not cease. She reviews other analytical options include time series analyses, an age-temperature growth model, and cohort tracking techniques.

A poor relationship between fish and otolith size at emergence has been documented. Meekan et al. (1998) explored the otolith to body size relationship from hatch to emergence in Atlantic salmon and concluded that difficulties in establishing an otolith to body size relationship at emergence could be explained by inaccurate size measurements, size-selective mortality in test fish resulting in truncation of the size range at emergence, and a lack of size correspondence over very short time periods. They found locating a consistent otolith axis of measurement, insufficient precision of fish measurement, and accurate fish aging from otoliths to be methodological challenges producing error of sufficient magnitude to obscure the relationship between otolith and fish size. Solving methods problems and pooling of data over longer time periods significantly improved the relationship.

Uncoupling between body and otolith growth may also be a result of a time lag in otolith response to changes in somatic growth rate. Some investigators have found the presence of a 3 to 21-day time lag between a change in somatic growth rate and otolith response (e.g. Neilson and Geen 1986; Molony and Choat 1990; Pepin et al. 2001). In contrast, Mugiya and Oka (1991) suggested that otolith growth reflects somatic growth on a daily basis, and that uncoupling documented by others reflects suboptimal experimental growth conditions. Campana and Neilson (1985) suggested that fish length corresponding to otolith size should be able to be estimated at each increment, as well as estimating instantaneous growth rate over short periods of time. Volk et al. (1984) found the 7-day average increment width predicted somatic growth rates well but concluded that uncertainty in the relationship increased with shorter time periods.

Mosegaard et al. (1988) and Campana (1990) have suggested that a lack of coupling between otolith and somatic growth may be the result of systematic variation in the relationship due to differences in somatic growth rates, since the otolith continues to grow after somatic growth has ceased (Mosegaard et al. 1988; Campana 1990; Wright et al. 1991; Dickey et al. 1997). Therefore, relatively slow-growing individuals may have otoliths that are disproportionately large for their body size. Otolith growth may be influenced by temperature, somatic growth, metabolic rate, and food ration (Greenberg and Brothers 1991; Hall 1991; Bradford and Geen 1992). Marshall and Parker (1982) documented differences in the body otolith size relationship between fed and unfed sockeye salmon. In contrast, Neilson and Geen (1982) found the ratio of otolith size to fish size of chinook salmon remained constant across a variety of experimental conditions modifying photoperiod, feeding frequency, and temperature. To avoid some of the problems of using increment width to estimate daily growth rate, Campana and Neilson (1985) and others reviewed within suggested plotting fish size versus increment count to study relative growth rates of fish from different habitats or environmental conditions. Coupling of otolith and somatic growth should be considered species, size, and life history stage specific (Bradford and Geen 1987; Neilson 1992).

Other problems linking otolith size and body size include variability in nucleus size and formation of accessory primordia and therefore inaccuracies in measurement from the nucleus (Campana and Neilson 1985). Use of multiple cohorts to reconstruct the growth otolith relationship (Carlander 1981) can lead to problems in backcalculating length from otolith increment information and the otolith to body size relationship produced. Although he discussed problems using scales, many issues he identified apply to the use of otoliths as well.

Methods for improving the otolith to body size relationship are reviewed by Neilson (1992) and Campana and Jones (1992) and include Campana‘s biological intercept (BI) method (Campana 1990), which corrects for differences in growth rate by tying otolith to somatic growth relationships of individuals with different growth rates to a common point in their histories, such as size at hatch or emergence. Use of this method counteracts the documented Lee’s phenomenon of underestimating back-calculated fish length. Another method for improving the relationship is the time-varying growth (TVG) method (Sirois et al. 1998), which adds an increment width weighting factor to the back-calculation of body size.

Table 4.10. A partial list of studies in which daily otolith increment deposition has been documented for salmonids.

Common Name	Scientific Name	Source
Atlantic salmon	*Salmo salar*	Wright et al. 1991
		Meekan et al. 1998
Chinook salmon	*Oncorhynchus tshawytscha*	Wilson & Larkin 1980
		Neilson & Geen 1982
		Gauldie 1991
		Zhang & Beamish 2000
Chum salmon	*Oncorhynchus keta*	Wilson & Larkin 1980
		Volk et al. 1984
		Fukuwaka 1996
		Fukuwaka 1998
Coho salmon	*Oncorhynchus kisutch*	Wilson & Larkin 1980
Pink salmon	*Oncorhynchus gorbuscha*	Wilson & Larkin 1980
		Courtney et al. 2000
Sockeye salmon/ kokanee	*Oncorhynchus nerka*	Wilson & Larkin 1980
		Marshall & Parker 1982
		Paragamian et al. 1992
Rainbow trout/ steelhead	*Oncorhynchus mykiss*	Wilson & Larkin 1980
		Campana 1983
		Mugiya, 1987a
		Mugiya, 1987b
		J.D. Neilson unpublished data as cited in Campana & Neilson 1985

CHAPTER 5

CONCLUSIONS

My findings show that size variation in age 0 westslope cutthroat trout (*Oncorhynchus clarki lewisi*) occurs at multiple scales in response to important environmental gradients. In Chapter 2, I found age 0 fish size and size variation to differ at all three scales examined: among areas, among streams, and within streams. Most variation occurred at the broadest scale. Age 0 trout tended to be larger and more diverse in systems that are warmer, lower elevation, and more productive, at all three scales. Age 0 size and size variation may be quite different among adjacent streams if they differ significantly in productivity and temperature. Similarly, age 0 size may be different within a stream, with fish that are smaller and less diverse more likely to occur upstream in response to longitudinal temperature gradients. Broad-scale watershed characteristics associated with productivity, such as geology and elevation, should be effective predictors of size and size variation at these broader scales, and instream productivity gradients should be associated with size and size variation at the scales at which they occur.

In Chapter 3, size variation was associated with habitat diversity at one of three scales studied, the reach scale. Larger and smaller fish tended to use habitats with different characteristics and different habitat types. Habitat units and unit types that contained larger age 0 individuals were more likely to be larger, deeper, with greater access to terrestrial and aquatic predators, and more diverse. Age 0 cutthroat trout will apparently move among habitat units as habitat needs change with increased size. This is consistent with my finding that at the finer habitat unit scale, habitats occupied by homogeneously- and heterogeneously-sized individuals did not differ. Age 0 salmonids appear to be highly mobile, consistent with findings of Kahler (1999). Habitat differences between habitat units occupied by large and small individuals suggest that predation risk and food delivery rate may be important factors mediating the habitat shift. Units occupied by smaller fish were shallower and slower velocity, limiting access to aquatic predators that may prefer smaller prey, but also with limited food delivery rates and limited cover from terrestrial predators that may prefer larger prey (Harvey and Stewart 1991). Deeper, higher velocity units would therefore be more appropriate for larger individuals, providing higher food delivery rates and cover from terrestrial and avian predators.

Temporally and spatially variable overwinter growth rate selection documented in Chapter 4 provides evidence for the value of size variation within and among populations. I found selection for fast growth rate in one stream and slow growth rate a second stream during one year, and no growth rate selection in either stream in one year, and found no overwinter selection for age in either stream during either year. Growth rate and age information obtained from mean otolith increment width and number of increments explained most of the variation in body length in both streams. Maintenance of size variation overwinter in both streams and temporally inconsistent patterns of overwinter selection suggest that size variation may have value within a population. Size variation may provide other values as well and thus be maintained within a population. For example, other temporally variable size-selective processes may be operating in this system, maintenance of size variation within a population may be a product of severe low frequency disturbance or climatic events, and size variation may limit the effects of competition. Documentation of these relationships was beyond the scope of my study. The extent to which size variation is maintained in these populations through selective forces versus the absence of mechanisms producing directional size selection remains unclear and will require additional study for clarification.

Development of compensatory mechanisms identified in Tom Lavin Creek in Chapter 4 suggests that size variation within this population may be of limited or secondary importance to the achievement of sufficient body size for overwinter survival, since these compensatory mechanisms appear to limit size variation within the population and increase mean size. Size selection favoring larger size is well-documented in age 0 fishes across diverse environments (Sogard 1997). In harsh environments, achievement of a minimum body size may limit diversification in size and life history characteristics associated with growth, such as emergence duration. In addition, if larger egg size is selected for in harsh environments associated with increased overwinter survival, other life history characteristics associated with egg size, such as fecundity, may be controlled by overwinter survival as well. Because life types differ in size, and therefore potentially egg size, salmonid life history types may have differential fitness across gradients of environmental harshness. Migratory life history types, with larger body size and therefore greater fecundity may have greater fitness in limited growth environments.

My results shed light on the uncertain relationship between scales of causal processes and ecological responses. Levin (1992) suggested that ecological response can be controlled by processes at broader scales, but that broader-scale patterns may be the cumulative response to processes occurring at finer scales. Horne and Schneider (1995) suggested that cause and response processes occur at the same spatial scales. My findings suggest that proximal causal processes and ecological responses occur at the same and broader scales. For example, I found in Chapter 2 that distribution of size variation in age 0 trout occurred at the same scales as variation in water temperature and productivity. However, the associated ultimate causal process, elevation, occurred at broader scales. Similarly, in Chapter 3 size variation was associated with habitat diversity at the reach scale, but valley width differences in aquatic habitat occurring at the stream scale controlled habitat characteristics and diversity at finer scales. In this latter example, although the immediate factor responsible for size variation appeared to be habitat diversity, processes occurring at broader scales were indirectly involved.

Although size variation is responsive to environmental gradients such as temperature and productivity, the response is apparently not simple and relationships are not strictly predictable. Organisms may adapt to stressful environments with phenotypic characteristics that differ from the norm (Lesica and Allendorf 1995; Hoffmann and Hercus 2000), including counter-gradient responses (e.g. Schultz et al. 1996; Conover et al. 1997; Yamahira and Conover 2002). In Chapter 4, I found evidence of adaptation to a harsh environment in reduced size variation along a temperature gradient, and relaxation of a life history characteristic in a more moderate environment. Although mean size followed the general pattern identified in Chapter 2, size variation appears to be a function not only of productivity gradients but also adaptation or phenotypic plasticity. Fewer phenotypic or life history strategies may be available for achieving sufficient body size to survive winter in harsh environments. My results are consistent with general theory that suggests variation in some characteristics may serve to minimize variation in, and hence buffer, other traits more closely linked to fitness (Caswell 1983).

MANAGEMENT AND CONSERVATION IMPLICATIONS

This study provides empirical evidence that conservation of phenotypic diversity in inland salmonids will require maintenance of habitat diversity across important environmental gradients and at multiple scales. My study provides evidence for the importance of temperature and productivity gradients for their association with diversification in age 0 size, development of life history responses to unproductive environments, and diversification in a life history characteristic, emergence timing. Other gradients and spatial scales may be important as well. I identified differences in instream habitat and relationships to watershed characteristics between wide and narrow valley streams but was not able to link landform to age 0 size characteristics. Additional important gradients may link to critical resources such as winter and summer refuge habitats and spawning substrates. The role and nature of disturbance across temporal scales, that affect critical gradients, the distribution of habitats and resources, and intraspecific phenotypic variation could also prove important in conservation and planning efforts (Reice et al. 1990).

Overlain on environmental gradients with apparently direct and simple effects on growth may be additional gradients that complicate observed patterns. These gradients may include environmental harshness, adaptability, or habitat sensitivity, as well as other physiological, behavioral, or life history gradients associated with growth. For example, elevation and temperature gradients are associated with variation in size and differences in life history variation. I anticipate that the varied expression of migratory life histories will also be linked to productivity, as Gross et al. (1988) suggest for diadromous fishes. Low elevation and wide valley cutthroat trout streams may be more degraded, sensitive to disturbance, and slow to recover. Ideally, management and conservation of inland trout could involve the overlay of current status, critical gradients, and known phenotypic and genetic structuring, which may occur at different and multiple spatial scales, to identify priority areas and appropriate scales of management.

Peripheral populations may be an important consideration in conservation and management strategies for this subspecies. Peripheral populations typically refer to geographically marginal populations that occur on the fringe of a species range. They may also include ecologically marginal populations that experience extreme biotic or abiotic conditions well within a species' range since both typically occupy unusual habitats, have lower abundances than core populations, and are often isolated (Lesica and Allendorf 1995). Genetic and phenotypic divergence from core populations can be common. Peripheral populations including ecologically marginal populations may thus represent an important component of intraspecific diversity and even sites of future speciation events (Skulason and Smith 1995). Life history characteristics that result in restricted gene flow, such as the homing characteristic of salmonids, tend to encourage formation of evolutionarily significant peripheral populations (Riddell et al. 1981). In inland salmonids, productivity gradients may encourage development of populations with divergent characteristics, providing further support for the maintenance of healthy populations across these gradients, as well as focused attention on populations at environmental extremes.

Fish species are often subdivided into more or less discrete populations and subpopulations (Berst and Simon 1981), characterized by their distribution, genotype, and phenotype and reflecting some level of reproductive isolation (Taylor 1991). Elucidation of fish population structure through examination of genetic and phenotypic variation within and among populations can help to focus and prioritize conservation and management efforts. Management for intraspecific diversity in cutthroat trout may benefit from consideration of the spatial distribution of genetic and phenotypic variation and the implications of each. Genetic studies of westslope cutthroat trout suggest that much of the genetic variation is among rather than within individual streams (Allendorf and Leary 1988). This suggests that they may be relatively sensitive to environmental variation among streams and have restricted gene flow. However, the Coeur d’ Alene subbasin does not display the higher level of genetic structuring at the stream scale typical of other westslope cutthroat trout populations (B. Rieman, unpublished data; Spruell et al. 1999). In Chapter 2, I found significant size variation among sites within a stream, suggesting a finer scale of diversification than has been demonstrated by available genetic information. Phenotypic variation can often indicate population structuring at finer spatial scales than indicated by genetic information (Utter 1981; Freeman-Gallant 1996). My study provides empirical support for the inclusion of phenotypic variation in evaluation of westslope cutthroat trout population structure and the sensitivity of this subspecies to relatively fine scale environmental gradients.

Finally, including westslope cutthroat trout habitat goals in land management efforts may contribute to the maintenance of natural aquatic habitat diversity, since strong linkages exist between watershed and aquatic characteristics (Likens and Bormann 1974). As I showed in Chapter 3, habitats vary at the stream scale between wide and narrow valley streams and at the reach scale habitat use is size-mediated. Because of the apparent dependency of age 0 habitats on large woody debris in wide valley streams, wide and narrow valley streams may differ in their sensitivity to management, maintenance of intraspecific diversity of cutthroat trout within and among streams may depend in part on recognition of the important differences and constraints of distinct landforms.

FUTURE RESEARCH

Future research directions specific to each chapter are suggested within those discussions; broad findings from this study suggest several additional important areas for future research. These include better understanding of the distribution of genetic and phenotypic diversity in inland salmonids and identification of environmental gradients that drive diversification and their scales of occurrence. Although considerable effort has been expended toward understanding genetic and life history variation in Pacific salmon, allowing for characterization and discrimination of discrete populations (e.g. Miller and Brannon 1981; Healey 1986); considerably less effort has been directed toward understanding genetic and life history variation in inland trout (Gresswell et al. 1994). Yet, many of the same conditions and mechanisms responsible for producing substructuring in salmon have been documented in trout. These include homing to natal streams (Riddell et al. 1981), genetic variation (e.g. Allendorf and Leary 1988), and exploitation of diverse habitats.

My findings suggest that the environmental characteristics and spatial positioning of a stream may affect intra- and inter-population variation in cutthroat trout. Size variation occurred primarily at the broadest spatial scale I studied, among areas or groups of streams that differed in elevation and temperature (Chapter 2). And, considerable differences in aquatic habitats and habitat diversity occurred among streams in different landforms (Chapter 3). Landscape patterns in elevation, valley width, geology, and drainage connectivity may function as broad scale predictors of habitat characteristics and distribution of phenotypic variation. Although considerable valuable information exists regarding relationships between landscape condition and physical and hydrological characteristic of streams (e.g. Leopold et al. 1963; Grant and Swanson 1995), relatively little inquiry has been directed at effects of broader scale landscape patterns on lotic habitats. Existing examples include: Benda et al. (1992); Nelson et al. (1992); Biggs (1995); Montgomery et al. (1996); Richards et al. (1996). Even less effort has been focused toward defining relationships with lotic intraspecific diversity (e.g. Schlosser and Angermeier 1995).

Understanding patterns and processes of phenotypic and genetic variation is critical to the understanding of evolutionary phenomena (Stearns 1989). Examination of the distribution of variation within a taxon can provide important information on the temporal and spatial nature of its environment as well as its relationship with that environment. Loss of diversity can result in reduced evolutionary flexibility and decline in fitness. Local adaptation and plasticity are sources of phenotypic variation that allow organisms to thrive in diverse environments. Adaptation through a phenotypic response to environmental conditions, even prior to genetic change, may be a common mechanism of evolutionary change in north temperate fish faunas, because selection acts on the phenotype and requires variation (Taylor and Bentzen 1993). Variation in some phenotypic variables may act to buffer an organism from environmental variability in order to maintain stability in traits more closely linked to survival and fitness (Caswell 1983). In Chapter 4, I demonstrated limited variation in size, which may have been influenced by compensatory mechanisms in a growth limited environment. Populations across a temperature gradient differed in their growth dynamics, maximizing growth within the harsh environment while allowing for size variation within a more moderate environment. Better understanding of the patterns of phenotypic variation and the mechanisms that influence fitness across diverse habitats would contribute to our ability to manage inland salmonids and conserve diversity across multiple spatial scales.

LITERATURE CITED

Abbott, A.M. 2000. Land management and flood effects on the distribution and abundance of cutthroat trout in the Coeur d' Alene River basin, Idaho. M.S. Thesis. University of Idaho, Moscow, ID.

Abbott, J.C., R.L. Dunbrack, and C.D. Orr. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). Behaviour 92:241-253.

Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340-346.

Adkison, M.D. 1995. Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? Canadian Journal of Fisheries and Aquatic Sciences 52:2762-2776.

Allendorf, F.W., D. Bayles, D.L. Bottom, K.P. Currens, C.A. Frissell, D. Hankin, J.A. Lichatowich, W. Nehlsen, P.C. Trotter, and T.H. Williams. 1997. Prioritizing pacific salmon stocks for conservation. Conservation Biology 11:140-152.

Allendorf, F.W., and R.F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170-184.

Alt, D.D., and D.W. Hyndman. 1989. Roadside geology of Idaho. Mountain Press Publishing Company, Missoula, MT.

Angermeier, P.L., and I.J. Schlosser. 1989. Species-area relationships for stream fishes. Ecology 70:1450-1462.

Arndt, S.K.A., R.A. Cunjak, and T.J. Benfey. 2002. Effect of summer floods and spatial-temporal scale on growth and feeding of juvenile Atlantic salmon in two New Brunswick streams. Transactions of the American Fisheries Society 131:607-622.

Averett, R.C., and C. MacPhee. 1971. Distribution and growth of indigenous fluvial and adfluvial cutthroat trout (*Salmo clarki*), St. Joe River, Idaho. Northwest Science 45:38-47.

Bailey, R.G. 1995. Description of the ecoregions of the United States. Inventory and Monitoring Institute, U.S. Department of Agriculture, Forest Service. http://www.fs.fed.us/institute/ecoregions/ecoreg1_home.html.

Baltz, D.M., and P.B. Moyle. 1984. Segregation by species and size classes of rainbow trout, *Salmo gairdneri*, and Sacramento sucker, *Catostomus occidentalis*, in three California streams. Environmental Biology of Fishes 10:101-110.

Baltz, D.M., B. Vondracek, L.R. Brown, and P.B. Moyle. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Transactions of the American Fisheries Society 120:166-176.

Bardonnet, A., and M. Heland. 1994. The influence of potential predators on the habitat preferenda of emerging brown trout. Journal of Fish Biology 45 Supplement A:131-142.

Beacham, T.D., and C.B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Transactions of the American Fisheries Society 119:927-945.

Beacham, T.D., F.C. Withler, and R.B. Morley. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 63:847-850.

Beamish, R.J., and G.A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735-743.

Bell, S.S., E.D. McCoy, and H.R. Mushinsky. 1991. Habitat structure: the physical arrangement of objects in space. Chapman and Hall. New York, NY.

Benda, L., T.J. Beechie, R.C. Wissmar, and A. Johnson. 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river basin, Washington State, USA. Canadian Journal of Fisheries and Aquatic Sciences 49:1246-1256.

Benoit, H.P., and P. Pepin. 1999. Interaction of rearing temperature and maternal influence on egg development rates and larval size at hatch in yellowtail flounder (*Pleuronectes ferrugineus*). Canadian Journal of Fisheries and Aquatic Sciences 56:785-794.

Berst, A.H., and R.C. Simon. 1981. Introduction to the proceedings of the 1980 stock concept international symposium (STOCS). Canadian Journal of Fisheries and Aquatic Sciences 38:1457-1458.

Berven, K.A., and D.E. Gill. 1983. Interpreting genetic variation in life-history traits. American Zoologist 23:85-97.

Bestgen, K.R., and B.J. Bundy. 1998. Environmental factors affect daily increment deposition and otolith growth in young Colorado squawfish. Transactions of the American Fisheries Society 127:105-117.

Betsill, R.K., and M.J. Van Den Avyle. 1997. Effect of temperature and zooplankton abundance on growth and survival of larval threadfin shad. Transactions of the American Fisheries Society 126:999-1011.

Biggs, B.J.F. 1995. The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. Freshwater Biology 33:419-438.

Bisson, P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. Murphy, K.V. Koski, and J.R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, future. Pages 143-190 *in* Streamside management: forestry and fisheries interactions. E.O. Salo, and T.D. Cundy (Editors). University of Washington College of Forest Resources, Seattle, WA.

Bisson, P.A., J.L. Nielsen, R.A. Palmason, and L.E. Grove. 1981. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 *in* Aquisition and utilization of aquatic habitat inventory information. N.B. Armantrout (Editors). Western Division American Fisheries Society, Symposium proceedings, October 28-30, 1981, Portland, OR.

Bisson, P.A., K. Sullivan, and J.L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262-272.

Boss, S.M., and J.S. Richardson. 2002. Effects of food and cover on the growth, survival, and movement of coastal cutthroat trout (*Oncorhynchus clarki*) in coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1044-1053.

Bozek, M.A., L.D. DeBrey, and J.A. Lockwood. 1994. Diet overlap among size classes of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in a high-elevation mountain stream. Hydrobiologia 273:9-17.

Bozek, M.A., and W.A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology 70:886-890.

Bradford, M.J., and G.H. Geen. 1987. Size and growth of juvenile chinook salmon back-calculated from otolith growth increments. Pages 453-461 *in* Age and growth of fish. R.C. Summerfelt, and G.E. Hall (Editors). Iowa State University Press, Ames, IA.

Bradford, M.J., and G.H. Geen. 1992. Growth estimates from otolith increment widths of juvenile chinook salmon (*Oncorhynchus tshawytscha*) reared in changing environments. Journal of Fish Biology 41:825-832.

Bradford, M.J., J.A. Grout, and S. Moodie. 2001. Ecology of juvenile chinook salmon in a small non-natal stream of the Yukon River drainage and the role of ice conditions on their distribution and survival. Canadian Journal of Zoology 79:2043-2054.

Brocksen, R.W., G.E. Davis, and C.E. Warren. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. Journal of Wildlife Management 32:51-75.

Brothers, E.B. 1978. Exogenous factors and the formation of daily and subdaily growth increments in fish otoliths. American Journal of Zoology 18:631.

Brothers, E.B. 1984. Otolith studies. Pages 50-57 *in* Ontogeny and systematics of fishes. H.G. Moser (Editors). Allen Press, Lawrence, KS.

Brothers, E.B., C.P. Mathews, and R. Lasker. 1976. Daily growth increments in otoliths from larval and adult fishes. Fishery Bulletin 74:1-8.

Brusven, M.A., and S.T. Rose. 1981. Influence of substrate composition and suspended sediment on insect predation by the torrent sculpin, *Cottus rhotheus.* Canadian Journal of Fisheries and Aquatic Sciences 38:1444-1448.

Bugert, R.M., and T.C. Bjornn. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. Transactions of the American Fisheries Society 120:486-493.

Bugert, R.M., T.C. Bjornn, and W.R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of the American Fisheries Society 120:474-485.

Bulak, J.S., J.S. Crane, D.H. Secor, and J.M. Dean. 1997. Recruitment dynamics of striped bass in the Santee-Cooper system, South Carolina. Transactions of the American Fisheries Society 126:133-143.

Butler, M.J.I. 1988. In situ observations of bluegill (*Lepomis macrochirus* Raf.) foraging behavior: the effects of habitat complexity, group size, and predators. Copeia 1988:939-944.

Campana, S.E. 1983. Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*). Canadian Journal of Zoology 61:1591-1597.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47:2219-2227.

Campana, S.E. 1992. Measurement and interpretation of the microstructure of fish otoliths. Pages 59-71 *in* Otolith microstructure examination and analysis. D.K. Stevenson, and S.E. Campana (Editors). Department of Fisheries and Oceans, Ottawa, CA.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197-242.

Campana, S.E., and C.M. Jones. 1992. Analysis of otolith microstructure data. Pages 73-100 *in* Canadian Special Publication of Fisheries and Aquatic Sciences. D.K. Stevenson, and S.E. Campana (Editors). Department of Fisheries and Oceans, Ottawa, CA.

Campana, S.E., and J.D. Neilson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014-1032.

Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries 6:2-4.

Carlile, D.W., J.R. Skalski, J.E. Batker, J.M. Thomas, and V.I. Cullinan. 1989. Determination of ecological scale. Landscape Ecology 2:203-213.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. American Zoologist 23:35-46.

Chambers, R.C. 1993. Phenotypic variability in fish populations and its representation in individual-based models. Transactions of the American Fisheries Society 122:404-414.

Chandler, G.L., and T.C. Bjornn. 1988. Abundance, growth, and interactions of juvenile steelhead relative to time of emergence. Transactions of the American Fisheries Society 117:432-443.

Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences 39:1208-1210.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345-357.

Chetelat, J., F.R. Pick, A. Morin, and P.B. Hamilton. 1999. Periphyton biomass and community composition in rivers of different nutrient status. Canadian Journal of Fisheries and Aquatic Sciences 56:560-569.

Claessen, D., C. Van Oss, A.M. De Roos, and L. Persson. 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology 83:1660-1675.

Claytor, R.R., H.R. MacCrimmon, and B.L. Gots. 1991. Continental and ecological variance components of European and North American Atlantic salmon (*Salmo salar*) phenotypes. Biological Journal of the Linnean Society 44:203-229.

Connell, J.H., and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121:789-824.

Connolly, P.J., and J.H. Petersen. 2003. Bigger is not always better for overwintering young-of-the-year steelhead. Transactions of the American Fisheries Society 132:262-274.

Conover, D.O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Transactions of the American Fisheries Society 119:416-430.

Conover, D.O., J.J. Brown, and A. Ehtisham. 1997. Countergradient variation in growth of young striped bass (*Morone saxitilis*) from different latitudes. Canadian Journal of Fisheries and Aquatic Sciences 54:2401-2409.

Conover, D.O., and T.M.C. Present. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83:316-324.

Conover, D.O., and E.T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends in Ecology and Evolution 10:248-252.

Cooper, S.D., S. Diehl, K. Kratz, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. Australian Journal of Ecology 23:27-40.

Copp, G.H. 1990. Recognition of cohorts and growth of larval and juvenile roach *Rutilus rutilus* (L.), using size-class ordination of developmental steps. Journal of Fish Biology 36:803-819.

Courtney, D.L., D.G. Mortensen, and J.A. Orsi. 2000. Digitized scale and otolith microstructures as correlates of juvenile pink salmon size. North Pacific Anadromous Fish Commission Bulletin 2000:337-345.

Cullinan, V.I., and J.M. Thomas. 1992. A comparison of quantitative methods for examining landscape pattern and scale. Landscape Ecology 7:211-227.

Daniels, R.A. 1987. Comparative life histories and microhabitat use in three sympatric sculpins (Cottidae: *Cottus*) in northeastern California. Environmental Biology of Fishes 19:93-110.

Day, F.P.J., and C.D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. Ecology 55:1064-1074.

den Boer, P.J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165-194.

Dickey, C.L., J.J. Isely, and J.R. Tomasso. 1997. Slow growth did not decouple the otolith size-fish size relationship in striped bass. Transactions of the American Fisheries Society 126:1027-1029.

Dolloff, A.C., and G.H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma.* Canadian Journal of Fisheries and Aquatic Sciences 2297-2306.

Donald, D.B., R.S. Anderson, and D.W. Mayhood. 1980. Correlations between brook trout growth and environmental variables for mountain lakes in Alberta. Transactions of the American Fisheries Society 109:603-610.

Dong, Q., and D.L. DeAngelis. 1998. Consequences of cannibalism and competition for food in a smallmouth bass population: an individual-based modeling study. Transactions of the American Fisheries Society 127:174-191.

Downes, B.J., P.S. Lake, E.S.G. Schreiber, and A. Glaister. 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. Ecological Monographs 68:237-257.

Dunnigan, J.L. 1997. The spatial distribution of cutthroat trout in the Coeur d' Alene River system, Idaho. Masters Thesis. University of Idaho, Moscow, ID.

Einum, S., and I.A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). Evolution 54:628-639.

Elliott, J.M. 1984. Growth, size, biomass and production of young migratory trout *Salmo trutta* in a Lake District stream, 1966-83. Journal of Animal Ecology 53:979-994.

Elliott, J.M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. the critical time for survival. Journal of Animal Ecology 58:987-1001.

Elliott, J.M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. II. fish growth and size variation. Journal of Animal Ecology 59:171-185.

Endler, J.A. 1973. Gene flow and population differentiation. Science 179:243-250.

Erkinaro, J., J.B. Dempson, M. Julkunen, and E. Niemela. 1997. Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. Journal of Fish Biology 51:1174-1185.

Everest, F.H., and D.W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91-100.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) in a British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 50:1198-1207.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483-498.

Francis, M.P., M.W. Williams, A.C. Pryce, S. Pollard, and S.G. Scott. 1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). Fishery Bulletin 91:159-164.

Freeman-Gallant, C.R. 1996. Microgeographic patterns of genetic and morphological variation in savannah sparrows (*Passerculus sandwichensis*). Evolution 50:1631-1637.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ.

Fretwell, S.D., and H. Lucas. 1970. On the territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:1-36.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Fukuwaka, M. 1996. Allometric back-calculation of individual growth for chum salmon otolith during early life. Scientific Reports of the Hokkaido Salmon Hatchery 50:113-116.

Fukuwaka, M. 1998. Scale and otolith patterns prove growth history of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 1998:190-198.

Garson, D.G. 2003. Chi-square signficance tests. http://www2.chass.ncsu.edu/garson/pa765/chisq.htm. PA765, Multivariate analysis in public administration. Department of Public Administration, North Carolina State University, World Wide Web online classnotes. retrieved November 26, 2003.

Garvey, J.E., R.A. Wright, and R.A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. Canadian Journal of Fisheries and Aquatic Sciences 55:2414-2424.

Gauldie, R.W. 1991. The morphology and periodic structures of the otolith of the chinook salmon (*Oncorhynchus tshawytscha*), and temperature-dependent variation in otolith microscopic growth increment width. Acta Zoologica 72:159-179.

Geffen, A.J. 1992. Validation of otolith increment deposition rate. Pages 101-113 *in* Otolith microstructure examination and analysis. D.K. Stevenson, and S.E. Campana (Editors). Department of Fisheries and Oceans, Ottawa, CA.

Gjedrem, T. 1976. Possibilities for genetic improvements in salmonids. Journal of the Fisheries Research Board of Canada 33:1094-1099.

Gleason, T.R., and D.A. Bengtson. 1996. Size-selective mortality of inland silversides: evidence from otolith microstructure. Transactions of the American Fisheries Society 125:860-873.

Glova, G.J. 1987. Comparison of allopatric cutthroat trout stocks with those sympatric with coho salmon and sculpins in small streams. Environmental Biology of Fishes 20:275-284.

Good, S.P., J.J. Dodson, M.G. Meekan, and D.A.J. Ryan. 2001. Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. Canadian Journal of Fisheries and Aquatic Sciences 58:1187-1195.

Graham, J.J., and D.W. Townsend. 1985. Mortality, growth, and transport of larval and Atlantic herring, *Clupea harengus* L., in Maine coastal waters. Transactions of the American Fisheries Society 114:490-498.

Grant, G.E., and F.J. Swanson. 1995. Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. *in* Natural and anthropogenic influences in fluvial geomorphology. American Geophysical Union Geophysical Monograph 89.

Grant, J.W.A. 1993. Self-thinning in stream-dwelling salmonids. Pages 99-102 *in* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. R.J. Gibson and R.E. Cutting (Editors). Canadian Special Publication of Fisheries and Aquatic Sciences 118.

Grant, J.W.A., and D.L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724-1737.

Grant, J.W.A., and D.L.G. Noakes. 1987. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis.* Journal of Animal Ecology 56:1001-1013.

Greenberg, L.A., and E.B. Brothers. 1991. Intrastream variation in growth rates and time of first otolith increment formation for young of the year *Etheostoma simoterum* (Cope) (Perciformes: Percidae). Journal of Fish Biology 38:237-242.

Gregory, S.V., G.A. Lamberti, and K.M.S. Moore. 1989. Influence of valley floor landforms on stream ecosystems. Pages 3-8 *in* Proceedings of the California Riparian Systems Conference. D.L. Abell (Technical Coordinator). USDA Forest Service General Technical Report PSW-110. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Gresswell, R.E., W.J. Liss, and G.L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51(Suppl. 1):298-309.

Gresswell, R.E., W.J. Liss, G.L. Larson, and P.J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. North American Journal of Fisheries Management 17:1046-1064.

Griffith, J.S.J. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265-273.

Griffith, J.S.J. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Transactions of the American Fisheries Society 104:440-447.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. Biological Journal of the Linnean Society 51:337-357.

Griffiths, D., and R.C. Kirkwood. 1995. Seasonal variation in growth, mortality and fat stores of roach and perch in Lough Neagh, Northern Ireland. Journal of Fish Biology 47:537-554.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47-48.

Gross, M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14-25.

Gross, M.R., R.M. Coleman, and R.M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239:1291-1293.

Grossman, G.D. 1980. Ecological aspects of ontogenetic shifts in prey size utilization in the bay goby (Pisces: Gobiidae). Oecologia 47:233-238.

Hall, D.L. 1991. Age validation and aging methods for stunted brook trout. Transactions of the American Fisheries Society 120:644-649.

Hamrin, S.F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47:223-232.

Hare, J.A., and R.K. Cowen. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415-2431.

Harvey, B., and A. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87:336-342.

Harvey, B.C. 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. Oecologia 87:29-36.

Harvey, B.C. 1998. Influence of large woody debris on retention, immmigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools. Canadian Journal of Fisheries and Aquatic Sciences 55:1902-1908.

Harvey, B.C., and C.D. Marti. 1993. The impact of dipper, *Cinclus mexicanus*, predation on stream benthos. Oikos 68:431-436.

Harvey, B.C., and R.J. Nakamoto. 1997. Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream. Canadian Journal of Fisheries and Aquatic Sciences 54:27-31.

Hawkins, D.K., and C.J. Foote. 1998. Early survival and development of coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead (*Oncorhynchus mykiss*), and reciprocal hybrids. Canadian Journal of Fisheries and Aquatic Sciences 55:2097-2104.

Hayes, J.W. 1995. Spatial and temporal variation in the relative density and size of juvenile brown trout in the Kakanui River, North Otago, New Zealand. New Zealand Journal of Marine and Freshwater Research 29:393-407.

Healey, M.C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. Pages 39-52 *in* Salmonid age at maturity. D.J. Meerburg (Editor). Canadian Special Publication of Fisheries and Aquatic Sciences 89

Healey, M.C., and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. American Fisheries Society Symposium 17:176-184.

Helfman, G.S. 1981. The advantage to fishes of hovering in shade. Copeia 1981:392-400.

Henderson, P.A., R.H.A. Holmes, and R.N. Bamber. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. Journal of Fish Biology 33:221-233.

Hitt, N.P. 2002. Hybridization between westslope cuttthroat trout (*Oncorhynchus clarki lewisi*) and rainbow trout (*O. mykiss*): distribution and limiting factors. M.S. Thesis. University of Montana, Missoula, MT.

Hoffmann, A.A., and M.J. Hercus. 2000. Environmental stress as an evolutionary force. BioScience 50:217-226.

Holmes, J.A. 1990. Sea lamprey as an early responder to climate change in the Great Lakes Basin. Transactions of the American Fisheries Society 119:292-300.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Horne, J.K., and D.C. Schneider. 1995. Spatial variance in ecology. Oikos 74:18-26.

Horner, N.J. 1978. Survival, densities and behavior of salmonid fry in streams in relation to fish predation. M.S. Thesis. University of Idaho, Moscow, ID.

Hughes, R.M., and J.R. Gammon. 1987. Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. Transactions of the American Fisheries Society 116:196-209.

Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board of Canada 26:1473-1483.

Huntingford, F.A., and C.G. de Leaniz. 1997. Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. Journal of Fish Biology 51:1009-1014.

Hutchings, J.A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis.* Evolution 45:1162-1168.

Imsland, A.K., A. Foss, and S.O. Stefannson. 2001. Variation in food intake, food conversion efficiency and growth of juvenile turbot from different geographic strains. Journal of Fish Biology 59:449-454.

Jobling, J., and T.G. Reinsnes. 1986. Physiological and social constraints on growth of Artic charr, *Salvelinus alpinus* L.: an investigation of factors leading to stunting. Journal of Fish Biology 28:379-384.

Jobling, M., and B.M. Baardvik. 1994. The influence of environmental manipulations on inter- and intra-individual variation in food acquisition and growth performance of Artic charr, *Salvelinus alpinus.* Journal of Fish Biology 44:1069-1087.

Johnson, D.W., D.A. Cannamela, and K.W. Gasser. 1983. Food habits of the shorthead sculpin (*Cottus confusus*) in the Big Lost River, Idaho. Northwest Science 57:229-239.

Johnson, S.L., F.J. Rahel, and W.A. Hubert. 1992. Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. North American Journal of Fisheries Management 12:118-124.

Jones, C. 1985. Determining age of larval fish with the otolith increment technique. Fishery Bulletin 84:91-103.

Jones, C.M. 1992. Development and application of the otolith increment analysis technique. Pages 1-11 *in* Otolith microstructure examination and analysis. D.K. Stevenson, and S.E. Campana (Editors). Department of Fisheries and Oceans, Ottawa, CA.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348-365.

Jonsson, B., S. Skulason, S.S. Snorrason, O.T. Sandlund, H.J. Malmquist, P.M. Jonasson, R. Gydemo, and T. Lindem. 1988. Life history variation of polymorphic Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. Canadian Journal of Fisheries and Aquatic Sciences 45:1537-1547.

Kahler, T.H. 1999. Summer movement and growth of individually marked juvenile salmonids in western Washington streams. MS Thesis. University of Seattle, Seattle, WA.

Kaplan, R.H., and W.S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin flipping" principle. American Naturalist 123:393-410.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82:1247-1259.

Keeley, E.R., and J.D. McPhail. 1998. Food abundance, intruder pressure, and body size as determinants of territory size in juvenile steelhead trout (*Oncorhynchus mykiss*). Behaviour 135:65-82.

Kinnison, M.T., M.J. Unwin, and T.P. Quinn. 1998. Growth and salinity tolerance of juvenile chinook salmon (*Oncorhynchus tshawytscha*) from two introduced New Zealand populations. Canadian Journal of Zoology 76:2219-2226.

Kirjasniemi, M., and T. Valtonen. 1997. Size-dependent over-winter mortality of young-of-the-year roach, *Rutilus rutilus.* Environmental Biology of Fishes 50:451-456.

Kirpichnikov, V.S. 1981. Genetic bases of fish selection. Springer-Verlag, New York, NY.

Klopfer, P.H., and R. Mac Arthur. 1960. Niche size and faunal diversity. American Naturalist 94:293-300.

Knight, C.A., R.W. Orme, and D.A. Beauchamp. 1999. Growth, survival, and migration patterns of juvenile adfluvial Bonneville cutthroat trout in tributaries of Strawberry Reservoir, Utah. Transactions of the American Fisheries Society 128:553-563.

Knudsen, K.L., and P. Spruell. 1999. Genetic analysis of westslope cutthroat trout in tributaries of Coeur d' Alene Lake. University of Montana. Report # WTSGL99-106. Missoula, MT.

Labbe, T.R., and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774-1791.

L'Abee-Lund, J.H., B. Jonsson, A.J. Jensen, L.M. Saettem, T.G. Heggberget, B.O. Johnsen, and T.F. Naesje. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta.* Journal of Animal Ecology 58:525-542.

L'Abee-Lund, J.H., A. Langeland, B. Jonsson, and O. Ugedal. 1993. Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. Journal of Animal Ecology 62:160-168.

Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman, and A.D. Steinman. 1989. Influence of channel geomorphology on retention of dissolved and particulate matter in a Cascade Mountain stream. Pages 33-39 *in* Proceedings of the California Riparian Systems Conference. D.L. Abell (Technical Coordinator). USDA Forest Service General Technical Report PSW-110. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Landry, F., J.R. Post, and E.A. Parkinson. 1999. Spatial ontogeny of lentic age-0 rainbow trout, *Oncorhynchus mykiss*: whole-lake manipulations of population size structure. Canadian Journal of Fisheries and Aquatic Sciences 56:1916-1928.

Lanka, R.P., W.A. Hubert, and T.A. Wesche. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society 116:21-28.

Lankford, T.E.J., J.M. Billerbeck, and D.O. Conover. 2001. Evolution of intrinsic growth and energy acquisition rates. II. trade-offs with vulnerability to predation in *Menidia menidia.* Evolution 55:1873-1881.

Larscheid, J.G., and W.A. Hubert. 1992. Factors influencing the size structure of brook trout and brown trout in southeastern Wyoming mountain streams. North American Journal of Fisheries Management 12:109-117.

Lee, D.C., J.R. Sedell, B.E. Rieman, R.F. Thurow, and J.E. Williams. 1997. Broadscale assessment of aquatic species and habitats. Pages 1073-1496 *in* An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great basins - Volume III. T.M. Quigley, and S.J. Arbelbide (Editors). USDA Forest Service, Portland, OR.

Leggett, W., and E. Deblois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32:119-134.

Lentz, H.S. 1998. Distribution and habitat of recently emerged young-of-the-year trout. M.S. Thesis. University of Montana, Missoula, MT.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1963. Fluvial processes in geomorphology. Dover Publications, Inc., New York, NY.

Lesica, P., and F.W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9:753-760.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Lewis, C.A., N.P. Lester, A.D. Bradshaw, J.E. Fitzgibbon, K. Fuller, L. Hakanson, and C. Richards. 1996. Considerations of scale in habitat conservation and restoration. Canadian Journal of Fisheries and Aquatic Sciences 53:440-445.

Li, H.W., G.A. Lamberti, T.N. Pearsons, C.K. Tait, J.L. Li, and J.C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123:627-640.

Likens, G.E., and F.H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. BioScience 24:447-456.

Litvak, M.K., and W.C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Marine Ecology Progress Series 81:13-24.

Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos 35:185-193.

Lonzarich, D.G., and T.P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. Canadian Journal of Zoology 73:2223-2230.

Luecke, C. 1986. Ontogenetic changes in feeding habits of juvenile cutthroat trout. Transactions of the American Fisheries Society 115:703-710.

Maclay, D.J. 1940. Tentative fish management plan: Coeur d' Alene National Forest. Panhandle National Forests, U.S. Forest Service. Coeur d' Alene, Idaho.

Mahon, R., and C.B. Portt. 1985. Local size related segregation of fishes in streams. Arch. Hydrobiol. 103:267-271.

Marshall, S.L., and S.S. Parker. 1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Canadian Journal of Fisheries and Aquatic Sciences 39:542-547.

Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. Journal of Wildlife Management 40:775-788.

Mason, J.C., and D.W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. Journal of the Fisheries Research Board of Canada 22:173-190.

May, R.M. 1994. The effects of spatial scale on ecological questions and answers. Pages 7 1-17 *in* Large scale ecology and conservation. R.J. Edwards, R.M. May, and N.R. Webb (Editors). Blackwell Sci., Pubs., London.

McCormick, M.I., and B.W. Molony. 1993. Quality of the reef fish *Upeneus tragula* (Mullidae) at settlement: is size a good indicator of condition? Marine Ecology Progress Series 98:45-54.

McDowall, R.M. 1994. On size and growth in freshwater fish. Ecology of Freshwater Fish 3:67-79.

McFadden, J.T., and E.L. Cooper. 1962. An ecological comparison of six populations of brown trout (*Salmo trutta*). Transactions of the American Fisheries Society 91:53-62.

McKern, J.L., H.F. Horton, and K.V. Koski. 1974. Development of steelhead trout (*Salmo gairdneri*) otoliths and their use for age analysis and for separating summer from winter races and wild from hatchery stocks. Journal of the Fisheries Research Board of Canada 31:1420-1426.

McLaughlin, R.L., and J.W.A. Grant. 1994. Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. Environmental Biology of Fishes 39:289-300.

Meekan, M.G., J.J. Dodson, S.P. Good, and D.A.J. Ryan. 1998. Otolith and fish size relationships, measurement error, and size-selective mortality during the early life of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55:1663-1673.

Meekan, M.G., and L. Fortier. 1996. Selection for fast growth during the larval life of Atlantic cod, *Gadus mordua* on the Scotian Shelf. Marine Ecology Progress Series 137:25-37.

Menge, B.A., and A.M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5:52-57.

Metcalfe, N.B., F.A. Huntingford, and J.E. Thorpe. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar.* Journal of Animal Ecology 57:463-474.

Meyer, K.A., and J.S. Griffith. 1997. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. Canadian Journal of Zoology 75:59-63.

Michener, W.K., T.J. Baerwald, P. Firth, M.A. Palmer, J.L. Rosenberger, E.A. Sandlin, and H. Zimmerman. 2001. Defining and unraveling biocomplexity. BioScience 51:1018-1023.

Mikheev, V.N., N.B. Metcalfe, F.A. Huntingford, and J.E. Thorpe. 1994. Size-related differences in behaviour and spatial distribution of juvenile Atlantic salmon in a novel environment. Journal of Fish Biology 45:379-386.

Miller, R.J., and E.L. Brannon. 1981. The origin and development of life history patterns in Pacific salmonids. Pages 296-309 *in* Salmon and trout migratory behavior symposium. E.L. Brannon, and E.O. Salo (Editors). Seattle, WA.

Miller, S.J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Transactions of the American Fisheries Society 111:527-530.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670.

Mills, C.A. 1988. The effect of extreme northerly climatic conditions on the life history of the minnow, *Phoxinus phoxinus* (L.). Journal of Fish Biology 33:545-561.

Milne, B.T. 1991. Heterogeneity as a multiscale characteristic of landscapes. Pages 69-84 *in* Ecological Heterogeneity. J. Kolasa, and S.T.A. Pickett (Editors). Springer-Verlag New York Inc., New York.

Miranda, L.E., and W.D. Hubbard. 1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80-87.

Mitchell, P.A. 1968. The food of the dipper (*Cinclus mexicanus* Swainson) on two western Montana streams. M.A. Thesis. University of Montana, Missoula, MT.

Mittelbach, G.G., and P.L. Chesson. 1987. Predation risk: indirect effects on fish populations. Pages 315-331 *in* Predation: direct and indirect impacts on aquatic communities. W.C. Kerfoot, and A. Sih (Editors). University Press of New England, Hanover, NH.

Molony, B.W., and J.H. Choat. 1990. Otolith increment widths and somatic growth rate: the presence of a time lag. Journal of Fish Biology 37:541-551.

Montgomery, D.R., T.B. Abbe, J.M. Buffington, N.P. Peterson, K.M. Schmidt, and J.D. Stock. 1996. Distribution of bedrock and alluvial channels in forested mountain drainage basins. Nature 381:587-589.

Montgomery, D.R., and J.M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. Geological Survey of America Bulletin 109:596-611.

Moore, K.M.S., and S.V. Gregory. 1988a. Response of young-of-the-year cutthroat trout to manipulation of habitat structure in a small stream. Transactions of the American Fisheries Society 117:162-170.

Moore, K.M.S., and S.V. Gregory. 1988b. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 45:1921-1930.

Morales-Nin, B., and Y. Aldebert. 1997. Growth of juvenile Merluccius merluccius in the Gulf of Lions (NW Mediterranean) based on otolith microstructure and length-frequency analysis. Fisheries Research 30:77-85.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology 68:362-369.

Mortensen, A., and B. Damsgard. 1993. Compensatory growth and weight segregation following light and temperature manipulation of juvenile Atlantic salmon (*Salmo salar* L.) and Arctic charr (*Salvelinus alpinus* L.). Aquaculture 114:261-272.

Mosegaard, H., H. Svedang, and K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in Artic charr (*Salvelinus alpinus*) as an effect of differences in temperature response. Canadian Journal of Fisheries and Aquatic Sciences 45:1514-1524.

Mugiya, Y. 1987a. Effects of photoperiod on the formation of otolith increments in the embryonic and larval rainbow trout *Salmo gairdneri.* Nippon Suisan Gakkaishi 53:1979-1984.

Mugiya, Y. 1987b. Phase difference between calcification and organic matrix formation in the diurnal growth of otoliths in the rainbow trout, *Salmo gairdneri.* Fishery Bulletin 85:395-401.

Mugiya, Y., and H. Oka. 1991. Biochemical relationship between otolith and somatic growth in the rainbow trout *Oncorhynchus mykiss*: consequence of starvation, resumed feeding, and diel variations. Fishery Bulletin 89:239-245.

Mullen, D.M., and T.M. Burton. 1995. Size-related habitat use by longnose dace (*Rhinichthys cataractae*). American Midland Naturalist 133:177-183.

Myrick, C.A., and J.J.J. Cech. 1996. The effects of elevated rearing temperatures and genetics on trout bioenergetics. Pages 41-47 *in* Applied Environmental Physiology of Fishes. C. Swanson, D. MacKinley, and P. Young (Editors). Physiology Section, American Fisheries Society, Bethesda, MD.

Neilson, J.D. 1992. Sources of error in otolith microstructure examination. Pages 115-126 *in* Otolith microstructure examination and analysis. D.K. Stevenson, and S.E. Campana (Editors). Department of Fisheries and Oceans, Ottawa.

Neilson, J.D., and G.H. Geen. 1982. Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production. Canadian Journal of Fisheries and Aquatic Sciences 39:1340-1347.

Neilson, J.D., and G.H. Geen. 1986. First-year growth rate of Sixes River chinook salmon as inferred from otoliths: effects on mortality and age at maturity. Transactions of the American Fisheries Society 115:28-33.

Neilson, J.D., G.H. Geen, and B. Chan. 1985. Variability in dimensions of salmonid otolith nuclei: implications for stock identification and microstructure interpretation. Fishery Bulletin 83:81-89.

Nelson, R.L., W.S. Platts, D.P. Larsen, and S.E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Transactions of the American Fisheries Society 121:405-426.

Nicieza, A.G., and N.B. Metcalfe. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology 78:2385-2400.

Nicieza, A.G., F.G. Reyes-Gavilan, and F. Brana. 1994. Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). Canadian Journal of Zoology 72:1603-1610.

Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Nielsen, J.L. 1994. Invasive cohorts: impacts of hatchery-reared coho salmon on the trophic, developmental, and genetic ecology of wild stocks. Pages 361-385 *in* Theory and application in fish feeding ecology. Deanna J. Stouder, Kurt L. Fresh, Robert J. Feller (Editors). Belle W. Baruch Library in Marine Sciences, Volume 18.

Nielsen, L.A., and D.L. Johnson. 1983. Fisheries techniques. American Fisheries Society, Bethesda, MD.

Nikol'skiy, G.V. 1969. Parallel intraspecific variation in fishes. Problems in Ichthyology 9:4-8.

NOAA. 2003. http://www.ncdc.noaa.gov/pub/, retrieved October 16, 2003.

Ojanguren, A.F., F.G. Reyes-Gavilan, and F. Brana. 1996. Effects of egg size on offspring development and fitness in brown trout, *Salmo trutta* L. Aquaculture 147:9-20.

O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2:63-69.

Ott, L. 1984. An introduction to statistical methods and data analysis. PWS Publishers, Boston, MA.

Panfili, J., and M.-C. Ximenes. 1992. Measurements on ground or sectioned otoliths: possibilities of bias. Journal of Fish Biology 41:201-207.

Pannella, G. 1980. Growth patterns in fish sagittae. Pages 519-560 *in* Skeletal growth of aquatic organisms. D.C. Rhoads, and R.A. Lutz (Editors). Plenum Press, New York, NY.

Paradis, A.R., M. Pepin, and P. Pepin. 1999. Disentangling the effects of size-dependent encounter and susceptibility to predation with an individual-based model for fish larvae. Canadian Journal of Fisheries and Aquatic Sciences 56:1562-1575.

Paragamian, V.L., E.C. Bowles, and Hoelscher. 1992. Use of daily growth increments on otoliths to assess stockings of hatchery-reared kokanees. Transactions of the American Fisheries Society 121:785-791.

Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28:1503-1510.

Pearsons, T.N., H.W. Li, and G.A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121:427-436.

Pepin, P., J.F. Dower, and H.P. Benoit. 2001. The role of measurement error on the interpretation of otolith increment width in the study of growth of larval fish. Canadian Journal of Fisheries and Aquatic Sciences 58:2204:2212.

Pepin, P., and T.H. Shears. 1995. Influence of body size and alternate prey abundance on the risk of predation to fish larvae. Marine Ecology Progress Series 128:279-285.

Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? American Naturalist 126:261-266.

Peters, R.H. 1983.The ecological implications of body size. Cambridge University Press, New York, NY.

Piet, G.J., J.S. Pet, W.A.H.P. Guruge, J. Vijverberg, and W.L.T. Van Densen. 1999. Resource partitioning along three niche dimensions in a size-structured tropical fish assemblage. Canadian Journal of Fisheries and Aquatic Sciences 56:1241-1254.

Poff, N.L., and J.V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental Management 14:629-645.

Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. American Zoologist 23:57-63.

Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12:225-251.

Post, J.R., and D.O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46:1958-1968.

Post, J.R., and A.B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 44:1840-1847.

Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333-451 *in* Predation: direct and indirect impacts on aquatic communities. W.C. Kerfoot, and A. Sih (Editors). University Press of New England, Hanover, NH.

Pratt, T.C., and M.G. Fox. 2002. Influence of predation risk on the overwinter mortality and energetic relationships of young-of-year walleyes. Transactions of the American Fisheries Society 131:885-898.

Quinn, T.P., and N.P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555-1564.

Rabeni, C.F., and S.P. Sowa. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1):252-259.

Railsbeck, S.F., and K.A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Transactions of the American Fisheries Society 128:241-256.

Ralston, S., and H.A. Williams. 1988. Numerical integration of daily growth increments: an efficient means of ageing tropical fishes for stock assessment. Fishery Bulletin 87:1-16.

Reice, S.R., R.C. Wissmar, and R.J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14:647-659.

Reinhardt, U.G. 1999. Predation risk breaks size-dependent dominance in juvenile coho salmon (*Oncorhynchus kisutch*) and provides growth opportunities for risk-prone individuals. Canadian Journal of Fisheries and Aquatic Sciences 56:1206-1212.

Reinhardt, U.G., and M.C. Healey. 1999. Season- and size-dependent risk taking in juvenile coho salmon: experimental evaluation of asset production. Animal Behaviour 57:923-933.

Reznick, D. 1981. "Grandfather effects": the genetics of interpopulation differences in offspring size in the mosquito fish. Evolution 35:941-953.

Rice, J.A., L.B. Crowder, and K.A. Rose. 1993. Interactions between size-structured predator and prey populations: experimental test and model comparison. Transactions of the American Fisheries Society 122:481-491.

Richards, C., L.B. Johnson, and G.E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53 (Suppl. 1):295-311.

Ricker, W.E. 1979. Growth rates and models. Pages 678-743 *in* Fish physiology VIII. bioenergetics and growth. W.S. Hoar, D.J. Randall, and J.R. Brett (Editors). Academic Press, Inc., New York, NY.

Riddell, B.E., and W.C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 38:308-320.

Riddell, B.E., W.C. Leggett, and R.L. Saunders. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the S. W. Miramichi River, N.B. Canadian Journal of Fisheries and Aquatic Sciences 38:321-333.

Rieman, B.E., D.C. Lee, and R. Thurow, F. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:1111-1125.

Rieman, B.E., and D.L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. Transactions of the American Fisheries Society 121:178-191.

Roff, D.A. 1992. The evolution of life histories. Chapman and Hall, New York, NY.

Roni, P., and T.P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:282-292.

Rosenfeld, J.S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585-593.

Rosgen, D.L. 1994. A classification of natural rivers. Catena 22:169-199.

Rot, B.W., R.J. Naiman, and R.E. Bilby. 2000. Stream channel configuration, landform, and riparian forest structure in the Cascade Mountains, Washington. Canadian Journal of Fisheries and Aquatic Sciences 57:699-707.

Ruzycki, J.R., and W.A. Wurtsbaugh. 1999. Ontogenetic habitat shifts of juvenile Bear Lake sculpin. Transactions of the American Fisheries Society 128:1201-1212.

Sale, P.F. 1991. Habitat structure and recruitment in coral reef fishes. Pages 197-210 *in* Habitat structure: the physical arrangement of objects in space. S.S. Bell, E.D. McCoy, and H.R. Mushinsky (Editors). Chapman and Hall, New York, NY.

Scarnecchia, D.L., and E.P. Bergerson. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. North American Journal of Fisheries Management 7:315-330.

Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. Annual Review of Ecology and Systematics 24:35-68.

Schlichting, C.D. 1989. Phenotypic integration and environmental change. BioScience 39:460-464.

Schlosser, I.J. 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 68:651-659.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. BioScience 41:704-712.

Schlosser, I.J., and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17:392-401.

Schmidt-Neilsen, K. 1984.Scaling, why is animal size so important? Cambridge University Press, Cambridge.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Schoener, T.W. 1983. Field experiments on interspecific competition. American Naturalist 122:240-285.

Schultz, E.T., D.O. Conover, and A. Ehtisham. 1998. The dead of winter: size-dependent variation and genetic differences in seasonal mortality among Atlantic silverside (Atherinidae: *Menidia menidia*) from different latitudes. Canadian Journal of Fisheries and Aquatic Sciences 55:1149-1157.

Schultz, E.T., K.E. Reynolds, and D.O. Conover. 1996. Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: geographic differences revealed by common-environment experiments. Functional Ecology 10:366-374.

Secor, D.H., and J.M. Dean. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis.* Canadian Journal of Fisheries and Aquatic Sciences 49:1439-1454.

Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford, and C.P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711-724.

Shepard, B.B., K.L. Pratt, and P.J. Graham. 1984. Life histories of westslope cutthroat trout and bull trout in the upper Flathead River Basin, Montana. Environmental Protection Agency, Region VIII, Water Division. Contract Number R008224-01-5. Denver, CO.

Shirvell, C.S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Canadian Journal of Fisheries and Aquatic Sciences 47:852-861.

Shirvell, C.S., and R.G. Dungey. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Transactions of the American Fisheries Society 112:355-367.

Shuter, B.J., J.A. MacLean, F.E.J. Fry, and H.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Sirois, P., F. Lecomte, and J.J. Dodson. 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. Canadian Journal of Fisheries and Aquatic Sciences 55:2662-2671.

Skulason, S., and T.B. Smith. 1995. Resource polymorphism in vertebrates. Trends in Ecology and Evolution 10:366-370.

Smith, R.W., and J.S. Griffith. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. Transactions of the American Fisheries Society 123:747-756.

Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion *versus* phenotypic modulation. American Zoologist 23:47-55.

Smoker, W.W., A.J. Gharrett, M.S. Stekoll, and J.E. Joyce. 1994. Genetic analysis of size in an anadromous population of pink salmon. Canadian Journal of Fisheries and Aquatic Sciences 51 (Suppl. 1):9-14.

Sogard, S.M. 1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. Canadian Journal of Fisheries and Aquatic Sciences 48:1862-1871.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129-1157.

Spruell, P., B.E. Rieman, K.L. Knudsen, F.M. Utter, and F.W. Allendorf. 1999. Genetic population structure within streams: microsatellite analysis of bull trout populations. Ecology of Freshwater Fish 8:114-121.

Stearley, R.F., and G.R. Smith. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. Transactions of the American Fisheries Society 122:1-33.

Stearns, S.C. 1983. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. American Zoologist 23:65-75.

Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. BioScience 39:436-445.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stein, R.A., S.T. Threlkeld, C.D. Sandgren, W.G. Sprules, L. Persson, E.E. Werner, W.E. Neill, and S.I. Dodson. 1987. Size structured interactions in lake communities. Pages

161-179 *in* Complex interactions in lake communities. S.R. Carpenter (Editor). Springer-Verlag, New York, NY.

Stevenson, D.K., and S.E. Campana. 1992. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117. Department of Fisheries and Oceans, Ottawa.

Sumpter, J.P. 1992. Control of growth of rainbow trout (*Oncorhynchus mykiss*). Aquaculture 100:299-320.

Sutton, T.M., and J.J. Ney. 2001. Size-dependent mechanisms influencing first-year growth and winter survival of stocked striped bass in a Virginia mainstream reservoir. Transactions of the American Fisheries Society 130:1-17.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207.

Taylor, E.B., and P. Bentzen. 1993. Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in northeastern North America. Evolution 47:813-832.

Templeton, A.R. 1994. Coadaptation, local adaptation, and outbreeding depression. Pages 152-153 *in* Principles of conservation biology. G.K. Meffe, and C.R. Carroll (Editors) Sinauer Associates, Inc., Sunderland, MA.

Thompson, J.D. 1991. Phenotypic plasticity as a component of evolutionary change. Trends in Ecology and Evolution 6:246-249.

Thompson, J.N., O.J. Reichman, P.J. Morin, G.A. Polis, M.E. Power, R.W. Sterner, C.A. Couch, L. Gough, R. Holt, D.U. Hooper and others. 2001. Frontiers of ecology. BioScience 51:15-24.

Thorpe, J.E. 1989. Developmental variation in salmonid populations. Journal of Fish Biology 35 Supplement A:295-303.

Thorpe, J.E. 1994. Salmonid flexibility: responses to environmental extremes. Transactions of the American Fisheries Society 123:606-612.

Thorrold, S.R., and D.M. Williams. 1989. Analysis of otolith microstructure to determine growth histories in larval cohorts of a tropical herring (*Herklotsichthys casterlaui*). Canadian Journal of Fisheries and Aquatic Sciences 46:1615-1624.

Thut, R.N. 1970. Feeding habits of the dipper in southwestern Washington. Condor 72:234-235.

Toneys, M.L., and D.W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. Transactions of the American Fisheries Society 108:415-419.

Trippel, E.A. 1993. Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwestern Ontario lakes. North American Journal of Fisheries Management 13:64-72.

Trippel, E.A., and F.W.H. Beamish. 1989. Lake trout (*Salvelinus namaycush*) growth potential predicted from cisco (*Coregonus artedii*) population structure and conductivity. Canadian Journal of Fisheries and Aquatic Sciences 46:1531-1538.

Trippel, E.A., and F.W.H. Beamish. 1993. Multiple trophic level structuring in *Salvelinus* - *Coregonus* assemblages in boreal forest lakes. Canadian Journal of Fisheries and Aquatic Sciences 50:1442-1455.

Turner, D.L., J.E. Ott, and E.D. McArthur. (in review). Classification and regression trees for ecological modeling: a case study using fire rehabilitation data. Journal of Range Management.

Urban, D.L. 2002. Classification and regression trees. Pages 222-232 *in* Analysis of ecological communities. B. McCune, and J.B. Grace (Editors). MjM Software Design, Gleneden Beach, OR.

Utter, F.M. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. Canadian Journal of Fisheries and Aquatic Sciences 38:1626-1635.

Van Den Avyle, M.J. 1993. Dynamics of exploited fish populations. Pages 105-135 *in* Inland fisheries management in North America. C.C. Kohler, and W.A. Hubert (Editors). American Fisheries Society, Bethesda, MD.

van Noordwijk, A.J. 1989. Reaction norms in genetical ecology. BioScience 39:453-458.

Van Winkle, W., K.A. Rose, and R.C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Society 122:397-403.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37:130-137.

Vayssieres, M.P., R.E. Plant, and B.H. Allen-Diaz. 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11:679-694.

Volk, E.C., D.G. Mortensen, and A.C. Wertheimer. 1995. Nondaily otolith increments and seasonal changes in growth of a pink salmon (*Oncorhynchus gorbuscha*) population in Auke Bay, Alaska. Pages 211-225 *in* Recent developments in fish otolith research. D.H. Secor, J.M. Dean, and S.E. Campana (Editors). U. South Carolina Press, Columbia, SC.

Volk, E.C., R.C. Wissmar, C.A. Simenstad, and D.M. Eggers. 1984. Relationship between otolith microstructure and the growth of juvenile chum (*Oncorhynchus keta*) under different prey rations. Canadian Journal of Fisheries and Aquatic Sciences 41:126-133.

Vondracek, B., W.A. Wurtsbaugh, and J.J.J. Cech. 1988. Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. Environmental Biology of Fishes 21:45-57.

Warlen, S.M. 1992. Age, growth, and size distribution of larval Atlantic menhaden off North Carolina. Transactions of the American Fisheries Society 121:588-598.

Weeks, S.C. 1993. Phenotypic plasticity of life-history traits in clonal and sexual fish (*Poeciliopsis*) at high and low densities. Oecologia 93:307-314.

Werner, E.E. 1984. The mechanisms of species interactions and community organization in fish. Pages 360-381 *in* Ecological communities: conceptual issues and the evidence. D.R.J. Strong, D. Simberloff, L.G. Abele, and A.B. Thistle (Editors). Princeton University Press, Princeton, NJ.

Werner, E.E. 1994. Ontogenetic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. Ecology 75:197-213.

Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393-425.

West, C.J., and P.A. Larkin. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:712-721.

West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics 20:249-278.

Wilson, K.H., and P.A. Larkin. 1980. Daily growth rings in the otoliths of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 37:1495-1498.

Wilson, K.H., and P.A. Larkin. 1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry. Canadian Journal of Fisheries and Aquatic Sciences 39:1335-1339.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences 42:1668-1672.

Woody, C.A., J. Olsen, J. Reynolds, and P. Bentzen. 2000. Temporal variation in phenotypic and genotypic traits in two sockeye salmon populations, Tustumena Lake, Alaska. Transactions of the American Fisheries Society 129:1031-1043.

Wright, P.J., N.B. Metcalfe, and J.E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. Journal of Fish Biology 36:241-249.

Wright, P.J., D. Rowe, and J.E. Thorpe. 1991. Daily growth increments in the otoliths of Atlantic salmon parr, *Salmo salar* L., and the influence of environmental factors on their periodicity. Journal of Fish Biology 39:103-113.

Yamahira, K., and D.O. Conover. 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? Ecology 83:1252-1262.

Young, K.A. 1999. Environmental correlates of male life history variation among coho salmon populations from two Oregon coastal basins. Transactions of the American Fisheries Society 128:1-16.

Zhang, Z., and R.J. Beamish. 2000. Use of otolith microstructure to study life history of juvenile chinook salmon in the Strait of Georgia in 1995 and 1996. Fisheries Research 46:239-250.

Zhang, Z., R.J. Beamish, and B.E. Riddell. 1995. Differences in otolith microstructure between hatchery-reared and wild chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 52:344-352.