AGE STRUCTURE, GROWTH, AND FACTORS AFFECTING RELATIVE ABUNDANCE OF LIFE HISTORY FORMS OF BULL TROUT IN THE CLARK FORK RIVER DRAINAGE, MONTANA AND IDAHO

by

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APPROVAL

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Most of all, I thank my family, especially Jillian, Adrian, Joseph, and Virginia Zymonas, for the invaluable support and sacrifices that they contributed. The work devoted to completing this thesis is dedicated to Joseph Zymonas.

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ABSTRACT

Bull trout *Salvelinus confluentus* exhibit high variability in life history patterns. Better understanding of the underlying mechanisms is needed to assist conservation efforts. I assessed relationships among life history form, growth rates, age structures, and environmental variables, using pelvic fin rays and scales to estimate age and growth. First, I assessed the effects of pelvic fin ray excision on survival and growth of age-3 and age-4 bull trout. Survival and growth were similar between fin ray-excised and control fish within each age group, although a bacterial coldwater disease infection caused higher mortality in age-3 fish. Excised rays achieved a mean 42% regeneration by six months. Second, I developed methodology for using pelvic fin rays to estimate age and growth. Suitability of fin ray sections was based on overall morphology, appearance of early annuli, and presence of a conspicuous dash in the nucleus. Back-calculation for juvenile and non-migratory bull trout produced real error (mean ± SE) of 4.1 ± 2.0% and absolute error of 7.2 ± 1.2% of known lengths one year prior. Ageing precision and accuracy of growth estimates using fin rays compared favorably to those from scales. However, obtaining adequate fin ray samples for large fish (>400 mm TL) proved difficult and additional work is needed to validate age and growth estimation procedures. Third, I analyzed age and growth of bull trout in relation to environmental conditions in study streams. Bull trout in predominantly migratory populations held lower proportions of individuals > age 3 during summer and generally displayed higher growth rates during ages 0 and 1 than those in resident populations. Migratory populations exhibited overall faster early growth, although not in all cases. Age-0 growth was positively associated with length of growing season, whereas age-1 growth was negatively associated with density of bull trout and positively related to presence of nonnative salmonids. Presence of the migratory life history was influenced by severity of barriers to migration and presence of nonnative brook and brown trout. These results suggest that the migratory life history may be encouraged by enhancing migratory corridors and juvenile rearing habitat in lower reaches of tributaries.

CHAPTER 1

INTRODUCTION

Bull trout are a char species native to mountainous regions of the northwestern United States and Canada. Habitat requirements of bull trout include cold water temperatures, low levels of fine sediment in spawning tributaries, and unimpeded corridors for migration among habitats (Rieman and McIntyre 1993). Past timber harvest, mining, and dam construction have degraded habitat conditions in many areas, and introductions of nonnative fish species have increased threats of competition, predation, and hybridization (Nelson 1965; Leary et al. 1993; Rieman and McIntyre 1993; Fredenberg 2002; Gunckel et al. 2002). Consequential declines in distribution and abundance of bull trout have prompted federal, state, and provincial agencies to designate the bull trout as a species of special concern or as threatened over much of its range (Federal Register 1999; Fish and Wildlife Division 2004; British Columbia Conservation Data Centre 2005).

One notable feature of bull trout ecology is a pronounced variability in life history, both within and among populations, that produces distinct differences in body size. A potamodromous species, bull trout commonly rear in small streams for one or more years before migrating downstream to large rivers or lakes. Higher productivity in downstream environments confers a growth advantage, and migratory individuals usually return to spawning tributaries at lengths from 400 to greater than 800 mm TL (McPhail and Murray 1979; Fraley and Shepard 1989; Rieman and McIntyre 1993). However, bull trout may also exhibit a resident life history, remaining in tributary streams during all life stages and rarely attaining sizes greater than 400 mm. Characteristics such as age structure, growth rates, and migration patterns may vary considerably among adjacent populations (Mogen and Keading 2005).

The mechanism controlling life history variation in bull trout has not been conclusively defined. Research on bull trout, related char species, and other salmonids has produced evidence linking life history to genetic and environmental factors, but a comprehensive explanation remains elusive (Secor 1999). Evidence for genetic control over life history variation in salmonids comes from genetic analyses indicating differences between forms (Skaala and Naevdal 1989; Vespoor and Cole 1989; Taylor et al. 1996), transplant or laboratory rearing experiments revealing a dependency of migratory tendency on parental life history (Jonsson 1982; Morita and Yamamoto 2001; Northcote 1981; Kaya 1989), and observations of reproductive isolation among sympatric forms (Jonsson and Hindar 1982; Skúlason et al. 1989). However, other studies have linked migration tendency to growth rates rather than inheritance (Hindar and Jonsson 1993; Økland et al. 1993; Bohlin et al. 1996). Genetic analyses have distinguished bull trout from different tributaries but not have not found differences between sympatric forms (Leary et al. 1993; Kanda et al. 1997; Spruell et al. 1999; Costello et al. 2003; Spruell 2003), and I am not aware of any study that has assessed the role of early growth in life history variation.

Better resolution of this question holds significance as a practical management issue as well as a matter of scientific interest. Management plans presently identify as goals both the promotion of the migratory form and the preservation of a diversity of life histories across the landscape (WWP 1998; USFWS 2002). The large-bodied migratory form, in particular, has declined in abundance but holds potential to improve the species' long-term status (Rieman and McIntyre 1993). Compared to residents, migratory individuals possess greater fecundity and competitive advantage, and they are more likely to colonize available habitats, supplement other populations, and promote genetic diversity (Rieman and McIntyre 1993). Also, spatial separation of migratory population components reduces the risk of elimination by stochastic events in a particular location. Management efforts to encourage particular life histories require additional information on factors influencing life history of bull trout.

The purpose of this study was to assess interrelationships among age structure and growth rates, biotic and abiotic environmental variables, and the occurrence of life history forms within bull trout populations. Of particular interest was the role of early growth in determination of life history form. Fisheries researchers commonly obtain age and growth data by analyzing hard parts such as scales, fin rays, or otoliths, but bull trout scales are difficult to interpret (Williamson and MacDonald 1997) and the threatened status of the species limits the availability of otoliths. For this study I proposed to estimate age and growth using pelvic fin rays because two previous studies of bull trout reported better ageing precision and higher ages with fin rays than scales (Williamson and Macdonald 1997; Gust 2001). However, this necessitated the completion of preliminary work in two areas. First, given the sensitive status of bull trout, I assessed the effect of partial pelvic fin removal on growth and survival of bull trout in a laboratory setting. Second, I conducted analyses to establish methodology for age estimation and back-calculation and to compare results obtained with pelvic rays to those obtained with scales and otoliths.

This thesis consists of three self-contained chapters pertaining to age, growth, and life history variation of bull trout. First, I describe a laboratory experiment conducted on a captive population of bull trout to assess the effect of pelvic fin ray removal on survival and growth (Chapter 2). Second, I evaluate the potential for using pelvic fin rays to estimate age and growth of bull trout in populations occupying widely different environments and exhibiting varying life history forms (Chapter 3). Third, I use pelvic fin rays and scales to describe age structures and growth rates in bull trout populations in the lower Clark Fork, Lake Pend Oreille, and Bitterroot drainages in Montana and Idaho, and I relate these characteristics to biotic and abiotic environmental factors and to life history (Chapter 4). Conclusions from the entire thesis are summarized in Chapter 5.

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CHAPTER 2

EFFECT OF PELVIC FIN RAY REMOVAL ON SURVIVAL AND GROWTH OF BULL TROUT

Introduction

Partial or complete fin removal is widely used in fisheries studies to mark fish (Guy et al. 1996) and to obtain rays or spines for age and growth analysis (DeVries and Frie 1996). In many species, otoliths and fin rays have greater ageing precision than scales, particularly for long lived individuals (e.g., Dutil and Power 1977; Sharp and Bernard 1988; Williamson and Macdonald 1997; Nakamura et al. 1998; Gust 2001; but see Hubert et al. 1987). Fin rays have been validated for ageing several salmonids, including brown trout *Salmo trutta* (Burnet 1969; Shirvell 1981), and chinook salmon *Oncorhynchus tshawytscha* (Chilton and Bilton 1986). Fin rays may be a useful alternative to otoliths for ageing in situations requiring a nonlethal sampling procedure, for example in studies of threatened species. However, fin ray removal may be an unacceptable ageing technique if it impairs growth or survival of rare species (Collins and Smith 1996).

Potential adverse effects of fin removal include a short-term physiological stress response (Sharpe et al. 1998) and a site for infection (Fry 1961). Potential longer-term impairments include reduced station-holding ability (Arnold et al. 1991), growth (Saunders and Allen 1967; Skaugstad 1990), and survival (Ricker 1949; Coble 1971; Nicola and Cordone 1973; Vincent-Lang 1993). Manifestation of these effects varies considerably depending on degree of fin removal and regeneration, and the particular fin, species, and size class studied (Mears and Hatch 1976; Bergstedt 1985).

The purpose of this study was to investigate whether the excision of the first three rays of one pelvic fin for the purpose of age and growth estimation affected growth or survival of bull trout. Bull trout are a federally listed ‘threatened’ species in the conterminous United States (Federal Register 1999) with strict restrictions on the number of fish that can be sacrificed for scientific or other purposes, hence limiting use of lethal sampling techniques such as otolith removal. Fin rays of bull trout offer an ostensibly nonlethal ageing alternative to otoliths while offering greater ageing precision and better resolution of annuli in older fish than scales (Williamson and Macdonald 1997; Gust 2001). I am not aware of published work that has addressed either the specific partial pelvic fin excision used here or any fin removal effects on bull trout. In a hatchery population of the closely related Arctic char *Salvelinus alpinus*, excision of an entire pelvic fin did not affect survival or growth relative to control fish (Skaugstad 1990). In this study, I compared growth, survival, and fin regeneration of fin ray-excised and control groups of bull trout 209-362 mm SL in the laboratory over 169 d, about the length of a normal growing season in Montana streams.

Methods

Bull trout used in this study were part of a cultured population at the U.S. Fish and Wildlife Service Bozeman Fish Technology Center in Bozeman, Montana. Fertilized eggs were originally obtained from a captive broodstock at the Creston National Fish Hatchery in Creston, Montana and reared for use in a temperature study (Selong et al.

2001). Fin erosion was evident on dorsal and caudal fins of most individuals but the pelvic fins showed little or no damage.

Prior to study initiation, bull trout developed symptoms of bacterial coldwater disease *Flavobacterium psycrophilum*, a common yet difficult to control infection in hatcheries (Nematollahi et al. 2003). Disease symptoms included lesions on or near the caudal peduncle, deterioration of the caudal fin, and continual swimming near the surface. About 14% of the population died after the onset of coldwater disease symptoms, and the study was delayed about two months until the source of infection was positively identified and mortality ceased. All fish had been similarly exposed to the pathogen prior to beginning this experiment; thus, the initial condition of control versus treatment groups was deemed unbiased. Fin excision can increase susceptibility to a pathogen (Fry 1961) and the infection was considered an added stressor more likely to adversely affect fin-excised fish than control fish. The coldwater disease pathogen is considered to be naturally ubiquitous in bull trout waters in Montana (E. Ryce, Montana Department of Fish, Wildlife, and Parks, personal communication) and thus its presence represented a realistic threat encountered by wild fish.

The experimental design enabled comparison of treatment and control groups among all fish as well as by age class. Two age classes were examined: age-3 ($N = 33$; initial mean ± SD = 258 ± 23 mm SL; range 209—298) and age-4 ($N = 50$; initial mean ± SD = 335 ± 16 mm SL; range = 294—362). Age-3 individuals were representative in size of adult bull trout resident in small headwater streams or of migratory subadult bull trout occupying larger rivers or lakes, whereas age-4 fish were similar in size to large resident or small migratory adult bull trout (Rieman and McIntyre 1993). At the start of the experiment (March 22, 2002), fish were anaesthetized with tricaine methanesulfonate, weighed to the nearest 0.1 gram, and standard length was measured to the nearest millimeter. A visual implant (VI) tag was inserted in the adipose tissue behind each eye, providing unique identification of the fish without affecting growth or survival (Zerrenner et al. 1997; Rikardsen et al. 2002). Individuals were randomly selected for fin excision, which involved excising the first three rays at the anterior edge of the left pelvic fin using surgical scissors (Figure 2.1). Fin rays were excised distal to the articulation with the basipterygium but as close to the base as possible. This achieved the condition of maximum severity and ensured inclusion of the early growth portion necessary for accurate age determination (Scidmore and Glass 1953; Chilton and Bilton 1986; Chapter 3). Excision of the leading three rays resulted in removal of about one-third of the pelvic fin.

Figure 2.1. Age-3 bull trout after excising leading three pelvic fin rays, showing location of cut and proportion of fin removed. Pelvic fin edges outlined for clarity. Note deteriorated caudal fin symptomatic of coldwater disease.

Nearly equal proportions of treatment and control bull trout were randomly placed into three circular fiberglass tanks (diameter, 1.2 m; flow rate, 23.8 L/min) to attain replicate compositions of 11 age-3 fish (6 treatment, 5 control) and 16 or 17 age-4 fish (9 treatment, 7 or 8 control) in each tank. Length distributions of treatment and control fish were similar within both age-3 ($t = 0.57$, df = 23, $P = 0.57$) and age-4 ($t = 0.68$, df = 43, $P = 0.50$) groups at the beginning of the experiment. Water temperature was maintained at constant 12° C and equal food rations approximating satiation levels (Selong et al. 2001) were added by hand once daily to each tank.

Examinations were conducted after one week and thereafter at roughly monthly intervals (34, 64, 99, 127, and 169 d) over a 5.5-month period. Fish were anaesthetized, identified by VI tag code, weighed, and measured. The condition of the wound area on fin-excised individuals was visually inspected and the degree of inflammation recorded as "none," "moderate," or "severe." Length of regeneration of excised rays was quantified to the nearest millimeter using a ruler. Because the leading ray typically regenerated at a slower rate than subsequent rays, mean length of the regenerating fin portion was used in analyses. To adjust for growth during the study, the length of regeneration was converted to a percentage of estimated total fin length. Estimated total fin length was derived from a pelvic fin length (PFL)-body length (BL) equation ($PFL = 0.141*BL - 11.7$; $r^2 = 0.72$; $P = 0.01$) obtained by regressing maximum length of the left pelvic fin (typically the second or third ray) on body length for 38 control fish.

All statistical analyses were conducted with the level of significance set at $\alpha = 0.05$. I assessed tank effects on survival of control and fin-excised groups with chi-square tests. Survival differences between control and fin-excised groups at each sampling were also evaluated with chi-square tests or with Fisher's exact tests if expected cell counts were less than five (Zar 1996). Effects of treatment, age group, and tank on relative growth [(end length – initial length) / initial length] (Busaker et al. 1990) at each examination were analyzed with ANOVA (general linear model, all factors fixed). Difference between age groups in the amount of regeneration attained by the end of the study was assessed with a *t*-test.

Water circulation failed in one tank on day 108, causing visible distress and elevated mortality (58% of the fish in that tank). Data collected from this tank after the previous sample date (day 99) were subsequently omitted from further analysis. Data for all three tanks through day 99 and for the remaining two tanks through day 169 were combined for analyses because tank effects on survival (day 99: $\chi^2 = 0.19$, df = 2, $P = 0.91$; day 169: $\chi^2 = 0.08$, df = 1, $P = 0.78$) and relative growth (day 99: $F = 1.06$, df = 2, $P = 0.36$; day 169: $F = 0.09$, df = 1, $P = 0.77$) were not significant.

Results

Fin excision had no apparent effect on survival. No mortality occurred before the first examination on day 8 (Figure 2.2). Survival was similar between fin-excised and control groups at each stage during the 169-d study (fin-excised: ≥ 73%, control: ≥ 69%; $\chi^2 < 0.04$; df = 1; $P > 0.85$). Survival differed significantly between age classes at all examinations from day 64 through the end of the study ($\chi^2 > 5.61$; df = 1; $P < 0.02$). At the end of the study, 94% of age-4 but only 36% of age-3 bull trout remained alive in the two unaffected tanks. Symptoms of advanced coldwater disease, namely lesions on the caudal fin and peduncle, were readily apparent in at least 58% of the age-3 mortalities (a minimum value because some mortalities were not inspected prior to disposal) and 40% of survivors. Despite differences in survival between the two age classes, fin excision did not affect survival within each age class (age-3: *N* survivors = 3 control, 5 fin-excised, Fisher's exact test: $P > 0.42$; age-4: *N* survivors = 15 control, 17 fin-excised, $\chi^2 < 0.03$; df = 1; $P > 0.86$). Statistical comparisons within the age-3 class should be regarded with caution because only three control and five fin-excised fish survived to the end of the experiment; nonetheless, nearly equal proportions of fin-excised to control fish survived in both the age-3 and age-4 groups.

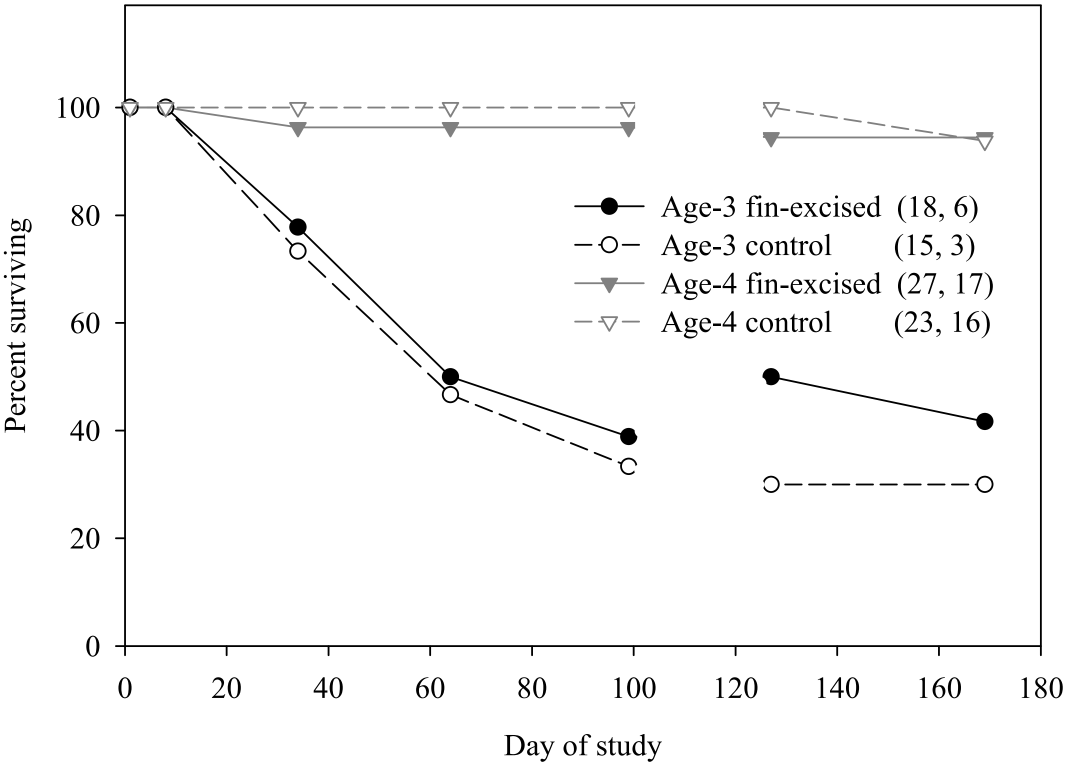

Figure 2.2. Percent survival of age-3 and age-4 bull trout with and without excised fin rays during the 169-day study. Percent survival is shown for all three test tanks from day 1 to day 99 and for the two tanks unaffected by a water supply failure from days 127 to 169. The first number in parentheses is the sample size for each age and treatment group for all three tanks at start of study; the second number is the sample size of the remaining two tanks at day 127.

Growth was similar between fin-excised and control fish. At the end of the study, mean relative growth in length was 12.5% (mean growth ± SE = 31 ± 4 mm) for the age-3 group and 4.5% (15 ± 1 mm) for the age-4 group (Figure 2.3). Fin excision did not affect growth at any point during the course of the study ($F \leq 0.77$, df = 1, $P > 0.38$). Although age-3 bull trout experienced high mortality, relative growth of treatment and control bull trout was similar in all three tanks at day 99 (fin-excised: 7.6 ± 0.8%, control: 7.6 ± 1.0%) and in the two unaffected tanks at the end of the study on day 169 (fin-excised: 12.9 ± 1.8%, control: 11.9 ± 2.2%).

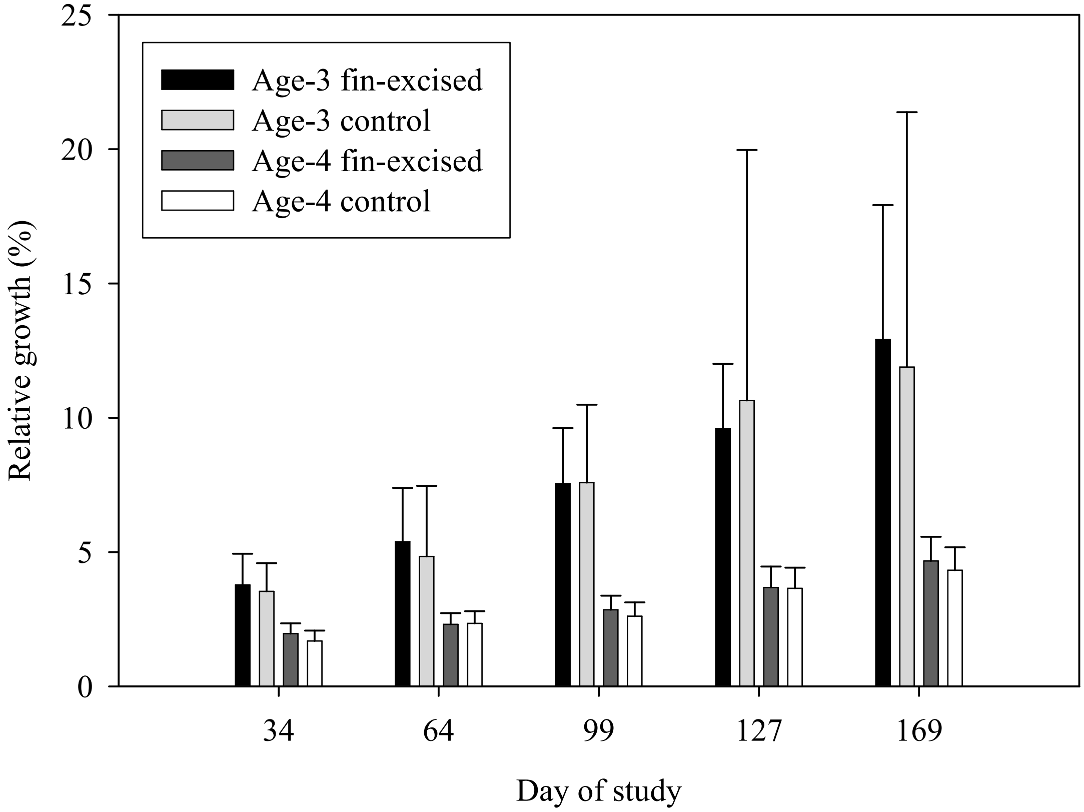

Figure 2.3. Relative growth (%) in length (mean + 95% CI) of age-3 and age-4 bull trout with and without fin ray-excision over the course of the study. Only data from the two tanks unaffected by water supply failure are included for days 127 and 169.

The wound area appeared to heal quickly in most fin-excised specimens. Severe inflammation (redness and swelling of tissue at distal end of remaining portion of cut rays) was apparent at the excision site in 46% of fin-excised fish on day 8 but declined to 4% by day 34. The fin-excision wound appeared completely healed in 56% of the fish by day 34 and in 96% by day 127. At the end of the study, the mean percentage of estimated total fin length regenerated was 42%, yielding a regeneration rate of 0.25%/d (Figure 2.4). Regeneration did not differ between age classes ($t = 0.17$, df = 7, $P = 0.87$) and appeared normal (all excised rays regenerating and straight) in 92% (22 of 24) of surviving fin-excised fish (Figure 2.5). The two cases of aberrant regeneration included one fish in which only one of the three excised rays regenerated, and another fish in which regenerated rays were sharply bent. I estimated that 90% fin regeneration would take about 370 days, assuming a similar regeneration rate (mean % regeneration = 0.0132 + 0.0024*days; $r^2 = 0.93$, df = 4; $P = 0.001$; age classes combined) (Figure 2.4).

Discussion

I found no evidence that the removal of pelvic fin rays affected growth or survival of captive bull trout. The lack of mortality in the 7-d period following fin excision and the rapid decline in inflammation suggested that stress and injury from handling (Ricker 1949; Sharpe et al.1998) were not severe. Long-term stress or physical impairment caused by fin excision was also apparently not great enough to adversely affect survival. These findings agree with numerous previous studies involving different species wherein the (more severe) complete removal of a paired fin did not adversely affect survival or growth (reviewed in Bergstedt 1985; Pratt and Fox 2002).

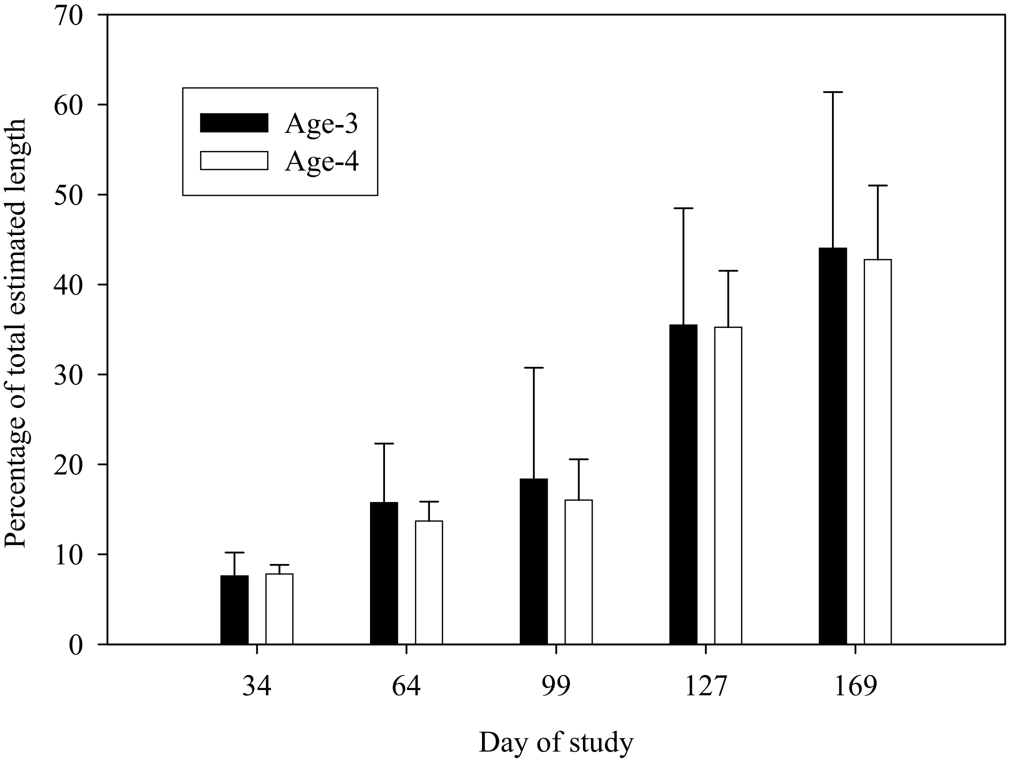

Figure 2.4. Percent of estimated total fin ray length (mean + 95% CI) regenerated by excised pelvic fin rays in age-3 and age-4 bull trout during the 169-d study period.

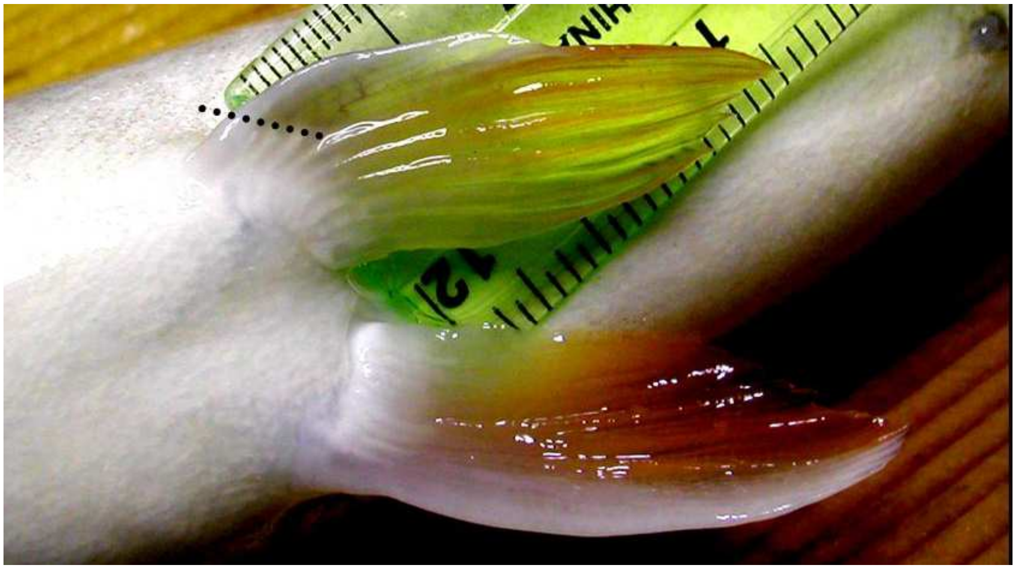

Figure 2.5. Regeneration of bull trout (374 mm TL) left pelvic fin rays 169 days after excision of first three rays. Approximate excision site indicated by dotted line.

Discussion

I found no evidence that the removal of pelvic fin rays affected growth or survival of captive bull trout. The lack of mortality in the 7-d period following fin excision and the rapid decline in inflammation suggested that stress and injury from handling (Ricker 1949; Sharpe et al.1998) were not severe. Long-term stress or physical impairment caused by fin excision was also apparently not great enough to adversely affect survival. These findings agree with numerous previous studies involving different species wherein the (more severe) complete removal of a paired fin did not adversely affect survival or growth (reviewed in Bergstedt 1985; Pratt and Fox 2002).

Two factors potentially contributed to lower survival of age-3 bull trout. First, age-3 fish were likely more susceptible to coldwater disease, which is typically more prevalent in small, young fish (Nematollahi et al. 2003). This is supported by the observation that a majority of mortalities showed signs of advanced coldwater disease. Second, an unanticipated additional stress may have been placed on the age-3 fish by cohabitation with the larger age-4 fish. Prior to the start of the experiment, the two age groups were housed in separate tanks. After mixing of age classes at the start of the trial, smaller fish frequently occupied the upper portion of the water column whereas larger fish were near the bottom. However, the surviving age-3 fish grew well, no agonistic behavior was observed, the fish were fed to satiation, and age-3 fish were too large to represent potential food items for age-4 fish. Whatever factor selectively affected the smaller fish did not appear to act differentially between fin-excised and control groups.

The presence of the coldwater disease pathogen, which occurs naturally in bull trout waters, was considered a potential stressor that could disproportionately affect fin ray-excised fish. Elevated infection rates have been linked to fin excision in previous studies (Fry 1961), but no difference was evident in our experiment. The coldwater disease infection was apparently not severe enough to mask the effect of fin ray excision, given the near complete survival of the age-4 group and similar survival rates between treatments within age groups. The specific mechanism of infection has not been conclusively identified for coldwater disease (Nematollahi et al. 2003), but the open wound caused by fin excision did not appear to be the main portal for new infection in my study as both control and treatment fish exhibited disease symptoms.

The fin regeneration observed in this study was similar to that in previous studies reporting nearly complete regeneration within one year (Stuart 1958; Eipper and Forney 1965; Coombs et al. 1990; Thompson and Blankenship 1997). Regeneration is typically more rapid and complete as the proportion of fin ray removed decreases (Eipper and Forney 1965; Thompson and Blankenship 1997) and with the amount of nervous tissue remaining (Geraudie and Singer 1985). Despite the close proximity of excision to the body, excised rays of most fish regenerated. The projected attainment of complete regeneration in about 13 months may underestimate the time required in the wild because the study was conducted under controlled conditions. A wild bull trout recaptured from Rock Creek near Noxon, Montana, 413 days after partial pelvic fin excision identical to that used in this study showed about 75% regeneration (0.18%/d) (Figure 2.6), slightly lower than the 0.25%/d rate we observed in the laboratory. Whether complete regeneration would be attained and the time required are not known, as the literature indicates that regeneration depends on factors such as the particular fin (Coombs et al., 1990), species (Wagner and Misof 1992), size class (Mills and Beamish 1980), temperature (Anderson and Roberts 1975) and extent of the cut (Thompson and Blankenship 1997).

Figure 2.6. Wild bull trout (281 mm TL) recaptured 413 days after partial fin excision, showing regeneration of excised rays (right pelvic fin, lower) in comparison with uncut fin (left pelvic fin, upper).

The absence of a significant reduction in survival or growth of fin ray-excised bull trout in our study, coupled with relatively rapid regeneration of excised rays, suggests that the effect of partial pelvic fin removal for ageing is likely nondeleterious to bull trout. However, further evaluation is warranted as I did not assess fin ray excision effects on smaller juveniles <200 mm or large adults >362 mm. Monitoring of survival, growth, and fin regeneration of fin ray-excised fish in the field is also recommended to verify our laboratory findings. It is not known whether partial pelvic fin excision would differently affect the abilities of bull trout to elude predators, capture prey, maneuver, or withstand pathogens present in the wild (Ricker 1949; Coble 1967; Nicola and Cordone 1973). However, the pelvic fins provide accessory maneuvering capability (Lagler et al. 1962) and are generally less critical to swim performance than other fins (McNeil and

Crossman 1979). Removal of only a portion of the fin should minimize detriment to the fish by allowing a level of continued functionality and reducing the area requiring subsequent regeneration. Further work on the use of fin rays for ageing threatened salmonids is recommended, as the high accuracy of ageing with fin rays coupled with minimal apparent side effects from their removal makes them an attractive alternative to scales and otoliths.

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CHAPTER 3

USE OF PELVIC FIN RAYS TO ESTIMATE AGE AND GROWTH OF BULL TROUT

Introduction

Anatomical structures such as scales, fin rays, and otoliths are routinely used to produce age and growth information for fish (Casselman 1990; DeVries and Frie 1996). Such structures have been found to periodically form visible marks attributable to seasonal variations in growth. Suitability of a given structure varies according to species, population, and specific application, and with proper interpretation, the appropriate structure may be used to obtain data integral to assessments of production, population dynamics, and the effects of natural and anthropogenic perturbations.

Age estimation with anatomical structures relies on the formation of identifiable marks at known time intervals (Casselman 1983). Generally, portions of the structures formed during fast growth periods alternate with visually distinguishable portions formed during slow growth periods. These differences are manifest as the relative spacing and completeness of circuli on scales (Jearld 1983) or, in bony structures, as bands having optical contrast caused by differences in the relative proportion of protein and mineral incorporated during growth (Casselman 1974; Simkiss 1974; Ferreira et al. 1999). Annual age is estimated by counting each completely formed winter growth zone, or annulus, along an axis radiating from the center of the structure to its edge. Distinctiveness of annuli depends largely on the degree of contrast between summer and winter growth conditions, structures typically being easiest to interpret in fish from populations subject to highly contrasting seasonal temperature differences (DeVries and Frie 1995).

Growth estimation using anatomical structures follows one of two general approaches. Estimated ages may be used in conjunction with measured body length at capture to generate length-at-age growth curves (Ricker 1975; Busaker et al. 1990). Alternatively, previous lengths at age can be back-calculated for each individual. Advantages of back-calculation include the capacity to either integrate or isolate effects of annual and intercohort variation, to standardize lengths obtained during the growing season as length at time of annulus formation, and to increase sample size by using lengths at multiple ages for individual fish (Francis 1990; Ricker 1992; DeVries and Frie 1995). Back-calculation procedures are generally based either on regression or proportional methods, with proportional methods considered more robust (Carlander 1981; Wiesberg and Frie 1987; Francis 1990). Appropriateness of a particular proportional formula depends on the nature of the relationship between the radius of the structure and the body length of the fish. If the regression of body length on structure radius intersects the origin, the direct proportion (Dahl-Lea) method may be used (Dahl 1907; Lea 1910). A y-intercept different from zero indicates the need for the intercept correction (Fraser – Lee) method (Fraser 1916; Lee 1920) or an alternative approach such as the Weisberg method (Weisberg 1986) or the body- or scale-proportional hypotheses (Francis 1990). Selection of a method warrants careful consideration because various methods and formulas may produce large differences in back-calculated lengths (Smale and Taylor 1987; Horppila and Nyberg 1999; Klumb et al. 1999b).

Validation procedures provide the best means to substantiate results of age and growth analyses. Without validation, a set of interpretations may be both convincing and inaccurate. For example, a reader may consistently miss the true first annulus, resulting in underestimation of age and overestimation of growth in the first year. Validation addresses this problem by confirming that results match biological reality. Methods include inspection of structures from fish of known age, length-frequency analysis, mark–recapture sampling, and marginal increment analysis (Beamish and McFarlane 1983; Campana 2001). Mark–recapture, marginal increment, and length-frequency analyses all suffer from the limitation that the true age of the fish is unknown. Verification studies, in which results from multiple structures are compared, may increase confidence in age estimates to a lesser extent (because the true ages of the specimens are typically unknown) but can also provide validation if results are equivalent among structures and one of the structures has been previously validated (Campana 2001).

Numerous studies have reported fin rays to hold potential advantages for age estimation, although reviews have been mixed. By the mid 1900s, use of rays had already been explored for several species (reviewed in Boyko 1950; Cuerrier 1951; Menon 1950). Pectoral rays have long been used to age sturgeons *Acipenseridae* (Chugunov 1925; Cuerrier 1951) but this method has recently come under scrutiny (Rien and Beamesderfer 1994; Hurley et al. 2004; Whiteman et al. 2004). Rays have been validated for ageing several species, including brown trout *Salmo trutta* (Burnet 1969; Shirvell 1981), Chinook salmon *Oncorhynchus tshawytscha* (Chilton and Bilton 1986), lake whitefish *Coregonus clupeaformis* (Mills and Beamish 1980), and white sucker

Catostomus commersoni (Beamish and Harvey 1969). Researchers have also reported relatively high precision with fin rays in comparisons among structures for ageing Arctic grayling *Thymallus arcticus* (Sikstrom 1983), river carpsuckers (Braaten et al. 1999), and bull trout (Williamson and MacDonald 1997; Gust 2001). Studies typically report annuli to be identifiable to greater ages in rays than on scales, with both structures considered non-lethal alternatives to other bony structures. However, investigators rejected use of rays in favor of other structures for Arctic char *Salvelinus alpinus* (Barber and MacFarlane 1987), largemouth bass *Micropterus salmoides* (Maraldo and MacCrimmon 1979), and spotted sea trout *Cynoscion nebulosus* (Ihde and Chittendon 2002). Cited problems included poor ageing precision and difficulties with sample preparation, identification of the first annulus, and distinction between true and false annuli. Even studies reporting favorable results with rays indicated that the first annulus may be indistinct or obscured by structural changes to the ray with increased age (Beamish and Chilton 1977; Shirvell 1981), and that marks on the outer edge of the structure may prove difficult to resolve (Shirvell 1981). A critical factor affecting the accuracy of age estimation using fin rays is the location at which the sample is taken from the fin. Fin ray cross sections vary markedly in appearance depending on the longitudinal position of the sample, and cross sections taken too distally from the body may not include early annuli (Beamish 1981; Sikstrom 1983).

Few studies have been published in which soft fin rays were used for back-calculation. Satisfactory results for white suckers were reported using the leading ray of the pectoral fin and an intercept correction formula (Chen and Harvey 1995; Mills and Chalanchuk 2004). Dorsal rays were used with the intercept correction method for river carpsuckers (Braaten et al. 1999) and with the direct proportion method for bighead carp *Hypophthalmichthys nobilis* (Schrank and Guy 2002). Validation was attempted in only one study, which involved the use of mark-recapture samples and the assumption that observed lengths at initial capture approximated lengths at annulus formation (Mills and Chalanchuk 2004). Hard spines have been used more widely for back-calculation, including those of catfishes *Ictaluridae* (Sneed 1951, Marzolf 1955) and several marine species (Anon. 1983; Sun et al. 2002), but structural differences between spines and soft rays complicate the direct transfer of techniques. Spines are usually sectioned at a specified position with reference to the basal groove or articulating process, whereas soft rays are biserial and show less structural symmetry. Thus, soft rays present greater challenges for standardizing sections and locating a consistent axis of measurement.

No validation studies addressing interpretation of age and growth of bull trout have been published. Most investigators have used scales (Bjornn 1961; Pratt 1985; Fraley and Shepard 1989; Connor et al. 1997; Mogan and Kaeding 2005) although two structure comparison studies have also been completed (Williamson and MacDonald 1997; Gust 2001). Dorsal rays provided better precision and higher ages than scales, but lower precision than otoliths for ageing bull trout from lakes and streams in northern British Columbia (Williamson and MacDonald 1997). A study comparing matched sets of seven structures for ageing bull trout between 200 and 800 mm TL reported highest precision with vertebrae, slightly lower precision with saggital otoliths and pelvic fin rays, and lowest precision with scales (Gust 2001). True accuracy of age estimates was not tested in either of these studies, but the results provide evidence that fin rays of bull trout are better than scales for age estimation and potentially back-calculation of growth.

Because removal of rays does not appear to adversely affect survival or growth (see Chapter 2), rays hold promise for use with sensitive populations in which minimization of detrimental effects is critical.

The purpose of this investigation was to evaluate the potential for using pelvic fin rays to estimate age and growth of bull trout in populations occupying widely different environments and exhibiting varying life history forms. In order to enhance comparability and accuracy of estimations, it was necessary to develop methodology for ageing and back-calculation of growth using pelvic rays because of the paucity of published information on the subject, particularly with respect to bull trout. Detailed criteria is available for identifying annuli on scales (Jearld 1983; Tanaka et al. 1968) but not for rays, and interpretation may be confounded by the particular species and life stage, environmental variability, presence of accessory marks (e.g., false annuli), and structural degradation as the fish ages (Beamish 1973; Beamish and Chilton 1977). Availability of mark-recapture samples presented an opportunity to attempt partial validation of annulus formation and back-calculation technique using bull trout populations having varying size distributions and growth patterns. Also, I compared ageing precision among fin rays, otoliths, and scales.

Methods

Sample Collection and Preparation

Fin rays, scales, and otoliths used in this investigation were collected from bull trout captured during electrofishing or trapping of eight streams in the lower Clark Fork

River drainage, Montana and Idaho, from 2001 through 2003 (see Chapter 4 for detailed description of sites and capture methods). The leading three or four rays from one pelvic fin were excised near the base (see Chapter 2) and placed in scale envelopes to dry. Fin ray samples were trimmed, set in epoxy, and cut into transverse cross-sections using a Buehler Isomet low speed saw. At least three consecutive sections were cut, the first section comprising the most proximal available portion of the ray. Thickness of sections averaged about 0.5 mm. Sections were polished using 400–1200 grit wet-dry sandpaper, and then affixed to a slide in sequential order using thermoplastic glue. Scales were removed from the area of the body ventral to the posterior edge of the dorsal fin and above the lateral line then stored in scale envelopes. Three non-regenerated scales in the best available condition from each fish were pressed into 0.56 mm cellulose acetate using a Carver hydraulic laboratory press at 71 degrees Celsius and 6800 kilograms hydraulic pressure for 4 minutes. Sagittal otoliths were collected only from 19 incidental electrofishing and trapping mortalities and from 6 post-spawn adult mortalities encountered during redd surveys in autumn. Preparation of otolith samples was similar to that of fin rays, with transverse sections cut through the nucleus.

Age and Growth Analysis and Quality Assessment

Samples were viewed under transmitted light at 40x to 400x power using a compound microscope. I rated the longitudinal fin ray region, R1—R5, for each cross section based on hemisegment morphology, an indicator of relative distance from the body (Appendix A). Analyses of consecutive cross sections from individual fish indicated that the number and appearance of annuli varied according to longitudinal position along the fin ray, as has been reported for other species (Beamish 1981; Sikstrom 1983; Ferreira et al. 1999), and that use of samples should be restricted according to fin ray region and the presence of a conspicuous mark in the nucleus (Appendix B). For bull trout < 300 mm, I used cross sections of only regions R2 or R3. Cross sections from more distal regions of the ray were excluded because the first annulus is typically not identifiable. For larger fish, I used only sections of region R1 or R2. Because the quality of the best available scales and otoliths varied considerably (e.g., portions of some scales missing or impression in acetate poorly defined; annuli on some otoliths indistinct) and affected confidence in age estimates, I rated these samples based on overall quality and interpretability and excluded those having poor structural integrity or which were poorly impressed in acetate.

Samples were interpreted without knowledge of fish size, sample date, or capture location in order to minimize bias (Casselman 1983). Annual growth in fin ray and otolith sections consisted of a pair of hyaline (translucent in transmitted light) and opaque (dark) bands, with the opaque band considered the product of fast, summer growth (DeVries and Frie 1995). The calendar birthday for every fish was considered to be January 1; thus, a sample showing a hyaline edge would be aged one year older if collected during spring prior to annulus formation than if collected in autumn. An annulus was counted at the point, progressing outward from the nucleus, at which an opaque zone replaced a hyaline zone. Annuli were only counted if bands were continuous around a majority of the ray (Shirvell 1981). The larger, ventral hemisegment of the fin ray was used for ageing because its marks were more conspicuous than those in the dorsal hemisegment. The third ray was used for analyses unless the second or fourth ray showed appreciably better definition. The first, leading ray was not used because it appeared to be less regular in shape and definition, as was reported for Chinook salmon (Chilton and Bilton 1986). Scale annuli were identified using standard criteria based on spacing and continuity of circuli around the scale (Jearld 1983). For all three structures, the same reader aged each sample on two separate occasions. If the two ages differed for a fish, the fin ray sample was analyzed a third time and assigned a final age or else excluded from analyses if confidence in the estimate was low.

I measured samples for growth estimation using a digital image analysis system. Images were captured with an Olympus camera mounted on a compound microscope and computer with Pixera Viewfinder 3.0© and Studio© software. Sigma Scan Pro© software was used to perform measurements on images. Samples were directly referenced through the microscope to aid in interpretation. The system was calibrated with a micrometer slide at the start of each session. Distances were measured along the "AS" axis of fin rays (anterior side, perpendicular to annuli; Figure 3.1) for use in back-calculation (Appendix C). Distances were recorded from the nucleus to each annulus and the edge of the ray. The origin of measurement in the nucleus was determined using a reference line connecting the dorsal indentation with the posterio-ventral corner of the ray section (Figure 3.1). For scales, distance between annuli was measured along a trajectory about five degrees offset from the anterior axis (Figure 3.1) because it offered the best overall structural integrity and interpretability. Annuli were marked at the last closely spaced circulus preceding a region of widely spaced, relatively well-defined circuli (Bilton and Robins 1971). Otolith cross sections were measured along the longest axis in the dorsal field (Figure 3.1)

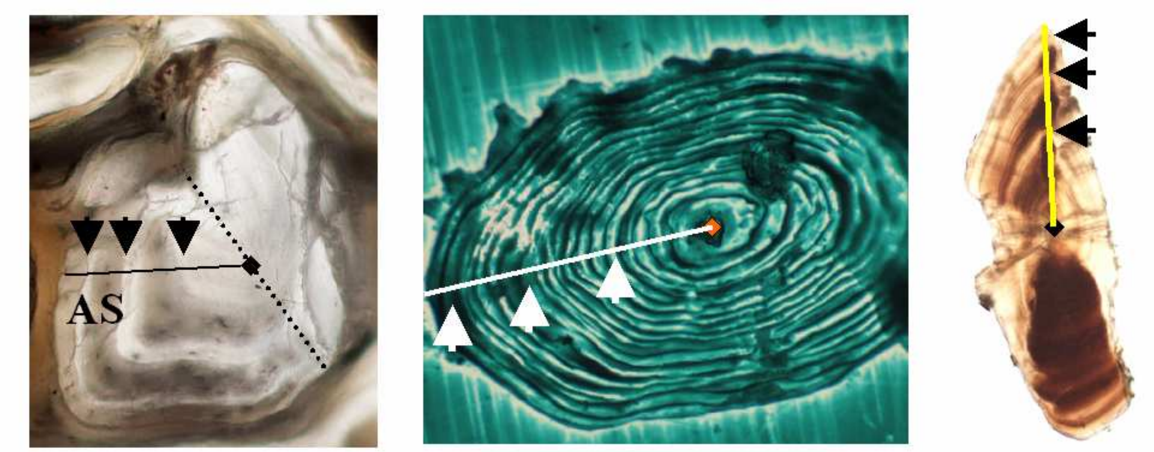

Figure 3.1. Measurement axes for pelvic fin ray, scale, and otolith from a bull trout (172 mm TL) collected on May 03, 2002. Arrows indicate annuli. Dotted line on fin ray indicates line of reference for origin of measurement.

The intercept correction (Fraser-Lee) technique (DeVries and Frie 1995) was used to back-calculate length at age (Appendix B). Appropriate formulas for back-calculation were first developed by regressing body length on structure radius for samples collected in tributary streams within the study area (Chapter 4). For pelvic fin ray samples from bull trout < 300mm TL, the intercept parameter ($\alpha = 20$) was obtained from a body—ray relation ($y = 863.37x + 19.306$; $r^2 = 0.93$) established using a random selection of 341 fin ray samples of morphology R1—R3 that included 20 (if available) samples from each 10-mm body length interval between 50 and 300 mm TL. For scales, random selection of up to five samples in each ten-millimeter length interval was used for lengths < 300 mm ($y = 863.37x + 12.5$; $r^2 = 0.84$; $N = 65$).

Validation

Annual Increment Formation. To confirm the formation of a single annual increment in the fin rays and scales of bull trout, I compared age estimates of fin ray pairs and scale pairs from 25 bull trout initially electrofished and PIT tagged in summer 2002 (range = 96—249 mm TL; mean ± SD = 155 ± 44 mm) and subsequently recaptured in summer 2003 (range = 136—265 mm TL; mean ± SD = 195 ± 38 mm) from the East Fork Bull River, Graves Creek, Prospect Creek, Rock Creek, and West Fork Thompson River ("tag—recapture sample set"). Rays were removed in 2003 from the pelvic fin opposite of that excised in 2002. However, two fin ray samples from recaptured fish were excluded because their atypical appearance suggested they were regenerated rays that had been previously excised during the initial capture in 2002 (Figure 3.2). Fin ray pairs from 16 fish and scale pairs from 22 fish were retained after excluding poor-quality samples. Suitable tag and recapture samples of both fin rays and scales were available for 14 fish. Validation required estimated age at recapture to exceed estimated age at initial capture by exactly one year. During age estimations, these samples were interspersed with those from fish captured only once and interpreted without knowledge of their membership in the tag—recapture set. Validation was compared between fin rays and scales using Fischer's exact test to accommodate small expected cell counts (Zar 1996).

Back-calculation. Accuracy of back-calculation using fin rays and scales was assessed using tag—recapture samples and a "virtual", or mathematical, marking procedure (Figure 3.3). The more common approach of comparing known body length of fish captured during winter to length at annulus formation was not possible because fish were captured during the summer growth period. Instead, the measured distance of

Figure 3.2. Transverse sections of regenerated pelvic fin rays collected one year after initially excised. Section at left is from a bull trout 169 mm TL; section at right is from bull trout 233 mm TL. Note the irregular shape and absence of well-defined banding. These characteristics were not observed in rays from any other individuals.

recent summer growth (opaque zone formation) along the radius on the initial capture sample was converted to a proportion of the total radius. The proportion was used to calculate a point on the radius of the recapture sample (obtained from the opposite pelvic fin) that approximated the radius at initial capture. This “virtual mark” was calculated as:

$$\text{Virtual mark} = AN_{recap} + [AN_{recap} * (OE_{tag} / AN_{tag})]$$

where

AN_{recap} = distance to the second-to-last annulus on the recapture sample collected in 2003,

AN_{tag} = distance from the nucleus to the last annulus on the initial capture sample collected in 2002,

OE_{tag} = measured distance of new opaque zone growth at the edge of the initial capture sample.

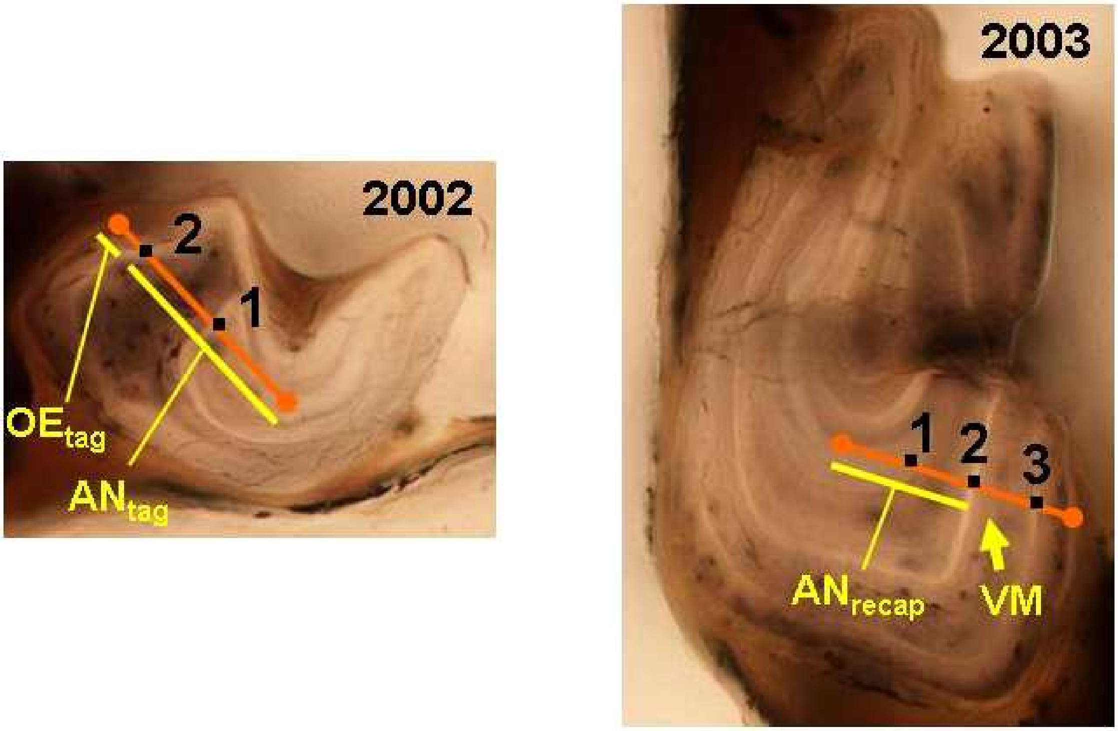

Figure 3.3. Tag (at left; right pelvic fin) and recapture (at right; left pelvic fin) samples from an individual bull trout that measured 138 mm TL when initially captured on 7/18/02 and 166 mm when recaptured on 7/15/03. Squares indicate annuli. Virtual mark (VM) approximated by arrow. Appearance of annuli differs between samples because of fracture in recapture sample and because recapture sample was excised relatively more distal from the body than was the initial capture sample. OE = opaque zone at edge, quantified along measurement axis; AN = distance from nucleus to last annulus; subscript indicates tag or recap sample.

Back-calculated length at the virtual mark should theoretically equal the measured length at initial capture. This procedure requires accurate identification of the same annulus in both samples, so only sample pairs for which estimated ages matched the predicted difference of one year were included. Differences between back-calculated lengths and actual lengths were evaluated using a paired *t*-test. Back-calculated length at the virtual mark was subtracted from measured length at initial capture to obtain an estimate of real error (positive or negative), which was then divided by measured length at initial capture to calculate percent error for each sample pair. Absolute values of error, which provide a better measure of bias in the method than real error (Mayer and Butler 1993), were calculated using the following formula to indicate magnitude of error without the canceling effect of opposite signs:

$$\text{Absolute percent error} = |(ML_{tag} - VM) / ML_{tag}|$$

where

ML_{tag} = Measured length in 2002,

VM = Back-calculated length to virtual mark on recapture sample.

To evaluate back-calculation beyond the single year addressed with the virtual mark, I used the tag—recapture samples to investigate precision of back-calculation up to four years prior to capture. Back-calculated lengths were compared between tag and recapture samples for all ages common to both (e.g., lengths at age 1 and age 2 for an individual that was age 2 when tagged and age 3 when recaptured). Although actual lengths of the fish at annulus formation were unknown, greater consistency between samples indicates better retention of proportionality with growth of the fish. Absolute error in both consistency and accuracy were compared between fin rays and scales using Wilcoxon rank—sum tests including only those fish for which both structures matched the expected age increase of one year.

Verification

Ageing Precision. Ageing precision with fin rays, scales, and otoliths was compared to quantify consistency of interpretation among structures. Matched sets of all three structures were available only from a limited number of incidental and spawning mortalities (19 juveniles 52–173 mm TL, mean ± SD = 111 ± 33; four large adults 465—520 mm TL) because the species' threatened status precluded lethal sampling. In addition, paired fin rays and otoliths without scales were available from two fish (504, 711 mm). An expanded set of 322 sample pairs (64–716 mm TL; mean ± SD = 165 ± 107) was used to compare fin rays and scales. Percent agreement and the coefficient of variation (Chang 1982; Campana 2001) were used to assess precision for each structure as well as agreement of final age estimates among matched fin rays, scales, and otoliths. Chi-square tests on the numbers of precisely (first and second readings agreed) and imprecisely (first and second readings disagreed) aged samples were used to assess difference in ageing precision between structure types.

Results

Validation

Annulus Formation. Annulus formation was more apparent on fin rays (88%; 14 of 16 fish) than on scales (68%; 15 of 22 fish), although the difference was not significant (Fischer's exact test: $P = 0.25$). Considering only the 14 fish for which both scales and fin rays were assessed, annulus formation was identified on 86% of fin ray pairs and 64% of scale pairs (Fischer's exact test: $P = 0.39$). In the two cases where estimated ages of fin rays did not match the expected increase of one year, early annuli on fin ray sections were difficult to decipher. Difficulty with scales was associated with identification of the first annulus as well as subsequent annuli.

Back-calculation. Validation procedures indicated reasonably accurate back-calculation both with fin rays (mean real percent error ± SE = 4.1 ± 2.0, absolute percent error = 7.2 ± 1.2; N = 14 fish) and scales (real percent error = 0.3 ± 3.0; absolute error = 9.2 ± 1.9; N = 16 fish). Measured length did not significantly differ from back-calculated length to the virtual mark for fin rays (paired t-test: $t = 1.38$, df = 13, $P = 0.19$) or scales ($t = 0.104$, df = 14, $P = 0.92$). Considering only the seven fish for which both structures matched the expected age increase, absolute percent error was lower for fin rays in five cases (mean difference ± SE = 6.2 ± 4.1), although a significant difference was not detected (Wilcoxon rank—sum test: $Z = -1.52$, $P = 0.13$).

Comparison of back-calculated lengths at annuli present on both tag and recapture samples (i.e., consistency) produced similar magnitude of error for both fin rays (absolute percent error = 8.2 ± 0.9; N = 33) and scales (8.9 ± 1.1; N = 48). Considering only the seven fish for which both structures matched the expected age increase, absolute percent error was lower for fin rays in seven of thirteen comparisons (mean difference ± SE = 3.1 ± 2.8) but the difference was non-significant (Wilcoxon rank—sum test: $Z = -0.94$, $P = 0.35$).

Verification

Ageing Precision and Structure Agreement. Ageing precision was overall higher with fin rays than scales but was negatively related to fish length for all structure types. Agreement between first and second age estimates for fin rays was 87% (CV = 3.4) overall, 90% for fish < 250 mm (N = 682), and 67% for fish ≥ 250 mm (N = 58). For scales, estimates agreed for 68% (CV = 7.4) of fish overall, 71% of fish < 250 mm (CV = 7.8; *N* = 142) and 55% of fish ≥ 250 mm (CV = 5.5; *N* = 33). First and second readings of otoliths agreed for all 19 small fish but only 3 of 6 large fish.

Agreement of estimated ages among structures varied by age classes examined. Ages estimated with otoliths and fin rays agreed for all 19 individuals in the juvenile out-migrant set, 16 of which were estimated to be age-1 or age-2. Scale ages agreed with those of otoliths and fin rays for all but one fish. For the large adult set, estimates agreed between five of six fin ray—otolith pairs and three of six scale—otolith pairs. Agreement between scales and fin rays from 18 migratory adults was low (33%), indicating higher ages from scales in 56% and lower ages in 11% of cases. Overall, estimates agreed for 77% of the 351 fin ray and scale pairs and no directional bias was evident, although disagreement increased markedly at age 5 and greater (Figure 3.4).

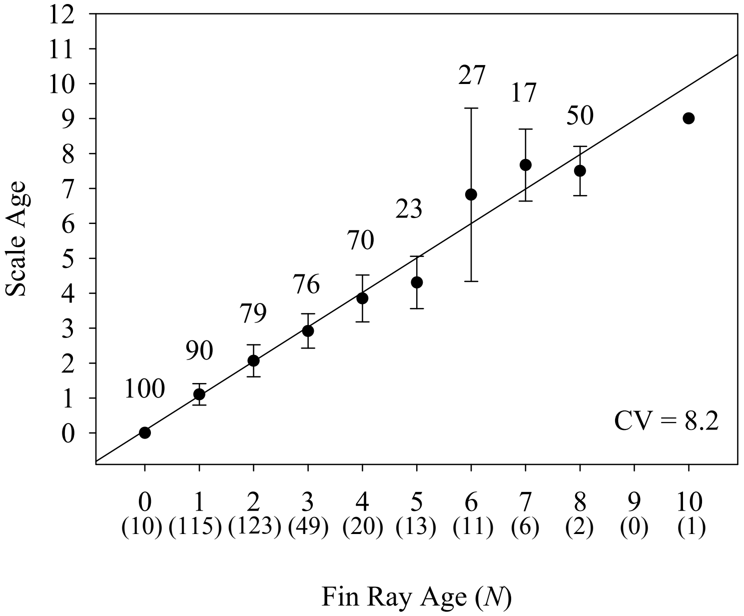

Figure 3.4. Agreement of age estimates for paired fin ray and scale samples for 351 individuals (mean ± 95% C.I.). Percent agreement listed above data points. Diagonal indicates 1:1 reference line. Sample sizes in parentheses.

Discussion

Pelvic fin rays proved to be effective structures for analysis of age and growth of bull trout. The relatively high degree of ageing precision achieved in this study was not unexpected and supports the results of previous work with pelvic rays (Gust 2001) and dorsal rays (Williamson and MacDonald 1997) of bull trout and with fin rays of other species (e.g., Beamish and Harvey 1969; Burnet 1969; Beamish and Chilton 1977; Sikstrom 1983). In these studies, higher precision and better resolution at higher ages was achieved with fin rays than with scales. The present evaluation served to confirm these findings for a different population of bull trout, to assess the performance of the reader, to test the influence of fin ray section region on age estimation, and to develop appropriate methodology for back-calculation.

Annulus formation in pelvic rays of tagged tributary-resident bull trout recaptured after one year at liberty was validated at a rate of 88%, with discrepancies arising from difficulty in discerning the first annulus in fin rays cut distally from the body rather than from inconsistent annulus formation. Validation success was lower with scales (68%) because patterns in circuli spacing and "cutting over" were less discernable and led to greater interpretive subjectivity. Although edge analysis and marginal increment analysis were not possible because no population was consistently sampled over the course of a year, available fin ray samples from bull trout < 300 mm TL indicated formation of an annulus (opaque growth visible at edge) between late April and early June. A hyaline (translucent) edge was apparent in some samples beginning in late August. Formation of the first annulus, a validation requirement of Campana (2001), was confirmed through inspection of fin ray sections collected in April and May from Trestle Creek bull trout that were too large to be newly emerged fry but small enough that it was highly unlikely they were age-2 (Downs and Jakubowski 2003).

Evidence from this investigation also indicates that pelvic fin rays are suitable for use in back-calculation. Validation tests using tag and recapture samples indicated a high level of accuracy (4.1% real error, 7.2% absolute error). This compares favorably with values reported for other structures and species, although variability in reported metrics and methods complicate direct comparisons. For example, use of the leading pectoral ray was found to produce overall 1.0 mm real error and 7.6 mm absolute error with white suckers at liberty for 1-3 years after marking, but percent error was not provided (Mills and Chalanchuk 2004). Using a series of oxytetracyclene marks formed 90 to 360 days prior on scales of sunfishes *Lepomis spp.*, back-calculation produced error generally less than 6% percent but varied from 0 to 19.2% (Klumb et al. 1999a). Comparing measured length of tagged smallmouth bass *Micropterus dolomieu* and walleyes *Sander vitreus* at annulus formation to lengths back-calculated using scales, mean error for individual age classes varied from –10 to +4% with the Fraser-Lee formula, and from -12 to +25% with the Weisberg method (Klumb et al 1999b). Mean absolute difference between length at the most recent annulus, back-calculated using scales, and mean observed length at time of annulus formation was about 9—13% at age-1 and 3—7% at age-2 through age-5 for pumpkinseeds *Lepomis gibbosus*, and about 25—31% at age-1 and 3—8% at age-2 through age-5 for golden shiners *Notemigonus crysoleucas* (Pierce et al. 1996).

The virtual mark procedure used in the present investigation has not been directly tested against other methods. However, the results of consistency tests (8.2% absolute error), in which back-calculation to a visible mark was compared between the tag sample and recapture sample, indicated that the fin ray retains proportionality from year to year and the virtual mark procedure is reasonably accurate. These tests rely on accurate identification of annuli on both samples, and ageing error would probably contribute relatively more error to back-calculated lengths with scales than with fin rays. Evaluations using tag and recapture samples were limited to tributary resident bull trout < 300 mm TL, of estimated age-1 to age-5 at initial capture, and at liberty for only one year after tagging, but these results supply the first evidence for the validity of back-calculation with pelvic rays of bull trout.

Age and life history influenced accuracy and precision of age and growth determination. High precision and reader confidence were achieved with all three types of structures from fish younger than age-3. Ageing precision and agreement was notably lower among all three structures for larger, older individuals. Difficulty distinguishing between true and false annuli was previously noted in fin rays and otoliths of large bull trout from Lake Pend Oreille in an unpublished, limited assessment conducted by fish ageing experts (MacLellan 1992). Complexity in the banding pattern could reflect the influence of environmental and physiological changes experienced while in the process of migration or while occupying larger downstream waterbodies, as these irregularities did not appear in the structures of individuals of similar age from populations having a predominantly resident life history. As an iteroparous species, migratory bull trout may undertake multiple spawning migrations and potentially even remain in tributaries for at least one full year rather than exiting immediately after spawning (e.g., West Fork Thompson River; Montana Fish, Wildlife, and Parks, unpublished data). Banding patterns were more regular and distinct on samples from some of the migratory individuals, indicating that rejection of difficult samples would likely increase precision and probably accuracy as well. However, selection or exclusion of samples demonstrating some particular feature presents the danger of causing mischaracterization of age and growth patterns in the population. Even for individuals with problematic fin rays or otoliths, confidence in age estimates was lower with scales than with rays or otoliths

Results of the above tests and comparisons suggest that pelvic fin rays of bull trout are useful for estimation of age and growth, given proper attention to collection and preparation. To limit error introduced by longitudinal variation in the ray, sections of region R2 (preferred) or R3 should be used for tributary resident bull trout <300mm. This has implications for collection of samples in the field, as only 15% of rays in the tag—recapture set, for example, were excised proximal enough to the body to provide sections of region R2. For large or old individuals (i.e., > 400mm or > age-7), the first annulus may be visible only in sections of region R1. Although measurements to the second or subsequent annuli have been used in procedures designed to circumvent problems with the loss of the earliest annuli in ray and spine sections (Surry and King 2003; Penha et al. 2004), the extent of variability in such measurements within and among populations makes this inappropriate with bull trout. Regardless of fish size, sections in which a dash mark is apparent in the center perpendicular to growth bands should not be considered reliable. The standard intercept correction procedure is suitable back-calculation with tributary resident bull trout but an alternative approach (e.g., a $\log_e$ modified Fraser—Lee equation or multiple trajectories corresponding to tributary and migratory growth stanzas) must be used for larger migratory fish. However, changes in the body—structure relation associated with migration make the comparability of back-calculated lengths at early ages of large fish to those of juveniles highly suspect.

In summary, pelvic fin rays provide a suitable structure for age and growth estimation with bull trout. Quality control and standardization of sections should be emphasized to reduce variability associated with longitudinal position of the cross section. Back-calculation methodology specific to fish size and life history should be used to maximize the accuracy and precision of resulting data and caution should be applied when comparing results with those from other studies. Further work is needed to validate ageing and back-calculation methodology for large, migratory adult bull trout and for ages more than one year prior to capture for smaller individuals.

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CHAPTER 4

AGE STRUCTURE, GROWTH RATES, AND FACTORS AFFECTING RELATIVE ABUNDANCE OF LIFE HISTORY FORMS OF BULL TROUT IN THE LOWER CLARK FORK RIVER DRAINAGE, MONTANA AND IDAHO

Introduction

Assessments of fish populations commonly involve consideration of life history characteristics. Life history, essentially the allocation of growth resources to ensure propagation of genetic material, is often described in terms of body size and timing in relation to migrations, maturation, fecundity, and longevity (Hutchings 2002). Corresponding demographic attributes of age, growth, maturity, sex ratio, and mortality provide a basis for monitoring population trends, estimating production, assessing habitat suitability, and predicting responses to management actions (Van Den Avyle and Hayward 1995). A particular life history may typify a species, but life history characteristics also differ across populations according to stochastic variation and adaptation to local environmental conditions (Taylor 1991; Hutchings 2002).

Bull trout life history is most broadly defined by migration patterns (Rieman and McIntyre 1993; McPhail and Baxter 1996). All bull trout hatch during spring in small to medium-sized headwaters streams where they typically rear for at least one year. Migratory life histories include the fluvial (riverine), adfluvial (lacustrine), and anadromous strategies, in which juveniles emigrate from tributaries to more productive rearing environments, sometimes encompassing distances exceeding 100 kilometers (Fraley and Shepard 1989; Swanberg 1997). Tributaries dominated by migratory life histories generally hold few fish 200—400 mm in length but contain larger individuals during the autumn spawning period (Fraley and Shepard 1989; Rieman and McIntyre 1993; Ratliff et al. 1996). Mature adults of migratory forms return to natal tributary streams at age 6 or older, having attained lengths of 400—800 mm or greater (McPhail and Murray 1979; Fraley and Shepard 1989) as a consequence of occupying more productive rearing habitats. The headwaters resident life history form, by contrast, remains in tributaries over the entire life cycle and exhibits a restricted range of movement, typically no more than a few kilometers (Jakober et al. 1998; Nelson et al. 2002). Residents reportedly mature at age 4 to age 6 and rarely exceed a length of about 400 mm (Rieman and McIntyre 1993; Bellerud et al. 1997; McCart 1997), although little has been published regarding demographic characteristics of resident populations. An iteroparous species, bull trout may spawn more than once, with adults of migratory and resident forms returning to their respective rearing habitats after spawning.

Life history variation occurs both within and among bull trout populations, often including the coexistence of multiple life history forms. Such coexistence, termed ‘partial migration’, is common among salmonid populations (Northcote 1992; Jonsson and Jonsson 1993). Sympatric forms of chars *Salvelinus spp.* may be reproductively isolated according to timing, location, or competition (Jonsson and Hindar 1982; Skúlason et al. 1989), but they have also been found to give rise to one another (Nordeng 1983; Kishi and Maekawa 2003), and individuals may even switch among strategies during the course of a lifetime (Nordeng 1983; Naslund 1990). In bull trout, life history forms occur in allopatry and in sympatry (Fraley and Shepard 1989; Nelson et al. 2002), individuals have been reported to switch strategies (Ratliff et al. 1996), and precocious males have been observed spawning with large, migratory females (Kitano et al. 1994;

Bellerud et al. 1997; James and Sexauer 1997). As with other members of the genus, a unified theory as to the underlying mechanisms behind adoption of a particular strategy has not been established.

One explanation for life history variation in bull trout centers on genetics. Evidence supporting the premise of inherited life history in Salmonidae includes results of laboratory genetics tests (Skaala and Naevdal 1989; Vespoor and Cole 1989; Taylor et al. 1996), as well as transplant studies (Jonsson 1982; Naslund 1993; Morita and Yamamoto 2001) and laboratory rearing experiments (Brannon et al. 1981; Northcote 1981; Kaya 1989) in which migration tendencies of the source population were retained. However, in other cases, genetic analyses have failed to distinguish between sympatric forms (Pettersson et al. 2001; Docker and Heath 2003). Also, differentiation of juveniles into distinct forms may not occur under uniform environmental conditions (Hindar and Jonsson 1993), discounting the influence of genetics. In bull trout, considerably greater genetic variation occurs among populations than within populations (Leary et al. 1993). Genetic analyses have revealed divergence among populations in different basins or tributaries (Kanda et al. 1997; Spruell 2003), among subpopulations within a tributary system (Spruell et al. 1999), and between resident and migratory forms separated by migration barriers (Costello et al. 2003). However, no divergence between life history forms has yet been reported, although the failure to date to detect a genetic difference does not rule out the possibility of its existence. No reciprocal cross or transplant experiments involving bull trout differing in life history have been published, although evidence for a genetic basis to life history was found in an unpublished study comparing seasonal thyroxine fluctuations in bull trout originating from migratory and resident populations (W. Fredenberg, U.S. Fish and Wildlife Service, unpublished data). Further, bull trout in isolated tributary populations may produce few out-migrants (Nelson et al. 2002), potentially indicating the existence of a selective mechanism similar to that reported in studies comparing salmonids from above and below waterfalls (Northcote 1981; Jonsson 1982).

A competing hypothesis suggests that life history form depends on early growth. According to this hypothesis, an individual must achieve a critical size or condition in order to trigger physiological processes related to either migration or maturation (Økland et al. 1993; Bohlin et al. 1996). Such thresholds may be considered points at which the benefits of one strategy begin to outweigh the benefits of the opposing strategy (Gross 1991; Hutchings 2002). For example, high growth may enable an individual to achieve a size suitable for successful spawning without risking migration, whereas poor growth may favor migration (Ricker 1938; Thorpe 1994; Morita et al. 2000). In this case, migration either represents a strategy pursued mainly by slower growing individuals within a population, or it is the norm in populations occupying habitats with limited growth opportunity (Thorpe 1994). This pattern of high growth rates leading to early maturation and reduced migratory tendency has been associated with high water temperature, high productivity, and low fish density (Gross 1991; Morita et al. 2000), and may function to rapidly increase population size where densities are low (L'Abee-Lund et al. 1990). However, faster-growing juveniles have also been found to migrate earlier in predominantly migratory populations of salmonids (Jonsson 1985; McCormick and Saunders 1987), and to become migrants in populations comprised of both migratory and resident components (Svenning et al. 1992; Kishi and Maekawa 2003). In these cases, migration probably confers a reproductive advantage that outweighs the risk of migration-related mortality (Gross 1991). Individuals having higher metabolism or dominant social status would be more likely to migrate (Metcalfe et al. 1993; Morinville and Rasmussen 2003). Existence of both a lower (or earlier) growth threshold corresponding to the decision to migrate and also a higher (or later) threshold corresponding to maturation as a resident may explain some of the variation (Dunston and Saunders 1997). Nonetheless, the relationship between early growth and subsequent life history form appears to vary both among and within species and populations.

Inconsistencies in both the genetics and early growth hypotheses may indicate the larger significance of the interaction of both factors. Genetics may regulate individual growth thresholds and metabolic capacities while environmental conditions influence the attainment of potential growth (Metcalfe 1993; Aubin-Horth and Dodson 2004). Evidence from reciprocal crosses and transplant experiments has shown genetics to influence the frequencies of different forms but the ratio to be modifiable by altering density or food availability (Nordeng 1983; Morita et al. 2000). In the case of bull trout, the failure so far to identify genetic difference between sympatric forms places heightened interest on resolving the influence of early growth in life history variation.

Assessment of the effect of early growth in wild populations requires consideration of biotic and abiotic factors that could influence growth rates or life history expression. Temperature regulates growth and habitat suitability through its effects on metabolism, food consumption, and immune response (Craig 1985; Jobling 2002). Bull trout have a lower growth optimum (13.2˚ C) than most North American salmonids (Selong et al. 2001), and their distribution in nature is distinctly related to temperature regimes (Rieman and Chandler 1999; Gamett 2002; Dunham et al. 2003). Productivity and fish densities influence growth by affecting food intake (Nordeng 1983; Gross 1991; Paul et al. 2000). Presence of introduced species may reduce suitability of downstream migration corridors and rearing habitat for bull trout. Brook trout, brown trout, and lake trout compete with and prey on bull trout, and brook trout also present hybridization risks (Nelson 1965; Leary et al. 1993; Fredenberg 2002; Gunckel et al. 2002). Finally, migration barriers present an obvious impediment to the success of migratory life histories and favor establishment of the resident form. Constructed barriers ranging from diversion dams to large hydroelectric facilities block passage in many watersheds. Also, agricultural irrigation withdrawals and increased sediment loads stemming from land use activities exacerbate dewatering of stream reaches, especially during late summer base flows. As a consequence, such artificial barriers may induce shifts in life history from predominantly migratory to resident (Morita et al. 2000).

Identification of mechanisms driving life history variation holds critical importance to management and recovery efforts. Recovery plans currently emphasize migratory life histories because of their higher fecundity, greater potential for genetic mixing and colonization of unoccupied habitats, and greater degree of insulation from stochastic and deterministic extinction risks (Rieman and McIntyre 1993). Specific to this study, recovery plans for the lower Clark Fork River drainage focus on boosting numbers of migratory populations and individuals while also protecting existing populations and genetic diversity (WWP 1998; USFWS 2002; Epifanio et al. 2003). A question of interest to fisheries managers is whether specific actions could be taken to encourage the production of migrants in tributaries dominated by the resident form. If genetics drives life history variation, then efforts must focus on protecting the remaining migratory stocks or introducing migratory stocks in concert with alleviating downstream mortality factors (McCart 1997; Nelson et al. 2002). Alternatively, the early growth hypothesis presents the possibility of encouraging expression of the migratory form by modifying environmental conditions that may affect juvenile growth rate (e.g., density, food availability, temperature).

The goal of this study was to evaluate the relationships among growth rate, age structure, environmental attributes, and life history variation of bull trout. The first objective was to characterize age structure, growth rate, age at out-migration, and spawning age in bull trout populations. Demographic diversity may have implications for persistence, for example where an event (e.g., predation) selectively impacts only a subset of the size classes present (Rieman and McIntyre 1993). Further, growth rate may affect the ability to withstand deterministic stresses such as habitat alteration (Rieman and McIntyre 1993). Numerous studies have used anatomical structures to derive age and growth information for the purpose of inferring life history (e.g., Svenning et al. 1992; Theriault and Dodson 2003), and the structures used in this study were pelvic fin rays and scales (Chapter 3). The second objective was to determine whether resident and migratory populations differ with regard to age structure and growth. The third objective was to assess the influence of biotic and abiotic environmental variables on growth rates and life history expression. The study area offered a mixture of resident and migratory populations in streams altered to various degrees by past land use activities. Specifically, I tested the following null hypotheses:

H_0 1: Age structure and growth rates of bull trout inhabiting tributary drainages during summer are similar both among populations and among life history groups (predominantly resident, migratory, or mixed populations).

H_0 2: Age at out-migration is similar both among populations and among life history groups.

H_0 3: Age structure of mature adults is similar both among populations and among life history groups.

H_0 4: Differences in life history expression are unrelated to abiotic and biotic variables including temperature, productivity, fish density, basin size, species composition, and degree of disruption to migratory corridors.

Study Area

This study included 15 bull trout populations in the Bitterroot, lower Clark Fork, and Lake Pend Oreille drainages in western Montana and northern Idaho (Figure 4.1). Past electrofishing, trapping, and redd surveys indicated that study streams supported various mixtures of resident and migratory components (WWP 1996; Moran 2002; Nelson et al. 2002; Liermann 2003; Liermann et al. 2003; Katzman 2003; Katzman and Hintz 2003). All tributaries in the lower Clark Fork drainage that supported bull trout populations, as well as proximate streams in the Lake Pend Oreille drainage, were initially included in 2002, and sites in the Bitterroot drainage were added in 2003 to increase the number of streams supporting resident life history components (Table 4.1).

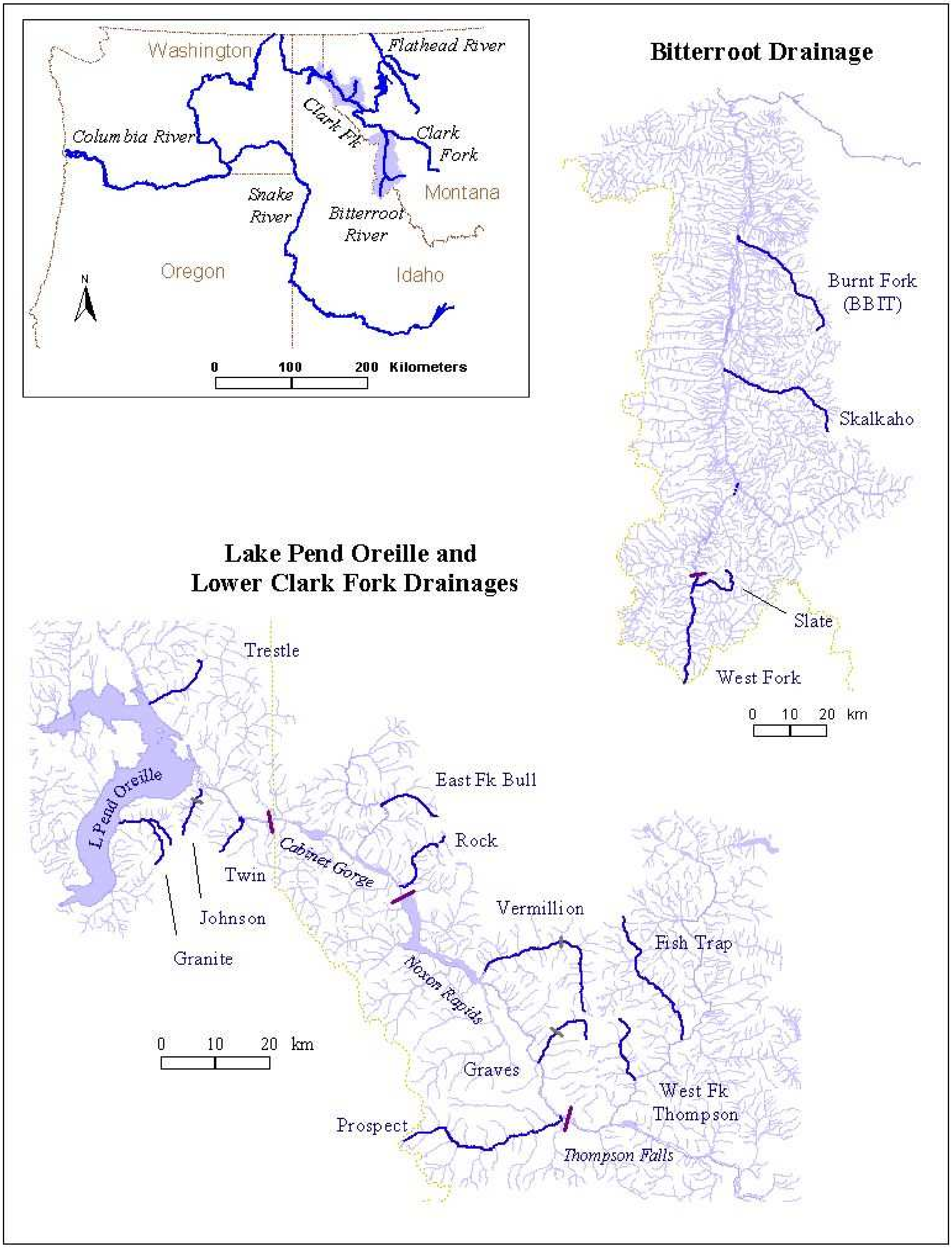


Figure 4.1. Study area, including study streams, main stem dams, and reservoirs. Inset shows location of study area within the northwestern United States.

Table 4.1. Study streams, life history, and years during which fish and habitat surveys were conducted (2 = 2002, 3 = 2003). Bold values indicate structures for age and growth analyses were collected. Asterisk indicates sufficient period of thermograph operation to allow calculation of duration of growing season.

Stream	Code	Dominant life history	Screw trap	Weir trap	Electro-fishing	Resident adults (hand nets)	Redd surveys	Conductivity	Macro-invertebrates	Temperature
					Lower Clark Fork (LCF)					
E Fk Bull	EBUL	Migratory	2, **3**	2, **3**	**2, 3**		2, 3	2, 3	3	2, 3*
Graves	GRAV	Migratory	2, **3**	2, 3	**2, 3**		2, 3	2, 3	3	3*
Prospect	PROS	Resident	2		**2, 3**	**3**	2, 3	2, 3	3	2, 3*
Rock	ROCK	Resident	2, **3**	2, 3	**2, 3**	**2, 3**	2, 3	2, 3	3	3*
Fish Trap	FTRP	Migratory		**2**	**2, 3**	**2**	2, 3	2, 3	3	2, 3*
Vermillion	VERM	Mix	**3**	**3**	**2, 3**	**2**	2, 3	2, 3	3	3*
W Fk Thompson	WTHO	Mix		**2**	**2, 3**	**3**	2, 3	2, 3	3	2, 3*
					Lake Pend Oreille (LPO)					
Granite	GRAN	Migratory		**2, 3**		3	2, 3	2, 3	3	
Johnson	JOHN	Migratory		**2, 3**		3	2, 3	2, 3	3	
Trestle	TRES	Migratory	1, **2**	**2, 3**		2, 3	2, 3	2, 3	3	2, 3*
Twin	TWIN	Migratory	**2**	**2, 3**	**2**		2, 3	2, 3	3	2
					Bitterroot (BIT)					
Burnt Fork	BBIT	Resident			**3**			3	3	3
Skalkaho	SKAL	Resident			**3**			2, 3	3	3
Slate	SLAT	Mix			2, **3**			2, 3	3	2, 3
W Fk Bitterroot	WBIT	Mix			**2**, 3			2, 3	3	2, 3

All three drainages are constituents of the upper Columbia River basin. Base elevation increases from about 635 m at Lake Pend Oreille to 1185 m at Darby, Montana in the Bitterroot drainage, but high mountain ranges dominate the landscape (maximum elevation about 3300 m in the Bitterroot Mountains, 2500 m in the Cabinet Mountains). Upper watersheds are typically steep, heavily forested, and largely within national forest boundaries, whereas private land ownership occurs in lower reaches. Primary land uses in study watersheds have historically been logging and mining, with sparse residential development occurring in some of the lower valleys. Air temperature and precipitation exhibit considerable spatial variability throughout the study area as a consequence of the mountainous topography. Peak flows associated with snowmelt in May and June followed by base flows in August and September characterize annual hydrographs.

Lake Pend Oreille (LPO) is a large natural lake (area = 38,362 ha, maximum depth = 351 m) occupying the Purcell trench and surrounded by the Selkirk, Cabinet, and Bitterroot mountain ranges. This drainage generally receives the highest precipitation (84 cm annually at Sandpoint, Idaho) and lowest mean monthly maximum temperature (13.7° C) of the three drainages in the study area (WRCC 2005). The lake and its tributaries presently support several adfluvial bull trout populations, but three hydropower dams block access to populations in the lower Clark Fork River drainage that historically used the lake as rearing habitat (Pratt and Huston 1993). Two tributaries of Lake Pend Oreille (Trestle and Granite creeks), were included in this study. Also, two tributaries that enter the Clark Fork River just upstream of the lake (Johnson and Twin creeks) were considered as within the LPO drainage because they join the main stem below the first dam and are easily accessible from the lake. Trestle Creek supports the strongest run of migratory bull trout of any LPO tributary (mean 252 redds annually), whereas smaller numbers return to Granite Creek (33 redds), Johnson Creek (20 redds), and Twin Creek (10 redds) (Downs and Jakubowski 2003).

The lower Clark Fork (LCF) basin includes the main-stem Clark Fork River and tributaries along a 118-km reach from the Thompson River to Lake Pend Oreille. The lower Clark Fork River separates the Cabinet Mountains to the north from the Bitterroot Mountains to the south. Precipitation generally decreases from west to east, averaging 85 cm annually at Heron, Montana (near the Idaho border) and 58 cm at Thompson Falls (WRCC 2005). Tributaries in the Bitterroot Range tend to lose surface flow in their lower reaches due to sediment aggregation attributed to large-scale forest fires and past forestry activities, whereas relatively unstable Belt Series geology contributes to high sediment loads in the lower reaches of streams in the Cabinet Mountains (Pratt and Huston 1993; WWP 1996; Saffel and Scarnecchia 1995). Habitat conditions in the main stem Clark Fork River have been most obviously altered by three hydroelectric dams. Thompson Falls Dam is a run of the river facility built in 1913, whereas Cabinet Gorge (built 1951, impounded area = 1,377 ha) and Noxon Rapids (built 1958, impounded area = 3,523 ha) dams both create large reservoirs. None of these dams provides an effective fish ladder or bypass system, although a limited trap and haul program for bull trout and westslope cutthroat trout began in 2001 (Lockard et al. 2003b). Most tributaries within the LCF drainage formerly supported populations of migratory bull trout, but the amount of suitable spawning and rearing habitat has decreased, runs of returning adults have diminished, and bull trout no longer inhabit some historically occupied tributaries (Pratt and Huston 1993). This study included seven tributaries in this basin, four of which supported relatively strong migratory components (East Fork Bull River, Fish Trap Creek, Graves Creek, and Vermillion River) and three believed to support mainly resident populations (Prospect Creek, Rock Creek, and West Fork Thompson River). Additional streams (Deep, Marten, Pilgrim, and Swamp creeks, South Fork Bull River) sampled during the study period were not included in the life history analysis because capture efforts produced fewer than five bull trout.

The Bitterroot River (BR) joins the Clark Fork River about 300 kilometers upstream from Lake Pend Oreille. The river is bounded by the predominantly granitic Bitterroot Range to the west and the sedimentary Sapphire Range to the east. Precipitation averages 40 cm annually at Darby, Montana (WRCC 2005). Upper portions of the drainage fall within national forest boundaries, but agricultural and urban land uses in the lower basin are considerably more extensive than in the other two basins. Irrigation diversions and habitat degradation have created barriers to migration in downstream reaches of tributaries in the lower half of the drainage, effectively isolating populations in headwaters reaches of several streams (Clancy 1993; Nelson et al. 2002). Fluvial bull trout populations were formerly common but migratory individuals are now rare and restricted to the upper West Fork and tributaries above Painted Rocks Reservoir (Clancy 1993). Tributaries included in this study include two streams (Burnt Fork and Skalkaho creeks) that enter the main stem in the lower portion of the drainage and support isolated resident populations, and two streams (Slate Creek and the upper West Fork Bitterroot) that include a migratory component (Clancy 1993).

Fish Species

At least 30 fish species inhabit study area waters (Pratt and Huston 1992). Native salmonids include bull trout, westslope cutthroat trout *Oncorhynchus clarki*, and mountain whitefish *Prosopium williamsoni*. The remainder of the native fish assemblage consists of various catostomids, cottids, and cyprinids. Nonnative salmonids potentially detrimental to bull trout, including brook trout, brown trout, and rainbow trout *Oncorhynchus mykiss*, are widespread in all three drainages and commonly occupy the lower portions of tributaries. Lake trout, northern pike *Esox luscious*, largemouth bass *Micropterus salmoides,* and smallmouth bass *Micropterus dolomieu* are introduced predators found primarily in the main stem Clark Fork River and Lake Pend Oreille. Kokanee *O. nerka* have been introduced to Lake Pend Oreille, where they provide prey for bull trout.

Methods

Fin ray and scale collection

Fin rays and scales used for age and growth estimation were collected in 2002 and 2003 with the cooperation of agencies already conducting work in the study area. Avista Corporation, Idaho Department of Fish and Game (IDFG), Montana Department of Fish, Wildlife and Parks (MFWP), and the U.S. Fish and Wildlife Service (USFWS) provided fin rays and scales from the LPO and LCF basins. A Montana State University graduate student, Clint Sestrich, and MFWP provided samples for Bitterroot River tributaries. Detailed sampling procedures and results are presented in various reports (Moran 2003a, 2003b; Downs and Jakubowski 2003; Liermann 2003, Liermann et al. 2003; Lockard et al. 2003a, 2003b; Moran 2004a, 2004b; Sestrich 2005) and a summary of pertinent aspects is provided herein. I assisted agency crews and conducted supplemental sampling to collect structures and habitat data for use in testing study hypotheses.

Bull trout were captured by electrofishing, in screw or weir traps operated near tributary mouths, and with hand nets (Table 4.1). Electrofishing was conducted in July and August in 12 tributaries to assess population composition and to acquire structures. I refer to fish <400 mm captured during electrofishing surveys conducted in July and August as “tributary occupants” (avoiding the life history implications of the term “residents”). This group consisted primarily of juveniles of any life history, but could also include resident adults and possibly some small individuals that had undertaken a migration (e.g., “jacks”). Large bull trout (i.e., > 400 mm TL) were avoided during electrofishing to minimize disturbance of rare migratory adults, but few such individuals were encountered during electrofishing surveys. Rotary screw traps were operated at seven tributaries in the LCF and LPO drainages variably between March and August depending on conditions and availability of crews and equipment. High flows frequently prohibited operation of traps during snowmelt runoff in May and June. Weir traps in ten tributaries in the LCF and LPO drainages were operated beginning as early as July until as late as December, and these traps captured large- and small-bodied fishes moving upstream and downstream in separate holding boxes. Bull trout < 250 mm TL captured in screw or weir traps while moving downstream were considered to be “juvenile out-migrants.” Individuals >300 mm TL captured in weir traps while moving upstream into tributaries during July—November or leaving tributaries during late August—December were considered mature migratory adults. In September and October, when electrofishing is prohibited in bull trout streams to protect spawning adults, I used hand nets while snorkeling at night to capture mature, resident form bull trout as well as a sample of immature individuals for comparison in seven streams. Employing a modification of the method of Bonneau et al. (1995), I worked in an upstream direction and captured bull trout by slowly working a net underneath a fish and lifting it out of the water. Redd surveys were conducted in autumn and structures for age and growth analysis were collected from encountered spawning mortalities. Sex of bull trout captured after July was determined by presence of gametes, a swollen urogenital opening (Morita and Morita 2002), and obvious secondary sexual characteristics, such as a well-developed kype on males (McPhail and Baxter 1996).

The anterior three or four rays from one pelvic fin were removed using scissors or wire cutters, with the cut made as close as possible to the articulation with the body in order to capture the earliest annuli (Chapter 3). Scales were removed from an area ventral and posterior to the dorsal fin using a dull knife. All structures were placed in coin envelopes labeled with the weight and total length of the fish as well as the date and location of capture.

Age and growth estimation

Samples were prepared and analyzed using the method established in Chapter 3. For each fin ray sample, I categorized the readability of annuli based on the overall morphology of the sample (R1—R5; see Appendix A), clarity of annuli (A—E; A = high, E = unrecognizable), and ability to resolve the earliest annulus (A—E; A = high, E =

unrecognizable). Fin samples excised too distal from the body (i.e., morphology R4 or R5 for individuals < 300 mm TL, R3— R5 for individuals >300 mm, dash mark prominent in nucleus) or lacking distinct annuli were excluded from analyses (Appendix B). For scales, I excluded samples for which the pattern of circuli was not clearly discernable in the anterior field.

Presence of conspicuously wide opaque bands on fin rays or widely spaced circuli on scales constituted evidence of migration to more productive rearing habitat (Chapter 3). Increased growth could also result from a niche shift (e.g., to piscivory) (Werner and Gilliam 1984), so migration was assumed only where the contrast in increment width was substantial (width of an increment at least twice that of interior increments). The Fraser—Lee intercept correction formula ($\alpha = 20$) was used to back-calculate length at age from pelvic ray samples (Chapter 3).

Age structure was calculated using age—length keys (DeVries and Frie 1996). Fin rays were used to estimate ages of tributary occupants, out-migrants, and mature resident adults. Scales were used to estimate age of returning migratory fish because most fin ray samples from this group were categorized as R3—R5 morphology and early annuli were deemed unrecognizable due to overly distal excisions of the fin rays. I attempted to include a distribution of samples proportional to the number of individuals captured in each length interval (25-mm intervals for tributary occupants and out-migrants, and 50-mm intervals for returning migrants) in order to minimize bias (Kimura 1977), but poor sample quality imposed constraints for some sets. Out-migration age was defined as age at capture for juvenile out-migrants and also, as a separate dataset, as the first conspicuously wide growth band evident on scales of adult migrants. Spawning age was considered to be equivalent to age at capture for migrant adults >300 mm caught in weir traps and for mature residents captured using hand nets.

Life History Characterization

Tributary populations were categorized as predominantly resident, migratory, or mixed life history based on electrofishing data, trap catches, autumn snorkeling efforts, and analysis of fin ray and scale samples. Given the highly flexible nature of bull trout life history, most tributary populations probably contain some proportion of both migrants and residents except where barriers eliminate the possibility of return after emigration. Thus, the designation referred to the predominance of a life history form in a tributary. The primary criterion for life history designation was the abundance of bull trout captured migrating upstream into weir traps at stream mouths relative to the abundance of ripe resident bull trout captured during autumn or bull trout 200—400 mm electrofished during summer. Fin rays and scales were analyzed for evidence of a rapid increase in growth indicating migration to a more productive environment. Tributaries in which one life history form was not clearly dominant were categorized as "mixed."

Biotic and Abiotic Habitat Covariates

Fish assemblage and population information potentially related to growth of bull trout was derived from electrofishing and trapping data collected during 2002 and 2003 (Moran 2002; Downs and Jakubowski 2003; Liermann 2003; Liermann et al. 2003; Lockard et al. 2003a; Lockard et al. 2003b; Moran 2003a; Moran 2004a; Sestrich 2005). Densities of bull trout, brown trout, and brook trout > 75 mm TL captured during two-to-four pass electrofishing surveys were calculated using Zippin removal estimates and the program CAPTURE (White et al. 1982). Combined density of brook trout and brown trout relative to density of bull trout was used to describe abundance of non-native species known as competitors and predators to bull trout within tributary streams.

Conductivity and macroinvertebrate biomass were included as indicators of biological productivity. I measured specific conductivity using a field conductivity meter in 2002 and 2003. For the analysis, I used three measurements taken during base flows in September 2003 at randomly selected locations distributed within the stream reach of primary juvenile bull trout occurrence within each tributary. Point measurements at nine streams indicated that conductivity values during summer base flow was similar (mean difference = 4.6 μS/cm) in 2002 and 2003. Concurrent with the conductivity assessments in September 2003, I collected macroinvertebrates at each site by rapidly kicking the stream substrate in riffle and run habitats directly upstream of a 500-micron mesh kick net, gradually progressing upstream for three minutes at each site. Large debris was rinsed and removed, and the sample was preserved in 70% ethyl alcohol. In the laboratory, macroinvertebrates were picked from debris. For each sample, all animals larger than about 0.5 mm in body length were removed and stored in a separate vial. One-quarter of the remaining sample of smaller individuals was then isolated using a divider, picked, and stored in another vial. Both samples were placed in crucibles and dried in an oven at 105˚ C for four hours, then weighed. Dried samples were ashed in a furnace at 550˚ C for one hour and reweighed. Ash-free dry mass (AFDM) was calculated as the difference in the two weights (Platts et al. 1983). Subsample AFDM (animals less than 0.5 mm in body length) was multiplied by four and then added to the corresponding value for the larger animals to obtain a total for the sample.

Abiotic habitat variables included water temperature, stream watershed area, and presence of barriers. Water temperature was measured with electronic thermographs programmed for hourly readings. I deployed thermographs housed in perforated PVC tubing at relatively deep, concealed sites with moderate flow velocities in ten tributaries initially included in the study, two of which were subsequently omitted from the data set because fewer than five juvenile bull trout were captured (Table 4.1). These thermographs recorded temperatures from September 2002 to October 2003. Additionally, I obtained temperature data collected by management agencies during July—September of 2003 in four streams and 2002 in eight streams. Overall mean summer temperature was calculated for use in analyses because it was found to be most strongly associated with bull trout distribution and abundance in Utah streams (Gamett 2002). For consistency across the set of streams, the mean was calculated for July 18—September 30. Missing mean temperature values for 2002 were calculated using an equation ($y = 1.017\ x - 1.7806$; $r^2 = 0.94$) derived by regressing mean values in 2002 on mean values in 2003 for six sites measured in both years. Duration of growing season, defined as number of days above the critical growth minimum (Kennedy et al. 2003), was included as a second temperature variable and defined as 5.2 ºC based on results from a laboratory study (Selong et al. 2001). This metric was calculated only for a reduced set of eight streams where thermographs were deployed for an extended period that included spring and autumn (Table 4.1). I used point temperature measurements, as well as data from multiple thermographs installed in different stream reaches, to quantify longitudinal variation in temperatures. Watershed area above each sampling location at every tributary was measured using a GIS. Finally, I categorized the extent to which barriers impeded migration in each tributary based on field observations and consultation with agency biologists. Categories indicated the estimated degree of impassability between reaches supporting juvenile bull trout and the main-stem river or lake as follows:

0 = no barrier
1 = occasional, temporary low flow impediment
2 = passable only at high flows (e.g. June peak runoff)

Barriers in categories 1 and 2 were generally associated with sediment deposition in lower stream reaches or, in the Bitterroot basin, with flow diversion and low-head dams. A fourth category consisting of reaches above permanent natural barriers (i.e., falls) was dropped from consideration because electrofishing and snorkel surveys produced no evidence of bull trout occurrence above such barriers at Graves Creek, Johnson Creek, and Vermillion River.

Statistical Analyses

Age structure of out-migrants, returning adults, and tributary occupants among the different life history categories was analyzed using a combination of chi-square tests of independence and graphical methods. Age-0 individuals were excluded from analyses because capture methods were inefficient for bull trout less than about 75 mm TL. Statistical tests involving migratory populations included ages 1, 2, and a pooled ≥ 3 category because few tributary occupants exceeded age 3. For resident populations, age categories included ages 1, 2, 3, and ≥ 4 groups. Interannual differences in age structure for individual streams and differences within life history groups were analyzed with chi-square tests. Difference between migratory and resident life history groups in proportion of each age class was tested using Mann—Whitney *U*-tests on ranked percentages. Nonparametric tests were used because sample sizes were small and the data was often highly skewed or non-normal

Early growth was characterized using increment data from fin rays. Because bull trout were captured in several months from spring through autumn, back-calculation was necessary to standardize growth determinations. Only the most recently formed complete increment (i.e., age-0 growth = incremental distance from the focus to the edge of the first annulus in age-1 fish; age-1 growth = distance between the first and second annuli in age-2 fish) was used, providing maximum accuracy (Gutreuter 1987) and allowing comparison to the available habitat data most closely corresponding to the growth interval (Quist and Guy 2001). Sample sizes limited analyses to only age-1 and age-2 individuals of tributary occupant and out-migrant groups. Differences in growth between juvenile out-migrants and tributary occupants of the same age-group captured by electrofishing at each stream were tested with Mann—Whitney *U*-tests, and groups were pooled for subsequent analyses to characterize overall age structure in a tributary if differences were not significant. Interannual variation in growth between 2002 and 2003 was tested for individual streams using Mann—Whitney *U*-tests. Size-selective ‘removal’ from the population (e.g., due to differential survival or emigration) was tested by calculating length at age 1 for the year 2001 cohort in individual populations and comparing results for samples collected in 2002 to those collected one year later in 2003.

Dependence of early growth on environmental variables was modeled using forward stepwise linear regression and Mann—Whitney *U*-tests. Mean values of habitat variables at each stream were weighted according to the proportion of included ageing structures collected at the nearest sampling station. Sample sizes were insufficient to use individual reaches as the experimental units, and weighting was done to obtain values more likely to reflect the actual conditions experienced by the bull trout included in the analyses. For example, if 70% of age-1 samples from a tributary were collected at the upstream-most site, then the values for temperature, growing season, conductivity, and macroinvertebrate biomass samples collected closest to that site, fish densities at the site, and watershed area above the site would receive a weight of 0.7 when calculating mean values for that stream. For fish caught in traps, the unweighted mean for all upstream sampling stations was used. To handle non-normality, conductivity was $\log_e$-transformed. Because weighted habitat scores differed for age-1 and age-2 sample sets, separate regression analyses were performed for each. Also, separate regressions were performed for the age-1 set (age-0 growth) with and without growing season length because inclusion of this variable reduced the number of streams from nine to seven. Because of extreme non-normality, relative abundance of nonnative species was generalized to a binary presence—absence variable, and watershed area was categorized into small (< 9,600 ha) and large (> 19,000 ha) groups. These two variables were excluded from the regression analyses, and instead growth differences between groups were tested using Mann—Whitney *U*-tests.

Growth of mature resident bull trout was characterized with back-calculated lengths at all previous ages. Back-calculated lengths at ages 1—5 were compared among streams and between sexes using Mann—Whitney *U*-tests. To test for a relationship between early growth and size selective survival or maturation within resident populations, back-calculated lengths at age 1 and age 2 were compared between resident adults and juveniles (pooled ages 1 and 2) at each stream using Mann—Whitney *U*-tests. Differences in growth of mature and immature fish were identified by plotting growth trajectories for both types within each population.

The full set of 15 streams was used to assess relationships of life history to biotic and abiotic habitat covariates. Differences in overall (non-weighted) mean values of each habitat variable in 2003 among resident, migratory, and mixed populations were analyzed using Kruskal—Wallis tests. Because of a high incidence of zero values, relative abundance of nonnative brook and brown trout was generalized to a binary presence—absence variable, and difference among groups was tested using a Fisher exact test.

Results

Age and growth estimation

Only about half (48%) of the 751 fin ray samples examined were judged suitable for use in age and growth analysis. Quality of fin ray samples was better for small individuals (62% of fin rays from fish <250mm TL were suitable) but highly variable among individual field collection events. Poor quality of fin ray samples resulted primarily from excessively distal fin excision (96% of rejected samples), as indicated by fin ray morphology and characteristics of the nucleus (Appendix B).

Life history characterization

Field surveys generally supported the assessments of dominant life history made prior to the start of this study. Eleven of the fifteen study streams (73%) supported either predominantly resident (*N* = 4) or migratory (*N* = 7) life histories, whereas four streams supported a more even mixture (for detailed survey data see: Moran 2003a, 2003b; Downs and Jakubowski 2003; Liermann 2003, Liermann et al. 2003; Lockard et al. 2003a, 2003b; Moran 2004a, 2004b; Sestrich 2005). Exclusively resident populations occurred only at four tributaries where isolated by extensive reaches of subsurface flow or diversions (PROS, ROCK, BBIT, and SKAL). By contrast, no resident adults, but relatively large numbers of migratory adults, were found at the four streams in the LPO drainage (TRES, GRAN, JOHN, and TWIN). Large migratory adults entered five LCF tributaries (EBUL, FTRP, GRAV, VERM, and WTHO), but little evidence for a resident component was found at three of these (EBUL, FTRP, and GRAV). Four streams (SLAT, VERM, WBIT, and WTHO) could not be definitively classified as predominantly resident or migratory because migratory adults and also a relatively large proportion of individuals 200—400 mm were captured, and these sites constituted a third "mixed" category in analyses. Although few fish 200—400 mm TL occurred in the tributaries supporting the highest numbers of returning adfluvial migrants, this criterion was not entirely reliable because migratory individuals 200—400 mm were captured moving upstream into every weir trap in which bull trout were caught, and wide spacing of circuli and annuli on fin rays and scales (Figure 4.2a and b) suggested that some individuals 200—400 mm captured during electrofishing surveys in tributaries classified as migratory or as mixed had migrated to more productive habitats. Also, the fin ray sample for a 500-mm, age-12 or older (poor integrity of sample margin prevented more precise estimation) bull trout captured in an isolated reach of Prospect Creek evidenced no migration (Figure 4.2c), but rather a narrow banding pattern consistent with that of rays from resident individuals < 300mm at the same location (Figure 4.2d).

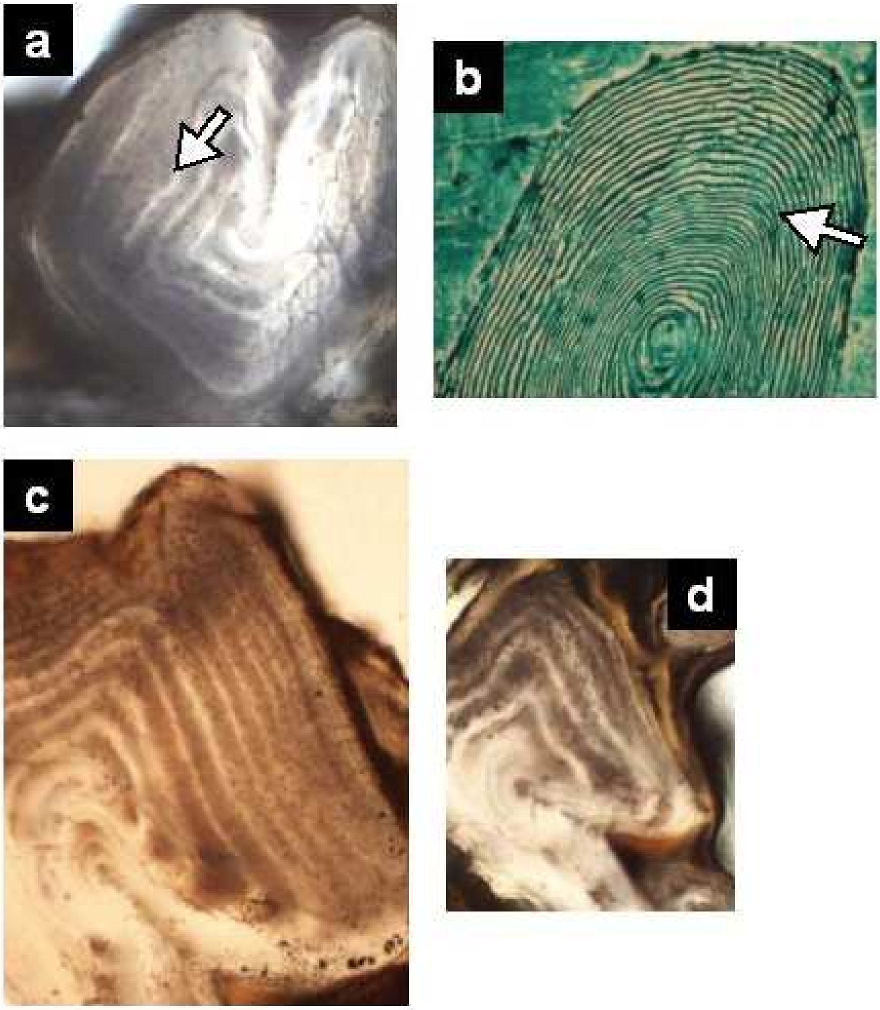


Figure 4.2. Evidence of life history in pelvic fin rays and scales. Arrow indicates increase in growth associated with migration to more productive main stem or lake environment apparent in fin ray of a 360-mm bull trout from West Fork Thompson River (a) and scale of a 259-mm bull trout from Twin Creek (b). Pelvic ray sections from two bull trout, 500 mm (c) and 242 mm (d), captured by electrofishing in Prospect Creek demonstrate a narrower banding pattern typical of tributary growth.

Age structure

Tributary occupants. Most bull trout (mean = 74%) captured in tributaries during July and August were age 1 or 2. Migratory and resident groups held similar proportions of age-classes 1—3 (both years combined; Mann-Whitney *U*-tests, all $P > 0.24$) but resident populations held significantly higher proportions of age-4 and greater fish than did migratory populations ($P < 0.01$) (Figure 4.3). Frequencies of ages 1, 2, and 3 differed between 2002 and 2003 for four of the six streams sampled in both years (Chi-square tests of independence; df = 2; EBUL: $P = 0.03$, FTRP: $P < 0.001$, GRAV: $P < 0.001$, PROS: $P = 0.60$, ROCK: $P = 0.25$, WFT: $P = 0.04$).

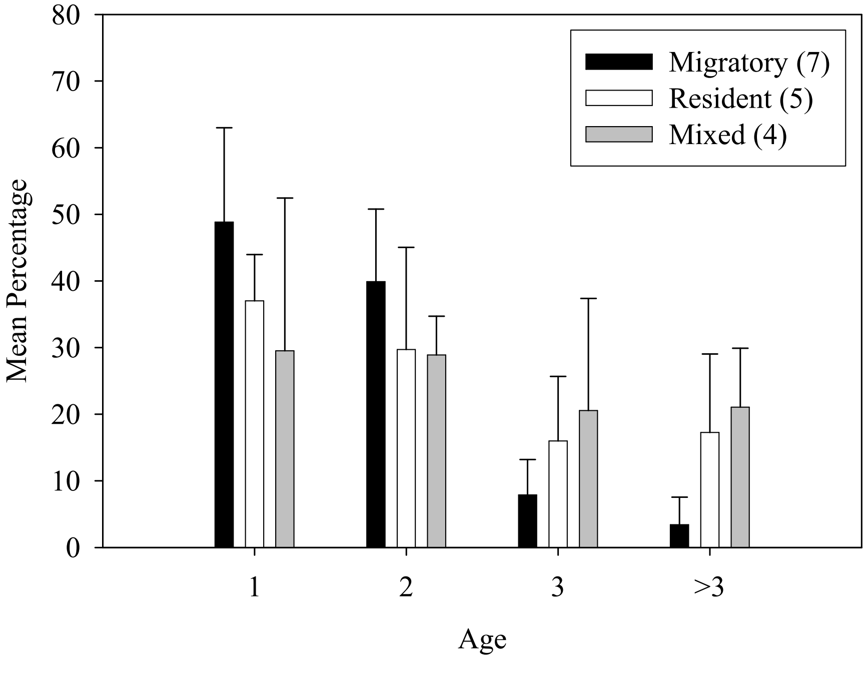
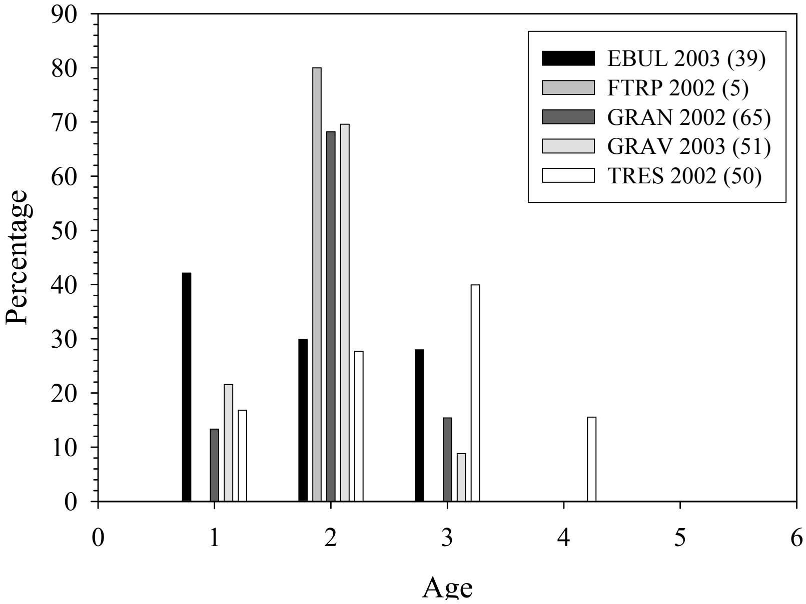


Figure 4.3. Age structure (mean percentage + 2 SE) of bull trout < 400 mm TL captured during electrofishing surveys in July and August of 2002 and 2003 in tributaries grouped by dominant life history. Number of tributary surveys in parentheses.

Out-migrants. Age structure of juvenile out-migrants differed between migratory and resident populations. In migratory populations, bull trout out-migrated mainly at ages 1—3 (Figure 4.4). Initiation of wide circuli spacing in scales (Figure 4.2) from 84 migratory adults captured moving upstream into weir traps indicated that out-migration at age 3 was most common (52%), followed by age 2 (23%) and age 4 (20%) (Figure 4.5). Among populations having a resident component, age of juvenile out-migrants at VERM was similar to that at migratory populations, whereas the majority of out-migrants were distinctly older at WTHO (age 4) and younger at ROCK (age 1). Also, trapping efforts at PROS in 2002 produced only two bull trout. Age distributions of out-migrants showed no consistent pattern of difference from those of tributary occupants at the five sites where paired collections were available (EFB, GRAV, ROCK, VERM, and WTHO).



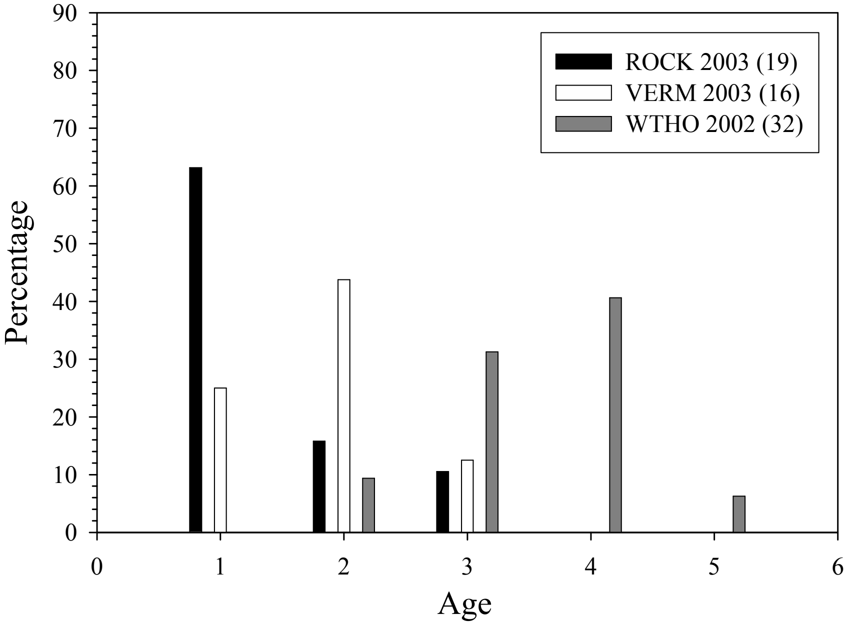


Figure 4.4. Out-migration age of bull trout in migratory populations (top) and resident (ROCK) or mixed (VERM, WTHO) populations (bottom) in 2002 and 2003. Number of samples aged for each stream provided in parentheses.

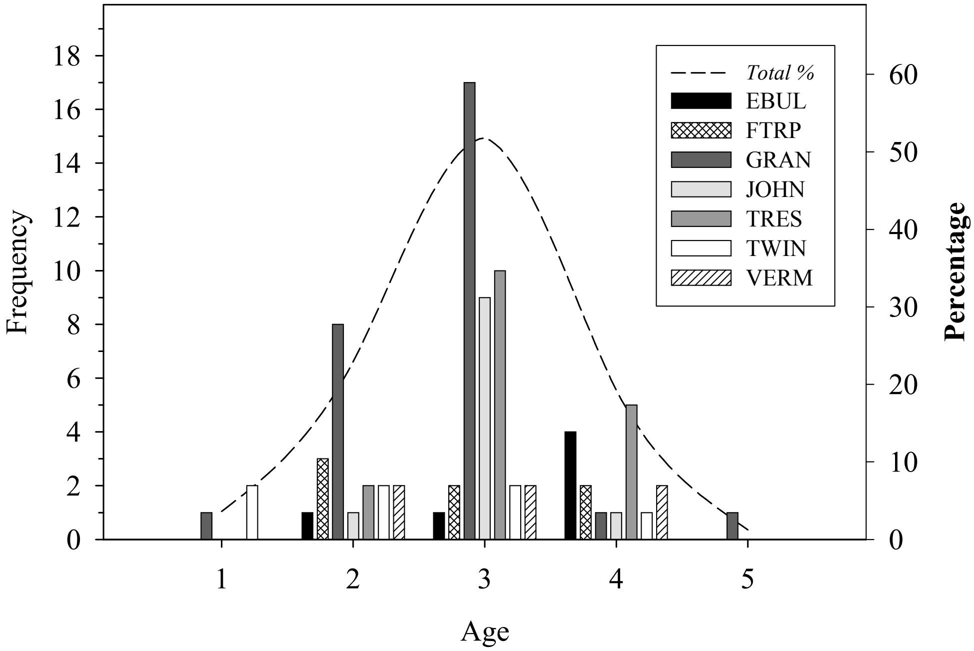


Figure 4.5. Estimated age at juvenile out-migration ($N = 83$) based on analysis of circuli spacing on scales of adult migratory bull trout. Dashed line indicates percentage for all samples combined.

Adults. Returning adult migrants captured in weir traps in the LPO drainage varied from age 4 to age 10, as estimated using scales (Figure 4.6). Overall, most fish were ages 6 or 7, although the distribution peaked at age 8 in one stream (JOHN). Characterization of age structure for tributaries upstream of Cabinet Gorge Dam (EBUL, FTRP, GRAV, and WTHO) was limited by capture of relatively few large individuals in traps and poor sample quality, but available samples suggested that fish of ages 4 and 5 comprised an overall greater proportion of the catch in LCF tributaries than in LPO tributaries.

Mature resident bull trout captured in autumn with hand nets varied from age 3—7 and peaked at age 6 (Figure 4.7). Mature residents had an overall younger distribution than migrants. Resident males (*N* = 23) outnumbered females (*N* = 8) and matured at a younger age (males = age 3, females = age 5) (Figure 4.8). Maturation began at an earlier age at ROCK (age 4) and PROS (age 5) than at WTHO (age 6). No fish < 200mm (*N* = 45) were mature. Analysis of samples from non-ripe fish 218—251 mm TL (mean = 232 mm; *N* = 18) from resident populations indicated that the oldest were age 5.

Most ripe resident bull trout were captured in three LCF streams (PROS, ROCK, and WTHO; 16 nights of effort; Figure 4.7), whereas a single ripe male was captured in FTRP (1 night) and no mature resident individuals or bull trout from 220—400 mm TL were found during surveys at GRAN (1 night), TRES (3 nights), or VERM (1 night). Bull trout exceeding 400 mm TL that appeared to be migratory females, based on large size, light coloration, and lack of a kype, were observed while snorkeling in two streams with relatively numerous residents (PROS: *N* = 1; WTHO: 1 fish observed on three occasions, 1-3 individuals total), but capture was not attempted. However, the narrow annuli spacing for a 500-mm individual (at least age 12) electrofished at PROS suggested a resident life history (Figure 4.2c), indicating that a low frequency of resident bull trout may attain greater size and age. Only one of the bull trout captured during autumn snorkeling efforts, a 360-mm male in WTHO, was judged migratory based on conspicuously wide age-4 and age-5 opaque bands in the fin ray sample (Figure 4.2a).

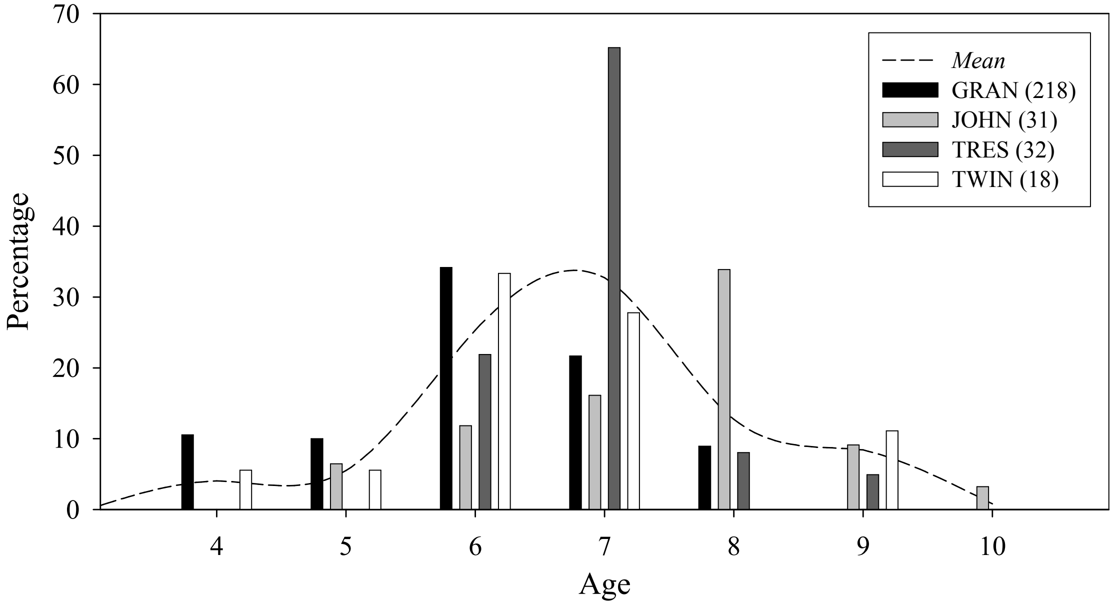


Figure 4.6. Age structure of returned migratory bull trout caught in weir traps in LPO basin tributaries in 2002. Sample size for each stream provided in parentheses. Dashed line indicates mean for all four streams

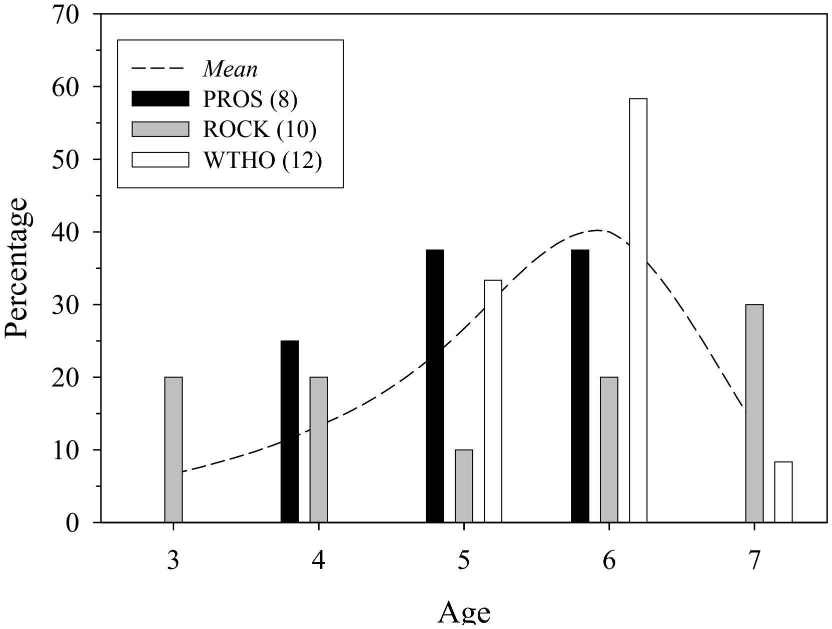


Figure 4.7. Age structure of mature resident bull trout captured with hand nets in autumn. Sample size for each stream provided in parentheses. Dashed line indicates mean of percentages for the three streams.

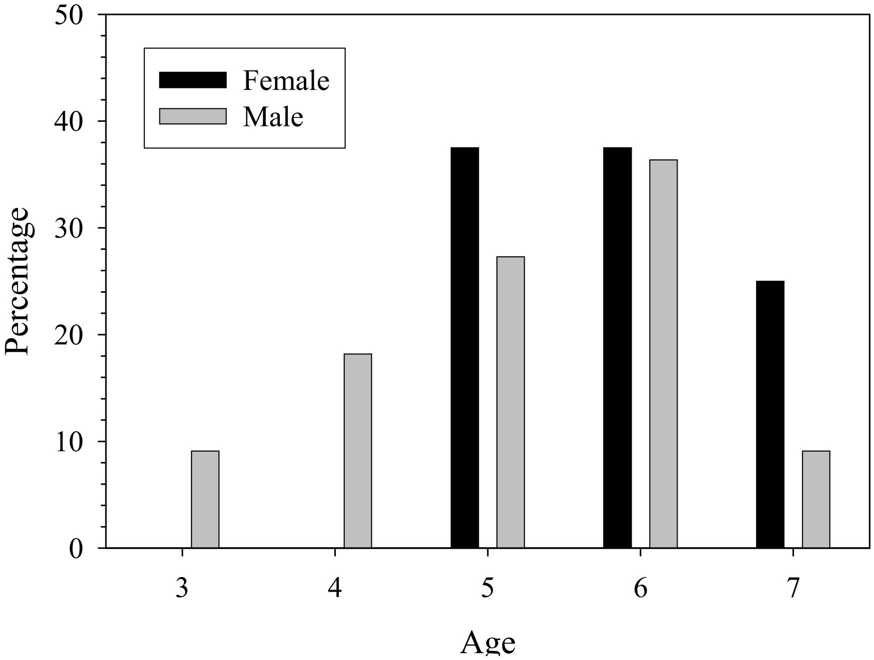
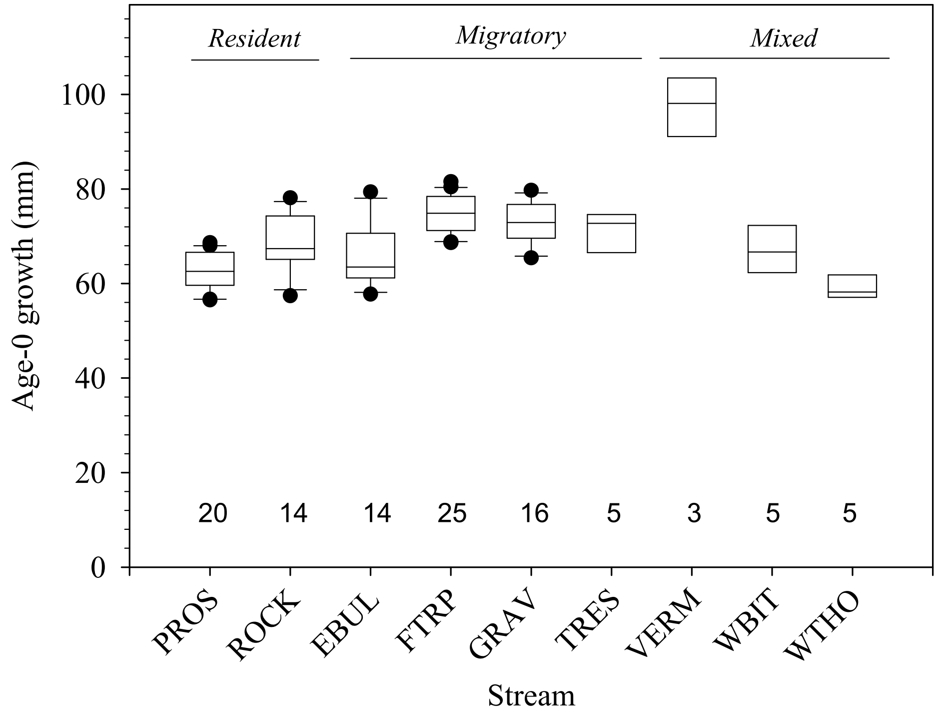


Figure 4.8. Age structure of mature resident female (*N* = 8) and male (*N* = 22) bull trout captured with hand nets in autumn.

Growth

Juveniles. Bull trout typically grew 60—80 mm (mean = 69.4 mm) in their first year and 35—55 mm (mean = 45.8 mm) in their second year (Figure 4.9 and Figure 4.10). Growth did not consistently differ between life history groups, although the group mean for migratory streams exceeded that for resident streams for both years and growth increments (samples collected in 2002: difference in group means for age-0 growth = 5.6 mm, age-1 growth = 2.1 mm; samples collected in 2003: age-0 growth = 0.7 mm, age-1 growth = 6.8 mm). Interannual variation was significant for two of the four age-0 growth comparisons (PROS and ROCK, 2003 > 2002; Mann-Whitney U-tests; both $P < 0.005$) and one of the six age-1 growth comparisons (PROS, 2002 > 2003; $P < 0.009$). Tributary occupants and out-migrants grew at similar rates within all populations except in EBUL (tributary occupants > out-migrants; Mann-Whitney *U*-test; $P = 0.001$). Thus, only electrofishing samples were used to describe EBUL age-0 growth, but trap and electrofishing samples were otherwise pooled for analyses to increase sample sizes. Back-calculated lengths at age 1 for the year 2001 cohort (sampled in 2002 and 2003) indicated that fish present in tributaries at age 2 were relatively large at age 1 in one resident population (PROS: $P = 0.024$) and relatively small at age 1 in one migratory population (FTRP: $P = 0.037$).

Adults. Mature resident adults in the LCF basin attained considerably smaller size than migratory adults of the same age in the LPO basin (Figure 4.11). Length differences between groups varied from 137 mm at age 4 to 266 mm at age 7. Among



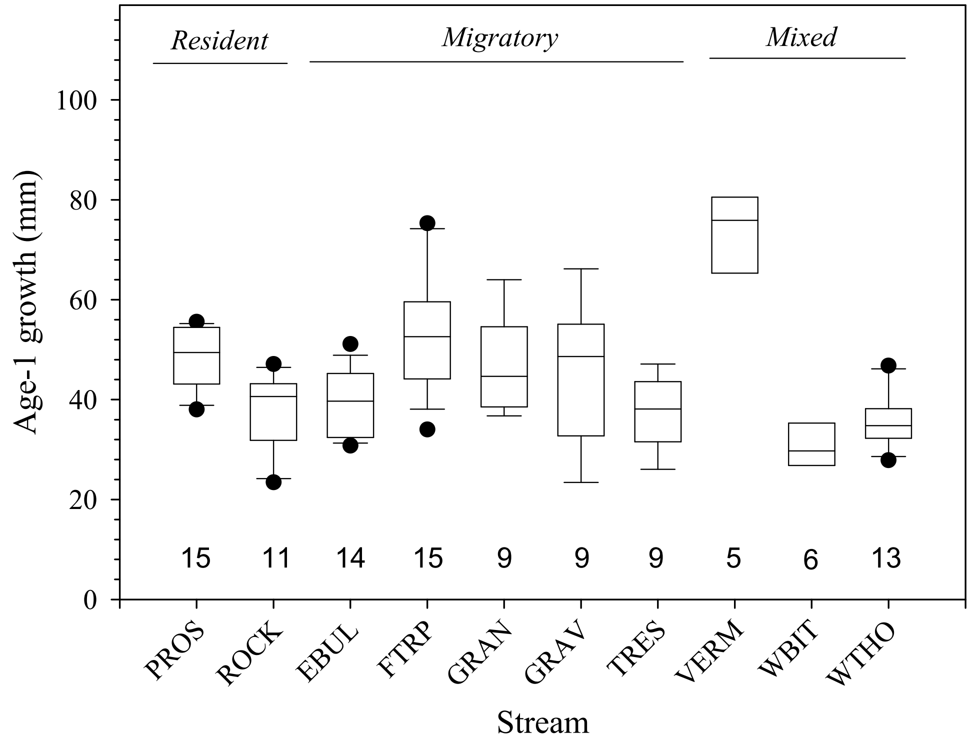
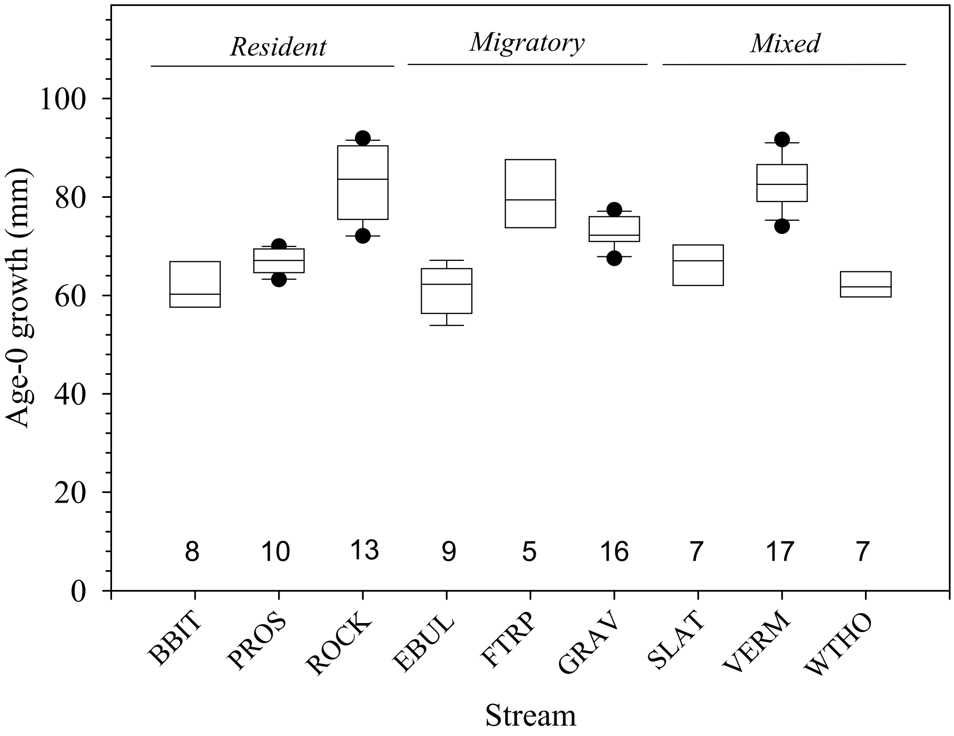


Figure 4.9. Age-0 (top) and age-1 (bottom) growth of bull trout captured in 2002. *N* provided above stream name. Boxes indicate 25th and 50th percentiles around the median; whiskers indicate 10th and 90th percentiles; solid circles indicate outliers.



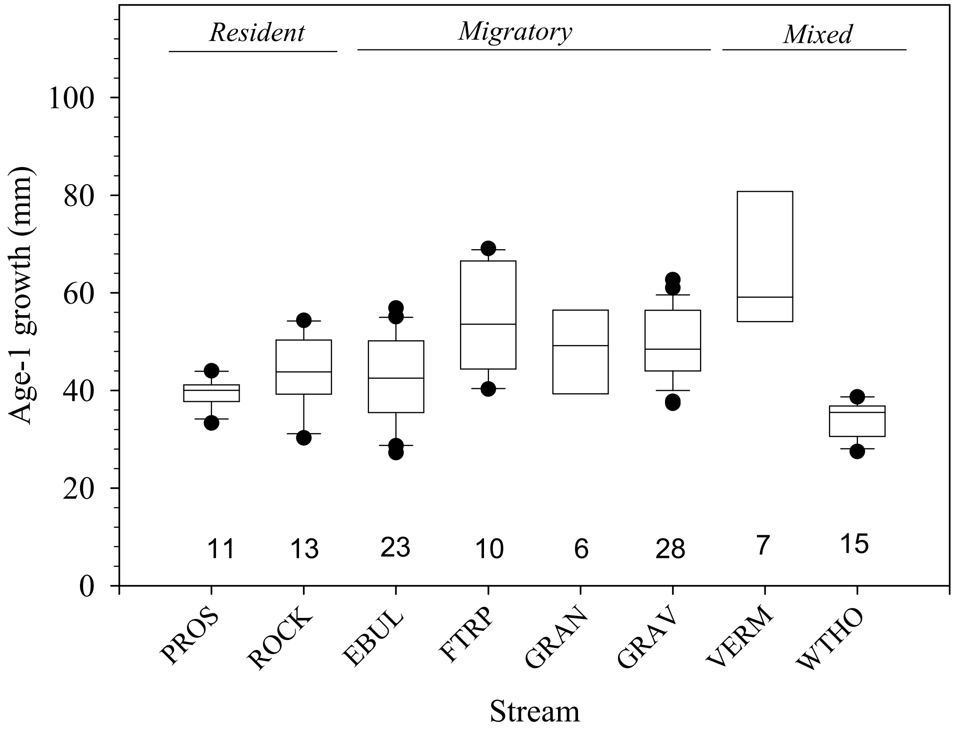


Figure 4.10. Age-0 (top) and age-1 (bottom) growth of bull trout captured in 2003. Boxes indicate 25th and 50th percentiles with encompassed median; whiskers indicate 10th and 90th percentiles; solid circles indicate outliers. *N* provided above stream name.

the three populations at which mature residents were collected, back-calculated lengths at age for mature residents showed a common growth trajectory but overall faster growth at PROS and ROCK than at WTHO (Figure 4.12). Length at age varied significantly among populations at age 1 (Mann-Whitney *U*-test; ROCK > WTHO: $P = 0.003$; PROS > WTHO: $P = 0.045$; ROCK > PROS: $P = 0.016$), age 2 (ROCK > WTHO: $P = 0.016$; PROS > WTHO: $P = 0.031$), and age 3 (ROCK > WTHO: $P = 0.019$), but not ages 4 or 5 (all $P > 0.10$). Females and males initially grew at similar rates then diverged, females being significantly larger at age 5 ($P = 0.045$), although this effect was not apparent in ROCK (Figure 4.13).

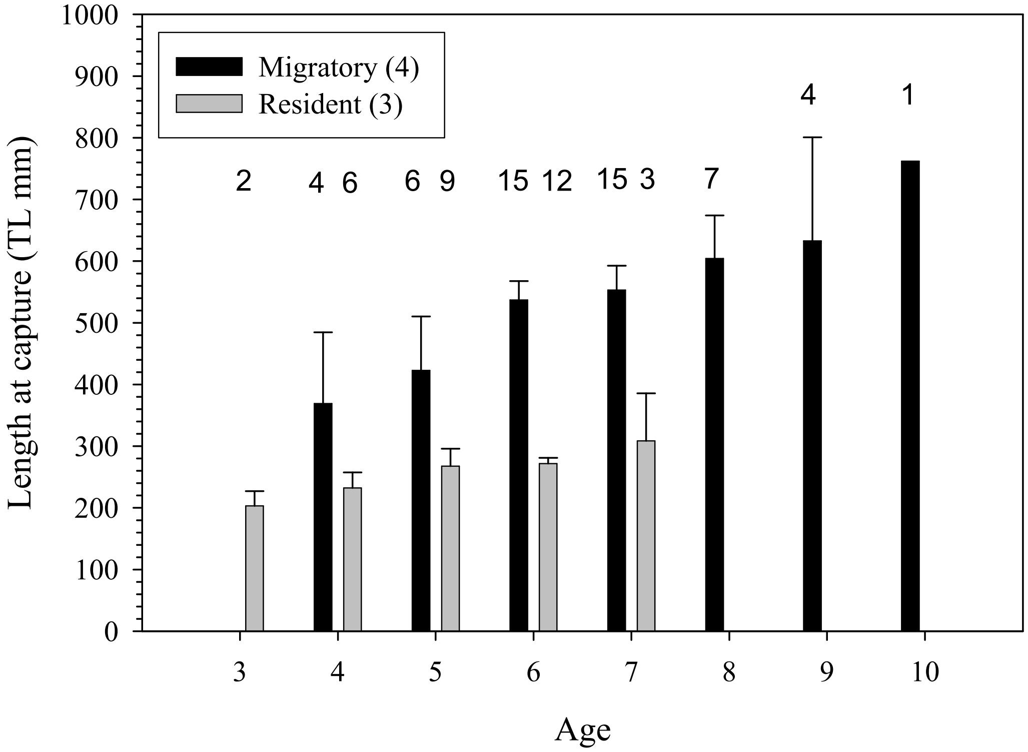


Figure 4.11. Length at capture for mature bull trout in autumn in four migratory and three resident populations. Bars indicate upper 95% confidence limit, *N* provided above bars. Number of streams provided in parentheses.

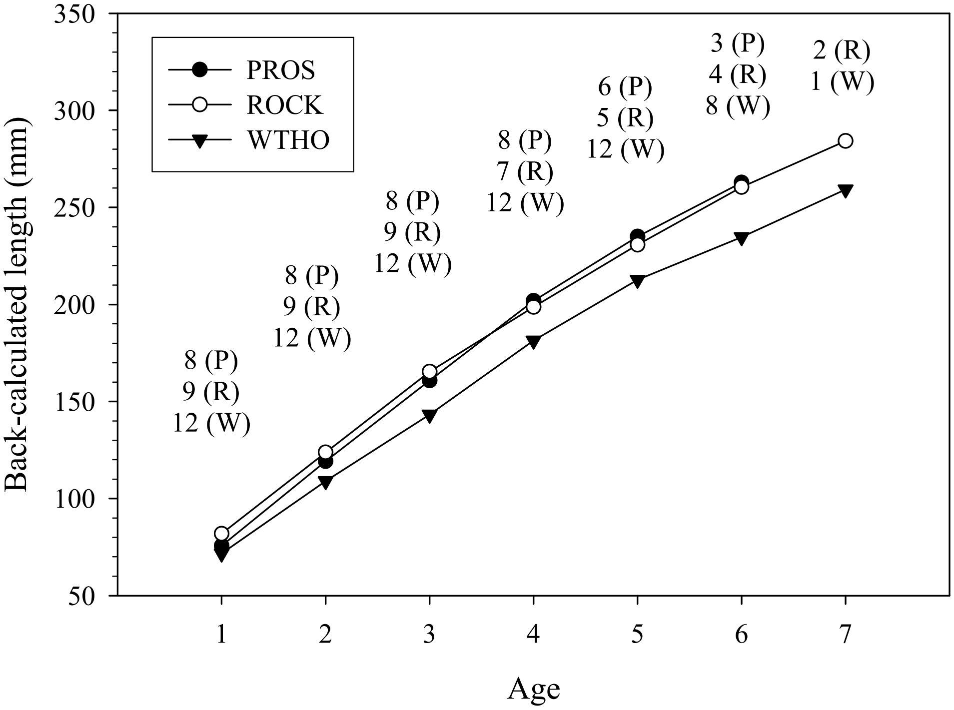
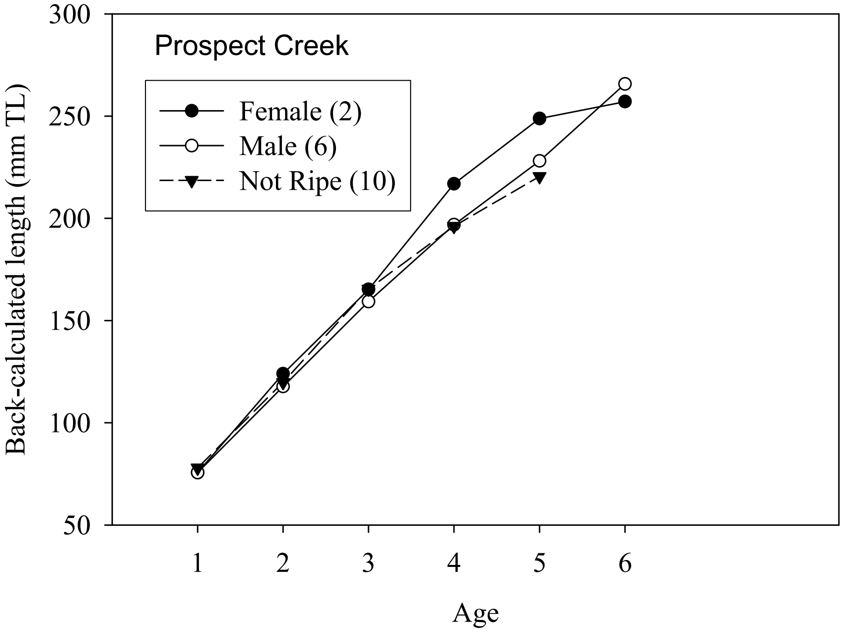


Figure 4.12. Mean back-calculated length at age for 29 mature resident bull trout in one mixed (WTHO = W) and two resident (PROS = P; ROCK = R) populations. *N* provided for each annulus and stream.



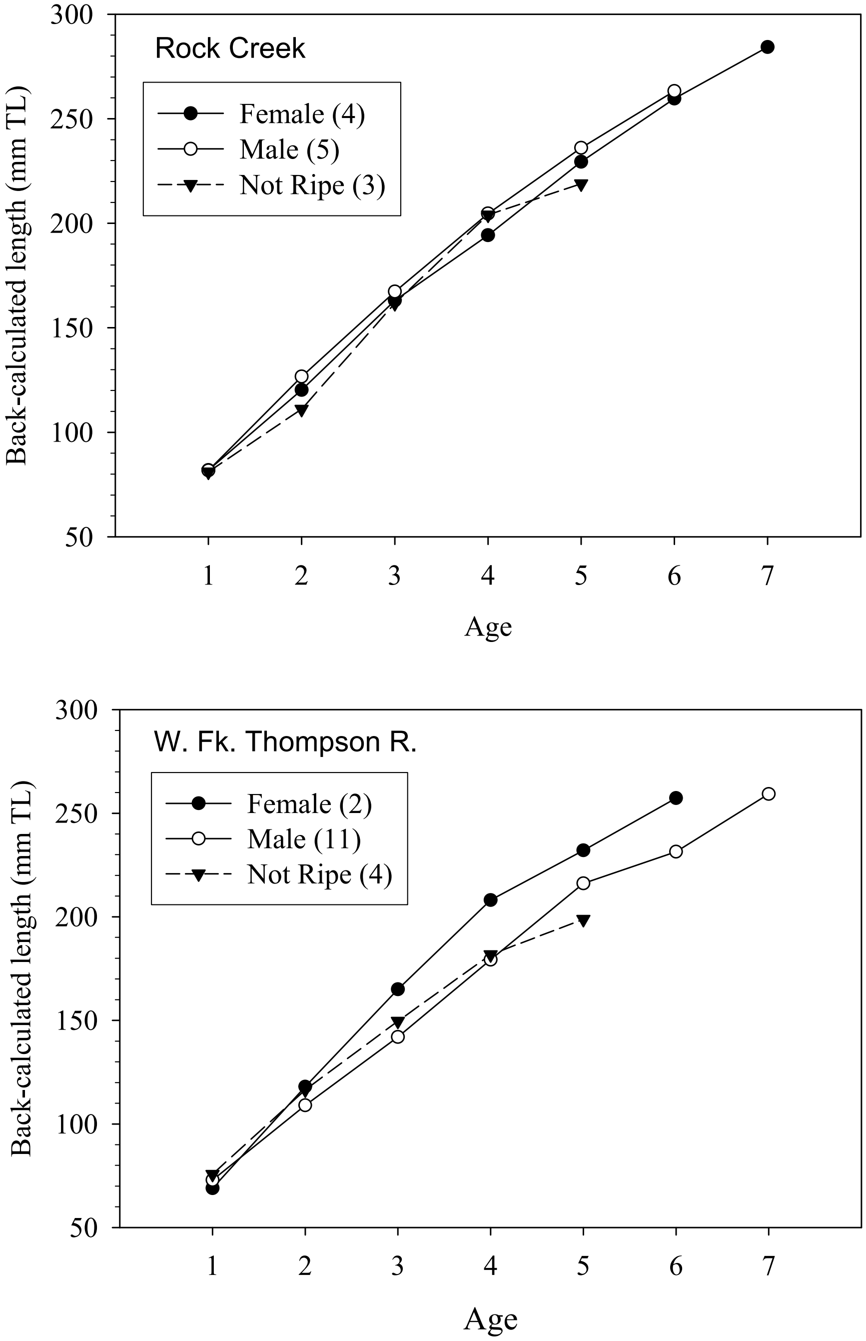


Figure 4.13. Mean back-calculated length at age for female, male, and apparently immature resident bull trout captured in autumn in three streams. *N* provided in parentheses.

Maturation in resident populations was positively associated with higher growth rates. Within each population, back-calculated lengths at ages 1 and 2 for mature residents significantly exceeded lengths at age for grouped ages 1 and 2 juveniles (Mann—Whitney *U*-tests: all $P < 0.03$). Although back-calculated lengths of immature individuals > 200 mm TL were similar to those of mature individuals at ages 1—4, lengths of immature fish at age 5 were consistently smaller at all three streams, suggesting that faster growing fish mature earlier whereas slower-growing ones remain immature for at least one additional year (Figure 4.13).

Biotic and Abiotic Habitat Covariates

Habitat conditions in reaches supporting juvenile bull trout showed considerable variation across the set of streams (Table 4.2) and longitudinally within streams. Watershed area fell into two distinct groups (< 9,600 ha, >19,000 ha). Nonnative brook and brown trout were absent in all sampled reaches of seven of the eleven streams where electrofishing was conducted, although previous surveys typically indicated their presence in lower tributary reaches or downstream water bodies. Temperature varied longitudinally along streams, with mean summer temperature measured by thermographs in lower reaches of six LCF streams 1.5 ± 0.3 º C (mean ± SE) warmer than corresponding values measured by thermographs in upper reaches (all thermographs situated within core bull trout rearing areas). Point measurements indicated a similar pattern, being 0.3 ± 0.1º C warmer at locations proximate to thermographs but 1.5 ± 0.2º C warmer at downstream sites in eight LCF and LPO streams. By comparison, the range of overall mean summer temperature values across all streams was only 2.0º C. Counterintuitively, the two temperature metrics, mean summer water temperature and length of growing season, indicated different effects (Spearman rank correlation, r = -

0.70). Macroinvertebrate biomass and conductivity, both considered indicators of biological productivity, were retained for relation to bull trout growth because they were only weakly correlated (*r* = 0.21).

Table 4.2. Mean values (unweighted) of habitat variables and barrier severity at each stream in 2003. Nonnative species presence indicates presence (P) or absence (A) of brook and brown trout within primary bull trout rearing areas and relative density (to density of bull trout) for streams where density information was available.

Stream	Macro-invertebrate biomass (mg)	Conductivity (µS/cm)	Mean summer temperature (ºC)	Growing season (days)	Bull trout density (#/100m)	Nonnative species presence	Watershed area (ha)	Barrier severity
BBIT	412	88.8	9.6	-	2.1	A	9529	2
EBUL	226	62.8	11.0	132	2.9	P (2.1)	5076	0
FTRP	318	149.6	10.0	155	1.3	P (0.1)	19483	1
GRAN	562	102.8	-	-	-	P	5965	1
GRAV	362	56.1	9.9	151	2.6	A	5124	1
JOHN	590	83.5	-	-	-	P	3683	1
PROS	133	24.3	10.5	126	4.3	A	4255	2
ROCK	405	13.5	9.9	154	2.8	A	3708	2
SKAL	1002	134.8	9.8	-	9.0	A	22817	2
SLAT	593	50.0	10.5	-	1.9	P (0.4)	4324	0
TRES	215	33.5	10.0	138	-	A	3437	0
TWIN	406	116.8	10.6	-	-	P	3192	0
VERM	587	55.2	9.0	183	0.8	P (1.1)	19379	0
WBIT	987	30.0	9.2	-	4.9	A	20883	0
WTHO	302	57.6	9.9	135	4.2	A	6613	0

Age-0 growth was most strongly related to length of growing season. Length of growing season was positively associated with growth and the only explanatory variable included in the forward stepwise procedure (Table 4.3). When growing season was excluded from analysis to maximize the number of included streams, no variable was significant. Age-1 growth of bull trout also was similar between tributaries having small and large watershed area, and between streams where nonnative brook or brown trout were present or absent (Table 4.4).

Table 4.3. Significant models explaining early growth of bull trout, developed using a forward stepwise regression procedure. Coefficient value indicates sign of relationship.

N streams	Variable	Coefficient	Coefficient SE	Coefficient *P*	*Model r^2*	Model *P*
			Age-0 growth			
7	Intercept	11.77	18.01	0.542	0.64	0.019
	Growing season	0.41	0.12	0.019		
			Age-1 growth			
7	Intercept	56.17	1.41	< 0.001	0.94	< 0.001
	Bull trout density	-3.3	0.37	< 0.001		

Table 4.4. Results of Mann—Whitney *U* – tests relating growth to binary environmental variables.

N streams	Variable	*U*	*P*
	Age-0 growth		
9	Watershed area	2.0	0.14
9	Nonnative species presence	11.0	0.81
	Age-1 growth		
7	Nonnative species presence	0.0	0.034
7	Watershed area	0.0	0.053

Age-1 growth was significantly related to bull trout density and presence of nonnative brook and brown trout (Table 4.3 and Table 4.4). The best model in the stepwise procedure included only bull trout density ($r^2 = 0.94$, $P < 0.001$, negative association). Age-1 growth was greater where nonnative competitors were present ($P = 0.020$) and also at sites having large watershed areas ($P = 0.053$).

Life history form was most closely associated with barrier severity and presence of nonnative brook and brown trout. All resident populations were found in upper stream reaches isolated from main-stem or lake habitats by low-head dams or extensive reaches of subsurface flow (i.e., barrier category 2), whereas migratory and mixed populations persisted only in stream reaches with minimal downstream barriers to migration (i.e., barrier categories 0 or 1; Table 4.2). Presence of nonnative competitors also differed among the three life history groups ($X^2 = 7.54$, df=2, $P = 0.023$), with brook and brown trout absent in core bull trout rearing areas in all four resident streams but present in six of seven migratory populations. Among mixed populations, brook and brown trout were absent at WBIT and WTHO but present at SLAT and VERM. These nonnative species did inhabit reaches downstream of the resident populations except at WTHO, where their presence was negligible throughout.

Discussion

Age structures and growth rates of bull trout in this study generally resembled those reported for other populations in the region. As expected, tributaries supporting migratory populations held relatively few bull trout during summer older than age 3 (Ratliff et al. 1996; Rieman and Macintyre 1993; Fraley and Shepard 1989; Mogen and Kaeding 2005a), whereas streams supporting the resident life history contained greater proportions of older fish. Early growth at most study streams was comparable to observations in the Flathead and St. Mary's drainages in Montana, and Priest Lake in Idaho (Bjornn 1971; Fraley and Shepard 1983; Mogen and Kaeding 2005a). Out-migration primarily at ages 2 and 3 conformed to previous reports for migratory populations (Fraley and Shepard 1983; Ratliff et al. 1996; Mogen and Kaeding 2005a). Estimated ages at juvenile out-migration for the set of returned migratory adults (range = 2—4, mode = 3) concurred with the results of a recent study using otoliths extracted from spawning mortalities at Trestle Creek (Downs et al. 2006). Ages of the majority of mature adults ranged from 5 to 7, as is typical of the species (Fraley and Shepard 1989; Ratliff et al. 1996; Mogen and Kaeding 2005a).

Exceptions to these typical observations tended to be associated with the resident life history. Atypical age distributions of out-migrants in study streams having largely resident populations may have indicated the influence of density dependent emigration than innate migration tendency (Chapman 1996). Mature residents demonstrated an overall younger age distribution than did migratory adults partly because the resident collection included a relatively high ratio of males to females (2.75:1), whereas ratios of migratory individuals may be more even or skewed toward females (McPhail and Murray 1979; Fraley and Shepard 1989; Downs and Jakubowski 2003). Males matured earlier than females and comprised a greater proportion of the collection of spawning individuals in resident populations. Residents first matured at sizes within the typical 200—400 mm range, but none were found within the 150—200 mm range reported for ripe males and females at some other locations (Bellerud et al. 1997; James and Sexauer 1997).

Barriers to migration exerted the most obvious influence over life history form. All four of the entirely resident populations were physically isolated rather than elective (or facultative) in nature (McCart 1997), occupying upper tributaries above extensive reaches of subsurface flow or water diversions. Such fish passage barriers present a potential source of mortality to out-migrating juveniles (May and Lee 2004) and exhibited greatest severity during base flow periods in late summer and autumn when most migratory bull trout enter spawning tributaries (Fraley and Shepard 1989; Ratliff et al. 1996; Swanberg 1997) and a pulse of juvenile bull trout may emigrate (Katzman and Hintz 2003; Liermann 2003; Lockard et al. 2003a; Downs et al. 2006). By contrast, the presence of elective residents (McCart 1997) was minimal where migratory adults returned in relatively high numbers. Also, whereas migratory individuals were found at all of the study streams lacking migration barriers (*N* = 11), evidence for an elective resident component was limited to the four ‘mixed’ streams where dams and associated reservoir conditions possibly restricted the success of the migratory life history. Thus, where migration offers reasonably high rates of return, the migratory form dominates and, in contrast to other salmonids, alternative mating tactics (i.e., sneaker males) and early maturation appear to offer little comparative advantage (Gross 1991). Interestingly, the absence of bull trout above permanent barriers (waterfalls) in the study area suggests either that bull trout populations never inhabited these sites or that complete isolation presents little chance of long term persistence for bull trout (Dunham and Rieman 1999; Morita and Yamamoto 2002).

Barriers also appeared to influence the association of bull trout life history form with presence of competitive nonnative species. Brook and brown trout were absent in primary reaches of resident bull trout occurrence at all but two streams, both of which contained mixed compositions of life histories (Slate Creek and Vermillion River), whereas these nonnatives were present at most migratory sites. Extensive reaches lacking surface flow on Prospect and Rock creeks apparently restricted upstream invasion and a selective barrier on the Vermillion River (China Gorge) constrained upstream passage of brown trout but not bull trout. In Bitterroot drainage streams, the lack of barriers between resident populations and nonnative species points to the probable importance of other habitat conditions that offer comparative advantage to bull trout (Paul and Post 2001; Rich et al. 2003). However, barriers at the two entirely resident sites in the lower Bitterroot drainage may restrict the detrimental effects of nonnatives by preventing upstream invasion of greater numbers or of larger fluvial forms. Only one stream in this study (West Fork Thompson River) lacked a migration barrier and contained both a resident bull trout component and negligible numbers of brook or brown trout.

The relationship of early growth to life history was inconsistent across sites. Within the migratory population showing slowest growth (EBUL), age-0 growth of out-migrants significantly exceeded that of electrofished individuals in the same cohort, and the collection of age-2 fish consisted of individuals that were relatively slow-growing during age-0, providing evidence that faster growth leads to earlier migration (Metcalfe et al. 1993; Morinville and Rasmussen 2003). Conversely, growth rates were slow at WTHO, where the proportion of resident to migratory adults was large and no barrier to migration was present. However, within resident populations, faster growth was also associated with earlier maturation. Higher rates of early growth among mature residents than among the collection of age-1 and age-2 juveniles at resident streams suggested a positive relationship between growth and residency, although results may also indicate size-selective survival or interannual variation. Samples collected from the year 2001 cohort in Prospect Creek in 2002 and 2003 pointed to either reduced emigration or better survival of larger individuals. Larger size of mature residents than of immature fish at age 5 also indicated that slower growing individuals delay maturation, as has been reported for white-spotted char (Morita and Morita 2002). Among the three populations where capture of mature residents was focused, higher growth rates were positively associated with earlier maturation. These findings point to the existence of a critical threshold size for maturation; however, no evidence was found to suggest that slower growth or reduced fitness was linked to migration.

Inconsistencies in these patterns across the full set of streams indicated a responsiveness of growth to environmental conditions, as did analyses revealing strong relationships of early growth to bull trout density, length of growing season, presence of nonnative brook and brown trout, and watershed area. One plausible interpretation is that these relationships reflect the availability of lower elevation habitats at streams having migratory populations, whereas most resident populations occupied only upper stream reaches having relatively high densities, small watershed areas, and short growing seasons. Previous investigation has indicated a negative relationship between early growth and total abundance of bull trout (Paul et al. 2000), but whether slow growth causes residency or rather arises as a corollary to higher densities or shorter growing season is unclear. Unfortunately, growth was determinable at an insufficient number of sites to permit more in-depth assessment in regression analyses of its relationship to life history. Interestingly, this pattern of high densities and slow growth in resident populations conflicts with observations for the white-spotted char, in which adoption of the resident life history above barriers was attributed to faster growth related to low densities (Morita et al. 2000).

Analysis of early growth differences among resident and migratory juveniles and adults from mixed populations was restricted by back-calculation limitations and resolution of field surveys. Differences in the body length—structure radius relationships for resident and migratory forms prohibited the use of back-calculation with structures collected from adults to compare early growth of sympatric resident and migratory of bull trout (Chapter 3). Relative proportions of resident and migratory individuals appeared to vary widely in mixed populations. For example, trapping data and analyses of fin rays and scales suggested that some resident-sized individuals in the Vermillion River may have undergone short-term migration (e.g., movement downstream for overwintering or upstream for thermal refuge in summer). By comparison, in the West Fork Thompson River, where fin rays evidenced slow tributary growth, resident adults were relatively abundant and migrants rare. Overall, the composition of migratory and resident forms was difficult to estimate with reasonable accuracy in mixed populations. Designation of life history relied partially on length frequency distributions and analyses of structures obtained during electrofishing surveys conducted prior to the spawning period, as trapping and autumn snorkeling efforts were too labor intensive to conduct at every site. Patchy distributions, presence of impassable barriers (Downs and Jakubowski 2003, Katzman 2003; Mogen and Kaeding 2005b), exploratory behavior, and spawning site infidelity (O'Brien 2001) all could alter perception of life history characteristics of a population. Moreover, the reproductive contribution of each form may differ as a result of fecundity, egg size, redd construction characteristics, or fitness of offspring.

A combination of factors ultimately led to smaller sample sizes than initially anticipated. First, because of intercohort and interannual variability, isolation of the most recent complete growth increment was necessary in order to compare populations and relate growth to environmental variables (Gutreuter 1987; Quist and Guy 2001). Back-calculation of all available growth increments for each individual, a practice commonly used to increase sample sizes (DeVries and Frie 1996), was inappropriate because of potential confounding by size-selective factors, the aforementioned back-calculation issues with resident and migratory forms, and interannual variation in abiotic and biotic habitat conditions, particularly given the observed differences in age structures and out-migration tendency between resident and migratory populations. Second, low abundances, patchy distributions, and trap inefficiency inhibited sample collection at many sites. Third, quality of fin ray samples was poor overall and many fin samples proved unusable, primarily because of excessively distal excision of fin rays. Previous papers reporting the use of salmonid fin rays noted the importance of excising rays as close as possible to the body (Shirvell 1981; Chilton and Bilton 1986), but quantitative criteria or an ageing validation study specific to bull trout were unavailable, and the concept of proximity to the body was found to carry a high degree of subjectivity among the numerous workers who collected samples in the field. Previous studies examining fin rays of bull trout used wholly intact fins removed from sacrificed bull trout (Williamson and MacDonald 1997; Gust 2001), and preliminary samples collected for this study were removed from mortalities gave an initial impression of substantially better sample quality than was subsequently found with excised rays. Small size of age-1 bull trout made proximal excision of only the leading few fin rays challenging in a field setting. Also, cutting rays in the field produces an uneven, fractured edge, and an additional length of ray was lost to trimming using the sectioning saw before achieving the first acceptable cross-section. With large individuals, acquisition of a suitable sample may require pushing against the abdomen and cutting through the relatively thick skin tissue obscuring the base of the rays or pulling a few entire rays. I found adequate samples to be readily obtainable from individuals <400mm TL, and I provide detailed criteria in Chapter 3 for assessing whether sections are proximal enough to include the first annulus, but additional work is required to better specify the proper technique for non-lethally obtaining pelvic ray samples from larger individuals.

Management recommendations and research needs

Results of this study provide indication that the migratory life history may be encouraged through management actions. In general, migratory populations exhibited faster early growth than resident populations, and growth itself was related negatively to bull trout density and positively both to watershed area and length of growing season. Reduction of barrier severity (i.e., excessive sediment, diversions) and improvement of rearing habitat in lower stream reaches could conceivably produce gains in all three factors by opening greater lengths of stream in lower watersheds and enhancing potential for movement among habitats. Efforts to increase production of out-migrants will provide little benefit, though, if emigration to productive downstream growth environments functions as an ecological trap (Battin 2004) and offers limited rates of survival and return. Preservation and establishment of resident populations deserves consideration as integral to maintenance of the full range of life histories across the landscape (Rieman and McIntyre 1993).

Greater resolution of the influences of genetics and environmental conditions on life history requires further study. Transplant or reciprocal cross studies should be conducted, guided by the large body of work that has been conducted on char species and other salmonids. Greater insight into factors affecting life history variation could be attained through a larger scale (e.g., > 30 populations) study assessing environmental variables at sites where available data indicates a predominantly resident or migratory life history. Age and growth assessment using bony structures of bull trout potentially provides useful information, but a true validation study is necessary for bull trout, particularly given the inherent difficulties characteristic to this species. Finally, alternative methods of detecting out-migration, perhaps involving electronic tag detection, telemetry, or use of alternative passive capture gears in downstream locations, should be investigated to assess movements during high flow periods when standard weir and screw traps prove inoperable.

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CHAPTER 5

CONCLUSIONS

The purpose of this research was to determine relationships among age structure, growth rate, life history, and environmental conditions in bull trout populations in the Clark Fork drainage of Montana and Idaho. I conducted a supporting laboratory investigation to evaluate the effects of pelvic fin ray excision on bull trout survival and growth. Additionally, I performed a series of tests to establish methodology for preparation and analysis of fin rays and to compare results to those obtained using scales and otoliths.

Effect of Pelvic Fin Ray Removal on Survival and Growth of Bull Trout

The sensitive status of bull trout limits the applicability of adverse sampling techniques. Although removal of fin rays is generally considered to be non-lethal based on investigations of complete or partial fin removal in other species, I conducted an investigation to gain additional information specific to the effect of fin ray excision on bull trout. Excision of the leading three rays (about one-third of the area) of one pelvic fin had no apparent effect on survival and growth of bull trout. Rates of survival and growth of fin-excised and control fish were nearly identical over the six-month period within both age classes examined. Mortality was high (64%) among age-3 fish, limiting the power of statistical tests within that group, but low (6%) among age-4 fish. Higher mortality of the younger, smaller fish most likely resulted from greater susceptibility to infection by bacterial coldwater disease. Regardless, mortality was equal between test groups within both age classes and indicated no detrimental effect from fin excision. Fin-excision wounds appeared to heal completely in most individuals by day 127. Excised rays regenerated normally in 92% of individuals and attained a mean 42% of estimated complete length by day 169.

The results of this study resembled those of numerous previous studies in which effects of fin clipping were negligible. However, the effect of fin excision may vary according to factors such as species, size class, fin, and amount of fin removed. This study included only bull trout ranging from 200—365 mm TL, and larger or smaller individuals could potentially be more adversely affected. Also, this study was conducted in a controlled laboratory setting, and the effect of fin excision in nature might be more severe because of stress from factors such as competition, predation, and exposure to pathogens. Nonetheless, fin excision proved non-deleterious in this investigation, supporting the contention that fin rays represent a non-lethal alternative to internal bones as structures for use in age and growth analyses.

Use of Pelvic Fin Rays to Estimate Age and Growth of Bull Trout

Previous studies have indicated that fin rays provide relatively high precision for estimating age of bull trout, but little information was available specific to preparation and interpretation of fin rays, particularly those collected in a field setting. Therefore, I performed several tests to establish methodology and evaluate the information gained from analysis of pelvic fin rays of bull trout. Based on these tests, I found fin rays to offer relatively high precision and accuracy, although samples from large fish presented some difficulty.

A primary challenge in the use of excised fin rays results from variability in the longitudinal point of excision (i.e., proximity to the body). Standardization of samples to maximize accuracy and comparability was achieved though examination of overall morphology and internal features. Morphology of transverse sections indicates relative proximity to the base of the ray and internal markings provide evidence as to the distinctiveness of the earliest annuli.

Fin rays provided better accuracy and precision of age and growth estimation for juvenile and resident bull trout than did scales. In general, fin rays showed more distinctive annuli than scales. Using tag and recapture samples, I established the most appropriate measurement technique and back-calculation formula for fin rays by evaluating a combination of accuracy and consistency criteria, and I found accuracy to be relatively high in comparison with values reported for other species and techniques. However, these results were obtained using tributary resident bull trout < 300 mm TL and back-calculation of values one year into the past.

Use of fin rays to estimate age and growth of large migratory bull trout requires further research. The relationship between body length and fin ray radius demonstrated a shift corresponding to migration and the relation was variable among individuals. Thus, the accuracy of back-calculation for large individuals and the level of comparability to results obtained for resident fish needs validation. Further, the pattern of annulus formation after out-migration from tributaries varies among fish, sometimes presenting difficulty in interpretation, and also requires validation. However, despite complications with fin rays, the scales and otoliths from these large migratory fish presented similar levels of difficulty.

Age Structure, Growth, and Factors Affecting Relative Abundance of Life History Forms of Bull Trout in the Clark Fork River Drainage, Montana and Idaho

Bull trout exhibit flexible life histories, but the mechanisms driving this flexibility have not been adequately defined. I used pelvic fin rays and scales to estimate age and growth of bull trout in populations supporting predominantly migratory, resident, or mixed life histories, and I related this information to potentially influential biotic and abiotic variables. In spite of a high frequency of unusable samples, this approach proved useful in providing substantial information on the characteristics of these populations and the factors influencing life history.

Barriers to migration and presence of nonnative brook and brown trout most strongly influenced life history. All four entirely resident populations, but no migrants, occupied reaches where extensive sediment deposition or irrigation diversions severely inhibited fish movement between tributary rearing areas and the main stem. Nonnative brook and brown trout were absent from core bull trout reaches at these sites, their abundances possibly limited by presence of barriers. However, the presence of brook trout above barriers but downstream of resident populations at two of these sites indicates the importance of other habitat variables (e.g., temperature, habitat complexity) in the persistence of resident bull trout.

Age structure and early growth rates generally differed between resident and migratory populations. Migratory populations held greater proportions of age-1 fish and fewer individuals > age 3 during summer than did resident populations. However, samples indicated fairly large interannual fluctuations in cohort strength. Age structure of out-migrants in migratory populations (typically dominated by ages 1—3) differed from those in populations supporting a strong presence of residents, potentially reflecting genetic selection against out-migration in resident populations. Early growth rates in migratory populations tended to exceed rates in resident populations, although not without exception. Age-0 growth was positively associated with length of growing season, whereas age-1 growth was negatively associated with density of bull trout. Age-1 growth was also greater in tributaries where nonnative brook or brown trout were present and greater in tributaries having large watershed areas above the core bull trout reaches.

The ability to test the early growth hypothesis was constrained by limited success in establishing and comparing growth records of sympatric forms. Few adequate samples were obtained from migrants at sites supporting both forms, and the comparability of early growth estimates back-calculated using structures obtained from resident and migratory adults is dubious. Better resolution of the relationship between early growth, migration tendency, and inheritance requires the completion of transplant or laboratory rearing experiments.

A comprehensive assessment of the results of this study suggests that the migratory form might be encouraged through reduction of severity of downstream migratory barriers and enhancement of bull trout rearing habitat in lower reaches. Lower tributary reaches potentially provide conditions for high early growth rates through longer growing seasons and lowered densities (a function of larger stream channels and greater rates of out-migration). Although resident populations may produce fewer out-migrants of ages 2 and 3, the out-migration ages most typical of returned adults, observations of migratory adults downstream of barriers below resident populations in autumn suggest a high potential for the migratory form to return naturally. Of course, success of the migratory form relies on adequate rates of survival in downstream waters (i.e., main stem rivers and lakes) as well as on the production of out-migrants. The risks to resident populations presented by invasion of nonnative salmonids upon barrier removal also deserve consideration.

APPENDICES

APPENDIX A:

PELVIC RAY SECTION RATING CRITERIA BASED ON MORPHOLOGY

Variability in the longitudinal point of excision requires the use of criteria to standardize fin ray samples. To develop such criteria for pelvic rays of bull trout, I analyzed consecutive transverse sections of pelvic fins from nine bull trout ranging from 79—660 mm TL. Samples were obtained primarily from mortalities, and the curved, rounded ends indicated that complete rays were included. At least seven consecutive sections were cut from each fin sample, beginning at the proximal end. Consecutive sections were separated by the blade width of 0.5 mm, and the thickness of sections averaged about 0.3 mm.

Fin rays (particularly the larger, ventral hemisegment) showed a consistent morphological progression in all fish, being round at the proximal end and distally widening and flattening toward the tips. Based on initial inspection of the cross sections, I subjectively classified sections as being from one of five reasonably distinct regions of the ray, R1—R5 (Figure 1):

R1 = circular shape, (most proximal end of complete ray);
R2 = dorsal edge indented with associated “arms” (Ferreira et al. 1999) about equal in length; indentation less than half of total height of hemisegment;
R3 = major and minor arms unequal in length; dorsal indentation more than half of total height of hemisegment; roughly comma-shaped;
R4 = arms exaggerated, wide “U” shape;
R5 = shallow “W” shape with arms divided into two separate parts.

The length of fin ray characterized by each morphology rating increased with body length, with several cross sections rated R1 or R2 obtained for the largest fish but typically only one or two sections of each rating R1—R4 obtained for the smaller fish.

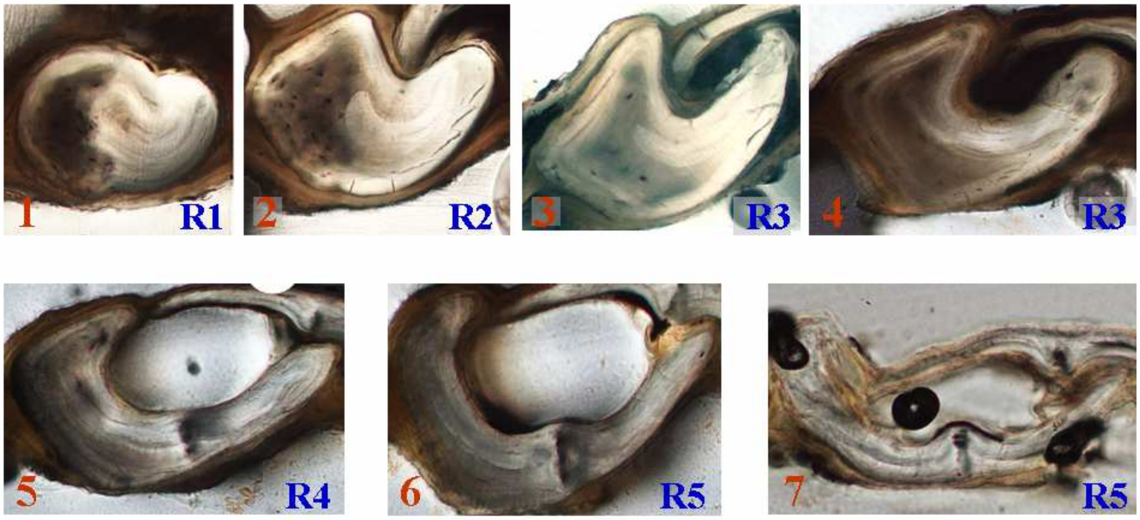


Figure 1. Consecutive transverse sections of third pelvic ray of a bull trout (138mm TL, age 2, captured in May at beginning of growing season) in progression away from the body. Lower left number in each photo indicates cross section number (1 - 7); letter in lower right indicates morphology rating (R1– R5).

APPENDIX B

EFFECT OF LONGITUDINAL POSITION ON AGE AND GROWTH ESTIMATION

To determine the effect of longitudinal position of the fin ray cross section on age estimation, I examined transverse sections showing successive morphologies R1—R5 from each of nine bull trout (range = 79—660 mm TL). All sections for each fish were first assigned a single age based on collective inspection of all sections. Three weeks later, each section was again aged, but in random order and using random numeric identifiers to prevent the reader from associating various sections of each sample. Difference between estimated age at first and second readings was used to detect patterns in interpretability across morphologies.

I investigated the influence of longitudinal position of the fin ray cross section on growth estimation by comparing back-calculated lengths at age among sections of morphologies R1—R4. To test for differences among regions, I used a repeated measures ANOVA, with all annuli pooled, and Tukey's pairwise comparisons. The intercept correction (Fraser-Lee) technique (DeVries and Frie 1995) was used for back-calculation (Appendix B):

$$[L_A = a + (L_C - a)(R_A/R_C)]$$

where

L_A = back-calculated length at annulus A,

a = intercept from body length—fin ray radius regression,

L_C = total length at capture,

R_A = fin ray radius at annulus A, and

R_C = fin ray radius at capture.

The effect of region on ageing precision differed between fish greater or less than 360 mm TL. For bull trout less than 360 mm, (79—360 mm TL, *N* = 7), first and second readings agreed for 100% of region R1 comparisons, 86% for regions R2, R3, and R4, and 71% of region R5 fin ray samples; in all cases, the difference in estimated ages was one year. Discrepancies resulted from difficulty resolving the innermost portion of the ray. For bull trout greater than 400 mm, (480 and 660 mm), only sections from regions R1 and R2 were suitable for ageing. Multiple sections were obtained from each region and consecutive sections within each region differed in quality. Early annuli in rays from these large individuals were indistinguishable in sections of region R3—R5, in which the central portion of the ray appeared as a relatively large hyaline area. Overall, growth bands were most distinct in the ventral and anterior portions of the ray but often discontinuous and difficult to resolve in the posterior portion of rays from all but the largest fish. Thus, with increasing body length, adequate representation of early annuli requires sections from more proximal regions.

Four common marks complicated discrimination of annuli. Fractures restricted the usefulness of the posterior field of rays in about one-half of samples, and their presence was not reduced by adjusting weight or cutting speed during sectioning (Figure 1A). A thin crescent-shaped mark was present in the nucleus of sections from regions R1—R3 from individuals <150mm TL (Figure 1A). Although this mark could be misinterpreted as the age-0 opaque zone, it appeared as a thin line within the nucleus rather than as an opaque zone surrounding a core area. False annuli were observed in rays from about 1/3 of the individuals and were generally distinguishable from true annuli by their thinness, visibility over a smaller portion of the ray, and presence in some cross sections but not others (Figure 1B). Finally, a dark "dash" in the nucleus, oriented perpendicular to annuli, was apparent in distal sections of each ray (Figure 1C). The dash was first visible in sections of region R5 from the smallest fish, but in sections of region R2 from the largest fish. In rays from the smallest individual examined (age-1, collected in spring at beginning of formation of opaque zone), this mark was first visible in the seventh cross section and corresponded to division of the hemisegment into two extremely thin, symmetrical components, as consistent with branching of the ray (Ferriera et al. 1999). In the distal portions (R4, R5) of rays from large fish, additional dash marks appeared to subdivide each of the halves associated with the first, central dash. These observations suggest that confidence in the accuracy of age estimates requires use of sections in which the dash mark is absent (regions R1—R4 for age-0 and age-1individuals, but only region R1 for large or old fish), as its presence indicates a high likelihood that the earliest annulus or annuli are indistinguishable. Also, analysis of more than one section from each fish may help to alleviate the influence of confounding marks.

Back-calculated length at age, including all annuli ($N = 88$) on fin ray sections from six bull trout 122—360 mm TL, differed among fin ray regions (Figure 2) (ANOVA: $F = 6.11$, df = 3, $P = 0.001$). Pairwise comparisons indicated significant differences for three pairs of regions (R1—R2: $P = 0.002$; R1—R3: $P = 0.01$; R2—R4: $P = 0.04$). Sections of morphologies R2 and R3 produced the most similar back-calculated lengths, varying less than 3%, whereas all other combinations varied 4.9-6.2% (Figure 2). These results suggest that if sections of region R2 are not available for all fin ray samples, variability may be minimized by restricting back-calculation to sections of regions R2 and R3 from bull trout less than about 360 mm TL.

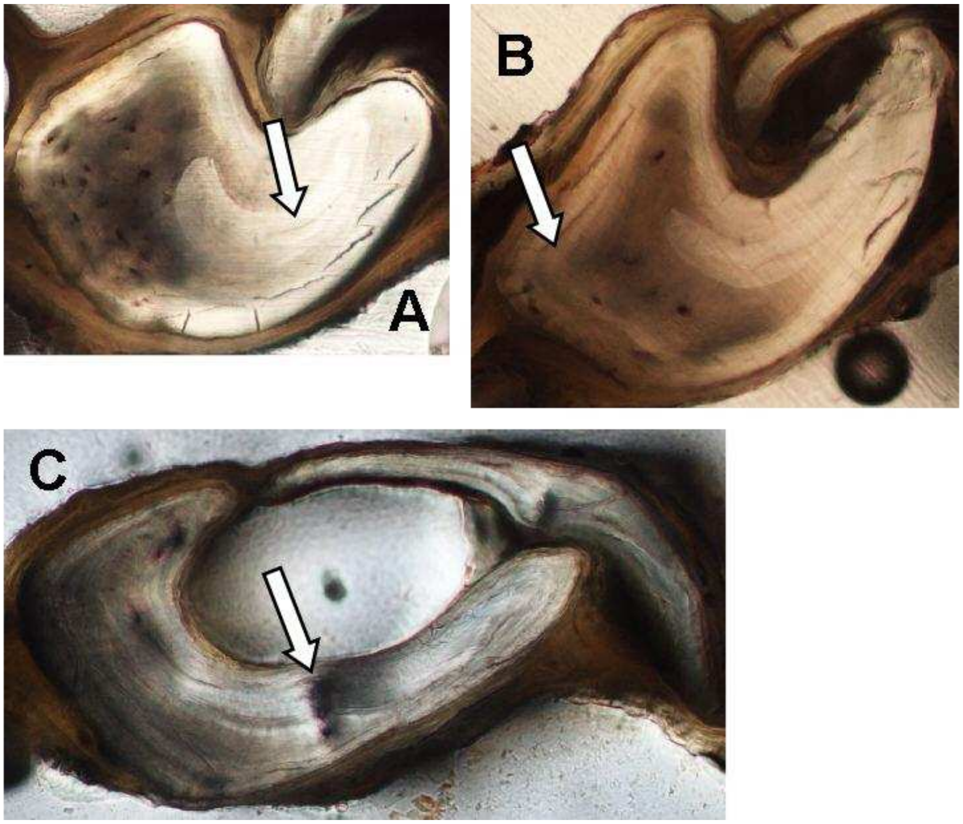
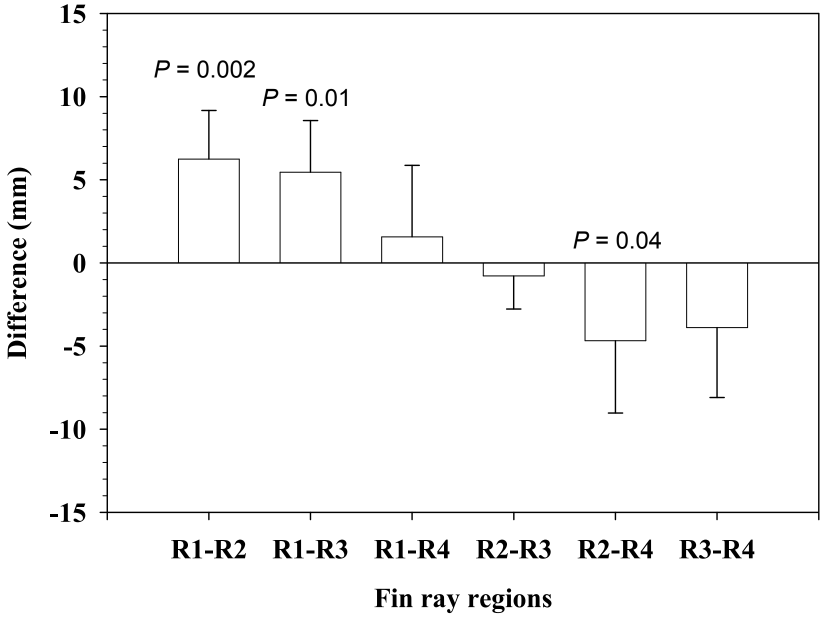


Figure 1. Extraneous marks on three sections of a pelvic ray from a bull trout (138 mm TL) captured from Trestle Creek during May, 2002. Arrows indicate crescent-shaped mark in nucleus (A), false annulus (B), and center dash (C). Relatively minor fractures are visible to the right of the nucleus in A and B.



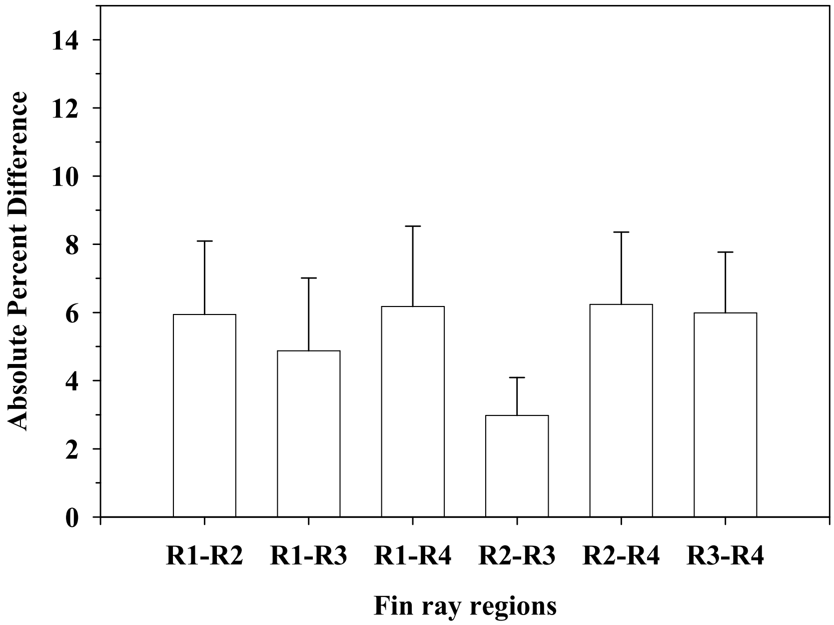


Figure 2. Real (top) and absolute (bottom) percent difference (mean + 95% C.I.) in back-calculated lengths at age between cross sections from different regions of individual fin rays. Includes all annuli (*N* = 88) on ray sections from six bull trout 122—360 mm TL

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APPENDIX C

COMPARISON OF AXES FOR MEASURING FIN RAY CROSS SECTIONS

Published literature offers little guidance on the use of soft rays for back-calculation. The longest axis has been generally recommended for measurement (Jearld 1983), but this portion of the pelvic fin ray (minor arm) is poorly defined in bull trout (Appendix 1). In studies of white suckers *Catostomus commersoni*, measurement of pectoral rays extended to the tip of the shorter but wider arm (Chen 1991; Mills and Chalanchuk 2004), but a curved trajectory would be necessary to follow the corresponding trajectory (major arm) in bull trout pelvic rays. Back-calculation in these studies was conducted using the Fraser—Lee method, and analyses of mark—recapture samples from suckers at liberty for 1—3 years produced overall mean error of 1.02 mm, absolute error of 7.6 mm, and no significant differences between actual and back-calculated lengths (Mills and Chalanchuk 2004). Dorsal rays have been used with the Fraser—Lee method and measurements along the longest axis for river carpsuckers (Braaten et al. 1999) and with the direct proportion method for bighead carp (Schrank and Guy 2002). Validation was not reported in either of these studies. No published studies have reported on back-calculation using fin rays from chars *Salvelinus* spp. or using pelvic rays from any species.

Body—Structure Relation

To determine relative suitability for back-calculation, I first assessed the relationship between body length and fin ray radius for three axes of measurement (Figure 1). These axes were selected because annuli were generally distinct, the fin ray was usually intact, and distances could be measured along a straight line from the nucleus. Least-squares linear regression was performed using 36 samples of region R2 or R3 from the tag—recapture set described in Chapter 3. Additional regressions were then performed after adding 12 samples from bull trout < 120 mm TL from the juvenile out-migrant sample set and also after further addition of 15 samples from the large adult sample set. Separate regressions were performed to identify effects of fish size and life history on the body—fin ray radius relation. Regressions were performed both with non transformed and $\log_e$ transformed data. Although regressions of body length on structure radius ideally involve equal representation of samples across the range of sizes and include samples all collected at the same time of year (Ricker 1992), the purpose of this analysis was obtain parameters required for initial development of back-calculation methodology using available samples.

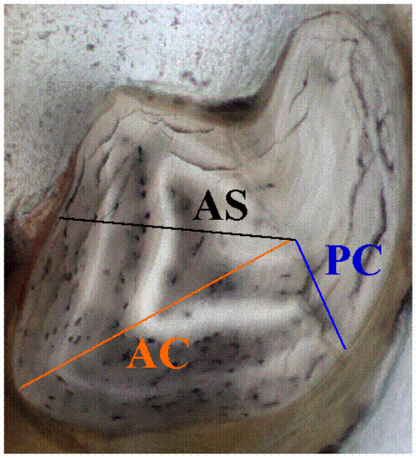

Figure 1. Cross section of pelvic fin ray showing three axes of measurement for back-calculation.

The highest coefficient of determination was obtained with the AS measurement axis in all cases except the non transformed "T—R + small + large" set, in which PC produced a marginally higher value (Table 1). Sets of calculations that did not include samples from large fish produced y-intercept values for AC and AS that were relatively close to the reported length at pelvic ray formation of 22 mm (Gould 1987), but the y-intercept for PC (56.2) was much higher and its use would preclude back-calculation of smaller lengths using the intercept correction method. $\text{Log}_e - \log_e$ transformation typically reduced the y-intercept value, whereas the effect on r^2 values was inconsistent and only minor. Expanding the size range of included fish increased r^2 values without exception and reduced the magnitudes of differences among axes; however, inclusion of samples from large bull trout introduced non-linearity into the relations for AS and AC and resulted in substantially increased variance at the upper portion of regressions for all three axes (Figure 2). $\text{Log}_e - \log_e$ transformation increased linearity and reduced heteroscedasticity for the AS and AC sets that included large fish.

These results suggest that both non-transformed and $\log_e - \log_e$ transformed Fraser—Lee back-calculation techniques are potentially appropriate for use with bull trout up to about 300 mm TL, a length range consistent with juvenile bull trout and most individuals in resident populations. The AS axis produced the highest r^2 values, although differences among axes were small when a relatively wide distribution of lengths was included. However, non-linearity in the relationship for larger bull trout (typically migratory populations) indicated the necessity either for use of transformed variables (Potts et al. 1998; Wilson et al. 2003) or for a more complex method that accounts for distinct growth stanzas (Frost and Lowry 1981; Laidig et al. 1991). All three axes produced high r^2 values after $\log_e - \log_e$ transformation, suggesting that further evaluation of the results of back-calculation for each axis is warranted.

Table 1. Body–structure relationships for three fin ray measurement axes, using three sets of samples with varying length ranges. Log_e transformations were performed on both length and radius. Listed y-intercept values for transformed relationships were back-transformed for comparison purposes. Bold values indicate relations from which y-intercept values were used as correction parameters in comparisons of accuracy and consistency of back-calculation among axes.

		AS axis		PC axis		AC axis	
Sample set	TL (mm)	r^2	Y-int.	r^2	Y-int.	r^2	Y-int.
Tag–Recapture	100-265	0.87	15	0.82	59	0.79	27
($\log_e$)		0.87	11	0.77	38	0.78	12
T–R + small	52-265	**0.93**	**11**	**0.90**	**53**	**0.88**	**21**
($\log_e$)		0.94	11	0.91	38	0.88	12
T–R + small + large	52-775	0.94	-47	0.96	45	0.92	-58
($\log_e$)		**0.96**	**6**	**0.95**	**28**	**0.93**	**6**

Back-calculation

Accuracy and precision of back-calculation for the three axes of measurement was tested using the tag—recapture samples and procedures described in Chapter 3. The Fraser—Lee formula (Appendix B) was used with non-transformed data. Calculations were also made using a modified formula with $\log_e$—$\log_e$ transformed variables {$L_A = \exp[a + (\log_e L_C - a)(\log_e R_A/\log_e R_C) + \text{MSE}/2]$, where MSE = mean square error from the body-fin ray regression, used to correct for transformation bias} (Potts et al. 1998; Wilson et al. 2003). Calculations were made using intercept parameters from the body—structure regressions that included samples from the tag—recapture set with additional small bull trout (herein noted as 'AS', 'PC', and 'AC'; see Table 1 for intercept parameter values). Sets of calculations were also made with parameters derived with additional large fish ('AS *', 'PC *', and 'AC *') to investigate the effects of including data from large

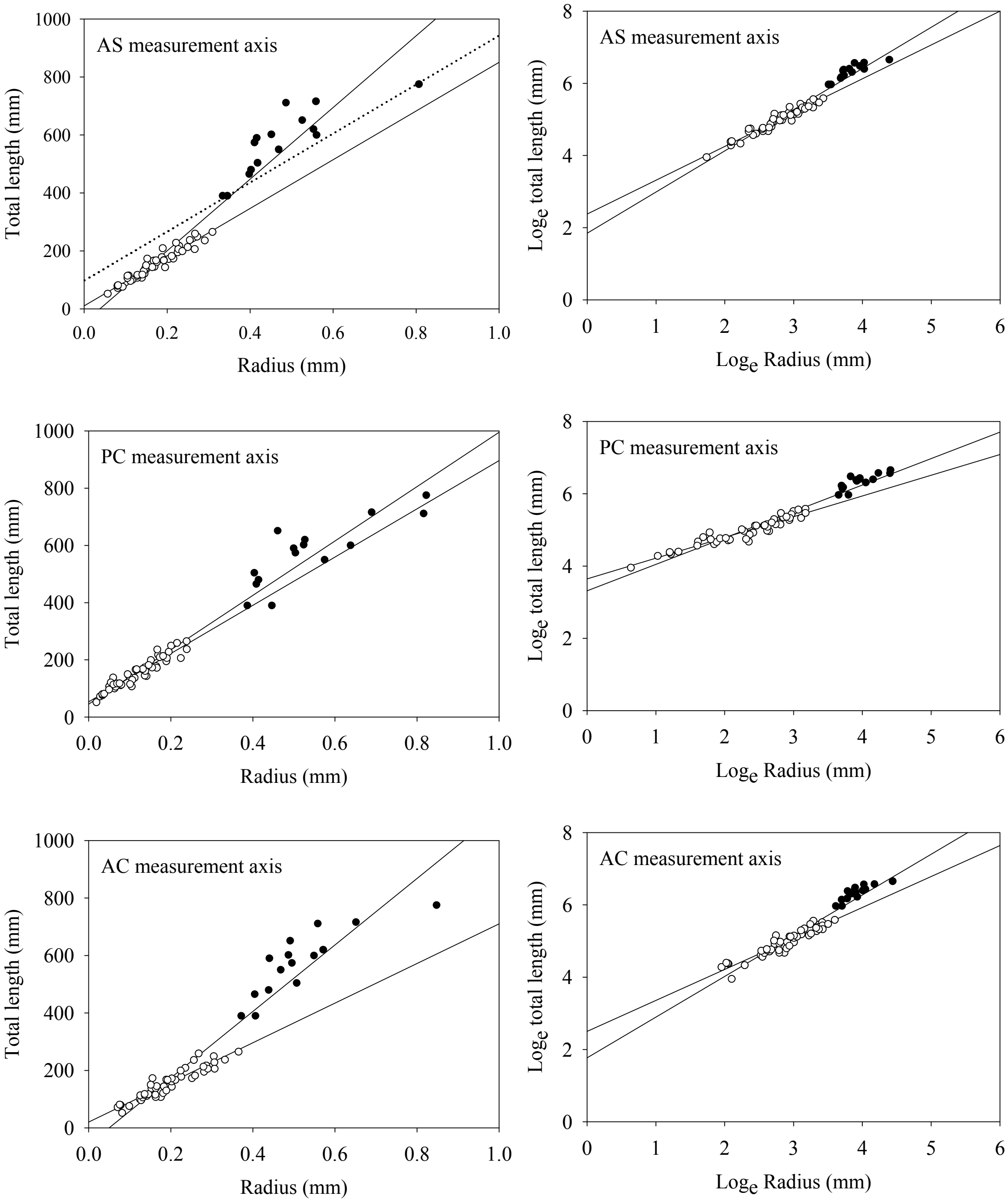

Figure 2. Body length—fin ray radius relations for three measurement axes. Non transformed variables at left; log$_e$—log$_e$ transformed variables at right. Solid lines depict regressions including all data points, whereas dotted lines include only bull trout < 300 mm TL (open circles).

migratory individuals when back-calculating lengths of substantially smaller, resident or juvenile fish. Significance of difference between actual, measured length and back-calculated length to the virtual mark was tested using a repeated measures ANOVA and Bonferroni paired comparisons with measured length as the control. As a second test of back-calculation accuracy, the propensity of each axis to produce unrealistic values was assessed by comparing actual length at initial capture to the length interval (back-calculated using the recapture sample) at annuli formed immediately preceding and following initial capture. Initial length was expected to fall within this interval, and values below the lower bound or above the upper bound constituted evidence of error. Finally, consistency (absolute percent error), or retentionof proportionality with growth of the fish, was compared among axes using a repeated measures ANOVA with Tukey's pairwise comparisons (family $\alpha = 0.05$).

Accuracy and precision varied according to the axis and formula used for back-calculation. Accuracy tests using the virtual mark produced < 5% real error for 9 of the 12 sets of calculations and < 7% absolute error for 5 sets (Table 2). ANOVA indicated significant differences among actual and back-calculated lengths ($F = 12.08$, df = 12, $P < 0.001$), and Bonferroni paired comparisons indicated significant differences between actual length and AC * ($P<0.001$), AS * ($P=0.04$), and PC ($P<0.001$). Mean percent error was nearly zero for AC, although absolute percent error was about equal between AC and AS. Transformation produced a reduction in mean percent error for five of the six sets of calculations, but no pattern was apparent for absolute percent error. Measured length at initial capture was within the length interval back-calculated using the recapture sample for every fish only for AS and $\log_e$AS (Figure 3). Actual length of only one fish fell outside the back-calculated length interval for $\log_e$AS *, PC *, and $\log_e$PC *. Consistency between tag and recapture samples (absolute percent error) was unequal among axes (*F* = 3.77, df = 10, *P* = 0.005) (Table 3). To meet parametric assumptions for the ANOVA, the AC * set was excluded (because it produced error that was an order of magnitude higher than that for all other sets) and the data set was transformed ($Y=Y^{\lambda}$, where $\lambda = 0.2$). Paired comparisons indicated the following significant differences (in absolute percent error): PC < $\log_e$AC*, PC < AS*, $\log_e$AS* < $\log_e$AC*. Ten of the sets of calculations produced <5% mean real error, and five sets (AS, $\log_e$AS, $\log_e$AS*, PC, and PC*) produced <8% mean absolute error.

Table 2. Accuracy of back-calculation (mean ± SE) using virtual mark. Asterisk denotes use of intercept correction parameter derived after inclusion of large bull trout (see Table 1). Final column gives percent of individuals for which real error was greater than zero, indicating underestimation of actual length at initial capture.

Axis	Error	| Error |	% Error	| % Error |	% Positive
AS	3.6 ± 2.0	8.2 ± 1.1	2.6 ± 1.6	5.9 ± 1.0	67
Log_e AS	3.4 ± 2.2	9.0 ± 1.1	2.4 ± 1.6	6.4 ± 1.0	67
AS *	-7.5 ± 2.7	10.1 ± 2.2	-5.6 ± 2.0	7.3 ± 1.7	71
Log_e AS *	-2 ± 2.5	8.8 ± 1.6	-1.4 ± 1.8	6.2 ± 1.2	67
PC	-14.7 ± 2.7	15.0 ± 2.6	-10.7 ± 2.2	10.7 ± 2.2	14
Log_e PC	4.3 ± 2.8	10.7 ± 1.7	3.1 ± 2.3	8.1 ± 1.6	62
PC *	-4.3 ± 2.2	9.2 ± 1.2	-2.7 ± 1.7	6.4 ± 1.1	62
Log_e PC *	2.4 ± 3.2	11.7 ± 1.9	-1.7 ± 2.6	8.9 ± 1.8	43
AC	0.1 ± 2.5	8.1 ± 1.7	0.0 ± 1.9	5.8 ± 1.4	62
Log_e AC	2.6 ± 2.9	9.7 ± 2.1	1.3 ± 2.4	7.0 ± 1.8	67
AC *	-14.2 ± 3.7	16.8 ± 3.1	-10.8 ± 3.1	12.6 ± 2.8	81
Log_e AC *	-4.9 ± 3.4	11.6 ± 2.4	-4.1 ± 2.8	8.7 ± 2.2	38

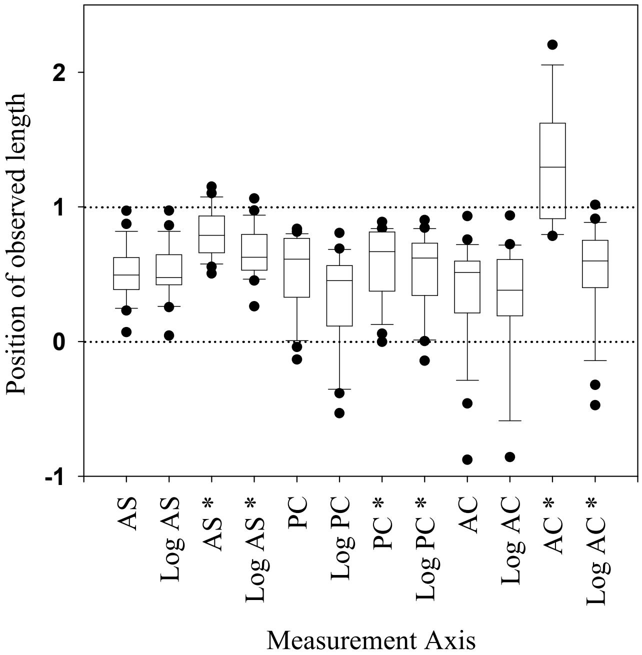

Figure 3. Position of observed length (tag sample) relative to back-calculated lengths at age (recapture sample). Lower dashed line represents standardized back-calculated length at the annulus preceding initial capture. Upper dashed line represents standardized length at the annulus preceding recapture. Boxplots depict median line within 25th to 75th percentiles (box), 10th to 90th percentiles (whiskers), and outliers (filled circles).

Table 3. Consistency (mean ± SE) of back-calculated lengths at age between tag sample and recapture sample collected one year apart. Positive real error values indicate that length back-calculated using sample collected in 2002 (when fish was younger and smaller) exceeded lengths from sample collected in 2003.

Axis	% Error	| % Error |	% Positive
AS	-4.6 ± 1.2	7.9 ± 0.8	26
Log$_e$ AS	-3.3 ± 1.2	7.3 ± 0.8	33
AS *	-2.3 ± 3.6	16.7 ± 2.9	53
Log$_e$ AS *	-0.4 ± 1.4	7.9 ± 0.9	48
PC	2.9 ± 1.0	6.5 ± 0.7	62
Log$_e$ PC	4.1 ± 1.9	10.7 ± 1.4	60
PC *	4.1 ± 1.1	7.4 ± 0.8	66
Log$_e$ PC *	7.2 ± 2.2	13.0 ± 1.7	69
AC	-4.0 ± 2.2	12.2 ± 1.6	38
Log$_e$ AC	-1.9 ± 2.5	13.0 ± 1.8	45
AC *	55.0 ± 38.7	116.8 ± 36.2	67
Log$_e$ AC *	0.8 ± 3.1	16.0 ± 2.2	53

The results of these tests suggest that the AS axis provides highest suitability for use in back-calculation. Three of the sets of calculations based on this measurement axis (AS, AS*, and $\log_e$AS*) scored well by all criteria. While AC produced highest accuracy according to the virtual mark, it also showed a relatively high number of instances in which the back-calculated range failed to capture the actual length, and consistency between tag and recapture samples was poor. PC* scored well in all tests and also retained linearity in the body—structure relation including large fish, but annuli proved to be more difficult to identify along the PC measurement axis than the other two axes, and location of the axis itself was more subjective and inconsistent. Use of intercept correction parameters obtained with regressions that included samples from large, migratory bull trout did not appreciably increase error if the body—scale relation was linear ($\log_e$AS*, PC*, $\log_e$AC*), but large error was incurred if the relation was non-linear (AS*, AC*). Calculations for AS, AS*, and $\log_e$AS * generally produced similar results. However, the modified formula using transformed data, particularly with an intercept correction parameter calculated using additional large fish, produced smaller lengths than the ordinary formula (Figure 4). Magnitude of differences increased with greater proportional distance back-calculated, but the relative accuracy of calculations two or more years into the past was not tested because the tag—recapture fish used in these analyses were limited to one year at liberty. Although one of the individual tests above might support the use of the PC or AC axes, analysis of the full set of results suggests that the AS axis represents the best overall choice for conducting back-calculation measurements.

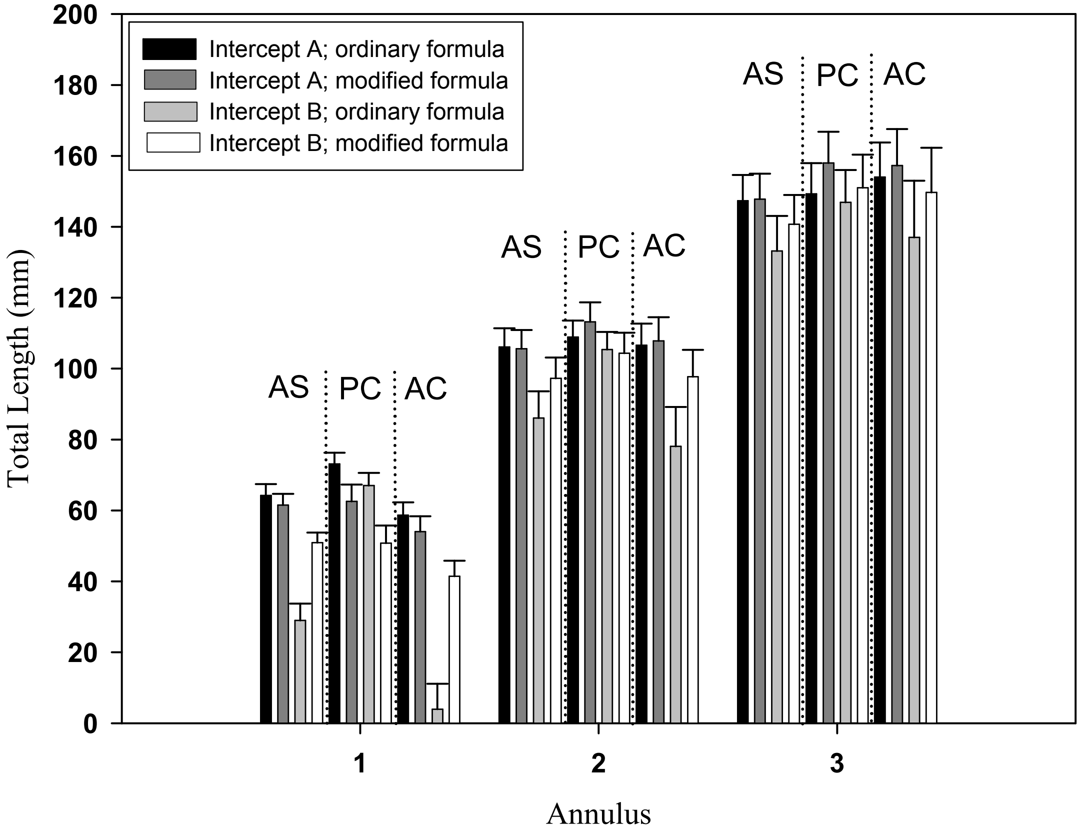

Figure 4. Back-calculated length at age (mean + upper 95% C.L.) for three axes of measurement using tag samples ($N = 21$) from the tag—recapture set. Intercept A indicates value for correction parameter derived with bull trout 52—265 mm TL; intercept B indicates value derived with bull trout 52—775 mm TL.

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