Comparison of methods to estimate the ages of bull trout in the Saint Mary River drainage, and an estimate of growth rates from scales

by Jarvis Jay Gust

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management

Montana State University

Abstract:

In November 1999, the U.S. Fish and Wildlife Service listed bull trout ('Salvelinus confluentus) populations in the contiguous United States as threatened under the Federal Endangered Species Act. Bull trout in Montana's Saint Mary River drainage system are unique because they are the only bull trout found east of the Continental Divide in the United States. This study compared bull trout ages estimated from scales, pelvic fin rays, sagittal otoliths, opercular bones, vertebrae, cleithra, and length frequency. Each aging technique had advantages and disadvantages in preparation and interpretation. Of the six hard parts examined, vertebrae appeared to be best for determining age of bull trout because the first and second readings were identical in 98% of the cases (N = 47).

Otoliths (N= 43) and fin rays were the next best in reproducibility (74%), followed by opercular bones and cleithra (62% and 57%, respectively; N= 47 for both). Age estimates from scales were poorest in reproducibility (37%; N= 711). Thirty-three scale samples from recaptured bull trout were available for comparisons between known increase in age and estimated increase in age. Those comparisons revealed that I underestimated the increase in age for fish less than 5 years old; fish 5 years old were accurately estimated; and the increase in age of fish older than 5 were over-estimated. Scales and fin rays produced less reproducible age estimates and probably less accurate estimates, but have the advantage of being obtainable through non-lethal sampling. Selection of aging techniques for bull trout should be based on the specific objectives of the intended study, and the advantages and disadvantages of using structures obtainable from non-lethal versus lethal sampling. Based on the analysis of scale samples, the mean back-calculated length of bull trout from the Saint Mary River drainage during the first 4-5 years of life was similar to neighboring adfluvial bull trout populations from Flathead Lake, Hungry Horse Reservoir, and Lake Koocanusa; however, older fish in those populations grew faster than bull trout in the Saint Mary population.

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APPROVAL

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Jarvis Jay Gust

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

In November 1999, the U.S. Fish and Wildlife Service listed bull trout (*Salvelinus confluentus*) populations in the contiguous United States as threatened under the Federal Endangered Species Act. Bull trout in Montana's Saint Mary River drainage system are unique because they are the only bull trout found east of the Continental Divide in the United States. This study compared bull trout ages estimated from scales, pelvic fin rays, sagittal otoliths, opercular bones, vertebrae, cleithra, and length frequency. Each aging technique had advantages and disadvantages in preparation and interpretation. Of the six hard parts examined, vertebrae appeared to be best for determining age of bull trout because the first and second readings were identical in 98% of the cases ($N = 47$). Otoliths ($N = 43$) and fin rays were the next best in reproducibility (74%), followed by opercular bones and cleithra (62% and 57%, respectively; $N = 47$ for both). Age estimates from scales were poorest in reproducibility (37%; $N = 711$). Thirty-three scale samples from recaptured bull trout were available for comparisons between known increase in age and estimated increase in age. Those comparisons revealed that I under-estimated the increase in age for fish less than 5 years old; fish 5 years old were accurately estimated; and the increase in age of fish older than 5 were over-estimated. Scales and fin rays produced less reproducible age estimates and probably less accurate estimates, but have the advantage of being obtainable through non-lethal sampling. Selection of aging techniques for bull trout should be based on the specific objectives of the intended study, and the advantages and disadvantages of using structures obtainable from non-lethal versus lethal sampling. Based on the analysis of scale samples, the mean back-calculated length of bull trout from the Saint Mary River drainage during the first 4–5 years of life was similar to neighboring adfluvial bull trout populations from Flathead Lake, Hungry Horse Reservoir, and Lake Koocanusa; however, older fish in those populations grew faster than bull trout in the Saint Mary population.

INTRODUCTION

Background

Bull trout (*Salvelinus confluentus*), a species of char (genus, *Salvelinus*), undergo some of the longest migrations of any trout in North America. The natural range of the bull trout is from northern California into Canada, including the Columbia and Saskatchewan River drainage in Montana (Brown 1971). Once considered to be a "trash" fish and the "cannibal" of Montana's streams, it was targeted for eradication in the early 1900s and also harvested commercially (Brown 1971; Fraley 1994). Today, bull trout are in decline and considered a species of special concern throughout the majority of their range in the contiguous United States. Bull trout are extinct in California, only reside in one river system in Nevada, and are currently considered "threatened" in many waters in Oregon, Washington, Idaho, and Montana (Fraley 1994). Causes of the bull trout decline are generally attributed to habitat disturbances, fragmentation, competition, and hybridization with nonnative species (Federal Register 1999). In November 1999, the U.S. Fish and Wildlife Service listed the Saint Mary-Belly River, Coastal-Puget Sound, and Jarbridge River bull trout populations in the United States as threatened under the Federal Endangered Species Act. This followed an earlier listing of the Columbia River and Klamath River bull trout population in June 1998. With this final rule, the bull trout is now listed as threatened throughout its entire range in the contiguous United States (Federal Register 1999).

Like other char, bull trout spawn from August through November and exhibit both

resident and migratory life-history strategies. Resident bull trout spend their entire lives in small tributary streams. Migratory bull trout live as adults in either a lake (adfluvial life-history form) or river (fluvial life-history form) and enter tributary streams to spawn. Their young rear for 2 to 3 years as juvenile fish in those tributaries. They reach sexual maturity in 5 to 7 years and are believed to predominantly return to the tributary where they reared to spawn and complete the life cycle. Size and age of bull trout at maturity is variable, depending upon life-history strategy. Growth of resident fish is generally slower than migratory fish; resident fish tend to be smaller at maturity and less fecund (Fraley and Shepard 1989; Goetz 1989). The long winter egg incubation, bottom-dwelling habits of the juveniles, and migratory top-predator adults, renders the species sensitive to environmental disturbances. All of these characteristics are believed to make bull trout a prime indicator of ecosystem and watershed health (Rieman and McIntyre 1993).

Bull trout are opportunistic feeders, with diets mainly a function of fish size and life-history strategy. Resident and juvenile bull trout prey primarily on invertebrate organisms. Migratory adults are principally piscivorous, preying on smaller fishes but have been known to eat frogs, snakes, mice and ducklings (Fraley 1994).

Bull trout in Montana's Saint Mary River drainage system are unique because they are the only bull trout found east of the Continental Divide in the United States. Bull trout apparently immigrated to the headwaters of the Oldman River drainage via postglacial dispersal routes originating in the Columbia refugium (Nelson and Paetz 1992). The headwaters of the Oldman River, an international drainage consisting of the Saint Mary-Belly River drainage and Canada's Waterton drainage, are tributary to the

Saskatchewan River. Bull trout in the Saint Mary River drainage include both the migratory (adfluvial, fluvial) and resident life-history forms. The migratory (fluvial) fishes have been reported to cross the international border into Canada (Mogen and Kaeding 2000).

Data on age and growth rates are vital to many aspect of fisheries management. Growth provides broad assessment of the environment, water chemistry, and endogenous conditions affecting fish. Therefore, growth is useful in evaluating habitat suitability, prey availability, and the influence of management activities (Devries and Frie 1996). Because information on the current status of bull trout in the Saint Mary River drainage is scant, data on the age and growth of bull trout collected as part of my study will serve as a baseline for the future.

The difficulty in determining the ages of bull trout with scales, otoliths, or any other hard body structures is due to a lack of reliable criteria from validation studies. Beamish and McFarlane (1983) outlined the importance of validating aging techniques. Although a study involving known-age fish is the only true means of validation, an alternative, indirect means of assessing the usefulness of an aging structure is to compare results obtained from several types of structures from each fish. In my study, estimated ages from scales, otoliths, cleithra, opercular bones, fin rays, and vertebra were compared to determine which of these hard parts provides the most reproducible age estimates.

Objectives

The goal of my study was to compare several available methods for estimating ages of bull trout in the Saint Mary River drainage. The first objective was to compare ages estimated from scales, fin rays, sagittal otoliths, opercular bones, vertebrae, cleithra, and length frequency. The second objective was to characterize growth rates among the various bull trout stocks in the Saint Mary River drainage, and to compare these data to information on bull trout in other drainages for which published data are available.

STUDY AREA

Aquatic Habitats

The Saint Mary River originates at Gunsight Lake, in Glacier National Park, and flows northeast about 10 km before entering Saint Mary Lake (Figure 1). Upon leaving the 15-km-long lake, the river flows onto the Blackfeet Reservation and continues northeast for about 2 km before entering Lower Saint Mary Lake (9 km long). From that lake, the river meanders northerly about 25 km to the international boundary, then continues north through shrub-grassland habitat about 55 km to Saint Mary Reservoir, a large, man-made impoundment. The Saint Mary River that flows from the reservoir joins the Oldman River about 8 km upstream from Lethbridge, Alberta.

Several major tributaries, all of which head in Glacier National Park and flow principally through forested habitats, enter the Saint Mary River (or its lakes) along its course (Figure 1). Although each tributary differs in physical characteristics that may be important to fish, all have in common the frequent occurrence somewhere along their length of natural year-round or seasonal barriers to the movements of fish.

Boulder Creek originates from snowmelt and flows northeast about 20 km before entering Swiftcurrent Creek, about 5 km above Lower Saint Mary Lake (Figure 1). About 6 km upstream from the park boundary, Boulder Creek flows become entirely subsurface as they pass through gravel-cobble alluvium for about 400 m during low-flow periods in late summer. The creek then emerges as groundwater upwelling and flows through a 3-km, low-gradient stretch characterized by braided channels and abundant

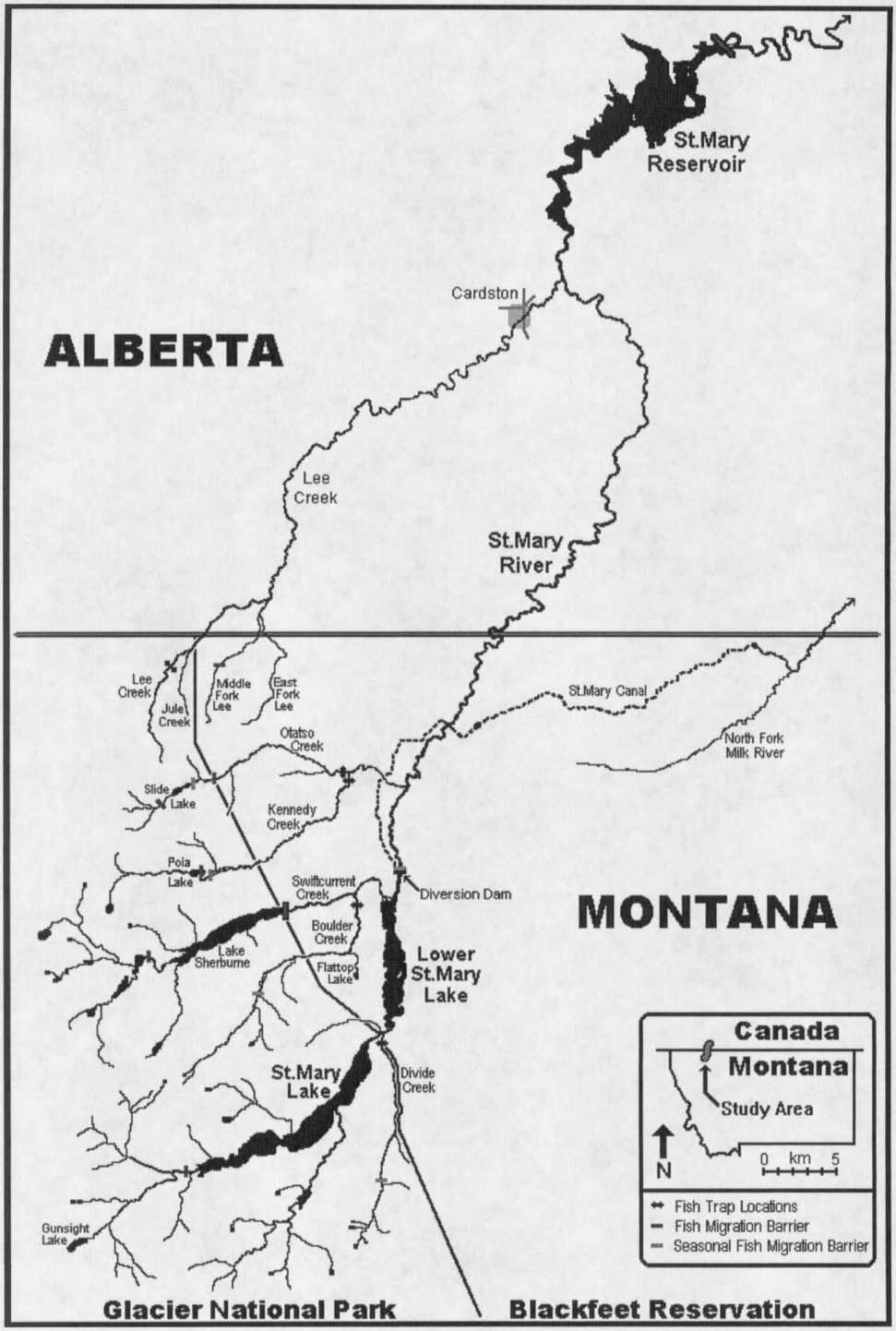

Figure 1. Study area, Saint Mary River drainage, U.S. and Canada.

damming by beavers. Because Boulder Creek has exhibited notably large, seasonal flows, much of the channel in the creek's lower reaches is wide, braided, and has substrates consisting predominantly of boulders and other large materials.

Swiftcurrent Creek originates at a series of lakes near the Continental Divide and enters Lower St. Mary Lake near the lake outlet. About 1920, Swiftcurrent Creek was impounded by placement of a 33-m-high dam at the park boundary, thereby forming Lake Sherburne (Figure 1). That reservoir has a maximum surface area of 648 hectares and storage capacity of nearly 84 million cubic meters.

Kennedy Creek originates at Kennedy Lake and flows northeast about 28 km before entering the Saint Mary River about 8 km downstream from Lower Saint Mary Lake (Figure 1). A 10-m-high waterfall occurs at the outlet of Poia Lake, about 5 km upstream from the park boundary on Kennedy Creek. Immediately downstream from Poia Lake, Kennedy Creek enters a high-gradient, boulder-strewn canyon. At the mouth of that canyon, about 0.7 km below the lake, the valley widens and the creek's gradient declines. In that stretch, Kennedy Creek disappears into the gravel-cobble alluvium during low-flow periods in late summer. About 300 m downstream, however, the creek emerges as groundwater upwellings and flows through a 1.5-km, low-gradient stretch characterized by braided channels and abundant beaver activity.

Otatso Creek originates at Otatso Lake and flows east about 18 km before entering Kennedy Creek, nearly 5 km above the Saint Mary River (Figure 1). A large waterfall (50 m high) occurs in upper Otatso Creek, 15 km upstream from the confluence with Kennedy Creek. Two kilometers downstream from the waterfall, Slide Lakes are formed

by a large landslide across Otatso Creek. Creek flows are entirely subsurface for nearly 100 m, i.e., while passing through the landslide, during all but seasonal high-flow periods. From that location, Otatso Creek flows through a 2-km-long, high-gradient, boulder-strewn canyon before flowing over a second waterfall (3 m high) about 12 km above the confluence with Kennedy Creek and near the park boundary. Downstream from that waterfall, Otatso Creek enters a canyon that has exposed, highly erodible, bear-paw shale walls that contribute substantially to the sediment load of the stream. Consequently, instream habitat in this lower reach is less diverse, and most substrates are armored.

Lee Creek and its tributaries (Jule, Middle Fork Lee, and East Fork Lee creeks) drain the northern-most area of the Saint Mary River drainage in Montana (Figure 1). Lee Creek originates as snowmelt and flows north about 11 km before crossing the international boundary. It then meanders about 50 km through mostly shrub-grassland habitat of southern Alberta, before entering the Saint Mary River near the town of Cardston.

Between 1914 and 1921, the U.S. Bureau of Reclamation built several water-control and delivery structures in the Saint Mary River drainage, as part of the Milk River Irrigation Project. Among those structures is a diversion dam 1.2 km downstream from Lower Saint Mary Lake (Figure 1). That dam, the Saint Mary Diversion, diverts water into the Saint Mary Canal, which conveys the water about 50 km–over the watershed divide and into Missouri River drainage–to the North Fork of the Milk River (Figure 1). In addition, Swiftcurrent Creek, which formerly flowed into the Saint Mary River

downstream from Lower Saint Mary Lake, was diverted into the lake itself. That allowed water released from Lake Sherburne to be diverted into the Saint Mary Canal.

Fish Species

The occurrences of natural year-round barriers to the movements of fish, along with the stocking of several nonnative fish species, have greatly influenced the historic and contemporary distributions of fishes in the Saint Mary River drainage. Waters upstream from those year-round barriers that were historically barren of fish include upper Swiftcurrent, Kennedy, and Otatso Creek watersheds, and the headwaters of the Saint Mary River (Fredenberg 1996; Figure 1).

Among the fish species native to the drainage, bull trout, westslope cutthroat trout (*Oncorhynchus clarki lewisi*), and mountain whitefish (*Prosopium williamsoni*) are believed to have occurred naturally in all the streams and lakes of the Saint Mary River drainage to which they had access, while lake trout (*S. namaycush*) inhabited only the Saint Mary and Lower Saint Mary lakes (Brown 1971). A degree of habitat partitioning between bull trout and lake trout may have resulted from competition between these highly piscivorous species (Donald and Alger 1993; Fredenberg 1996). Also indigenous to the drainage are northern pike (*Esox lucius*) and burbot (*Lota lota),* which inhabit the larger lakes, and white sucker (*Catostomus commersoni*), longnose sucker (*Cat. catostomus*), lake chub (*Couesius plumbeus*), trout-perch (*Percopsis omiscomaycus*), longnose dace (*Rhinichthys cataractae*), pearl dace (*Semotilus margarita*), mottled sculpins (*Cottus bairdi*), and spoonhead sculpins (*Cot. ricei*), which inhabit many of the

streams and lakes of the drainage to which the fish had natural access (Brown 1971).

Stocking of nonnative and native fishes in the Saint Mary River drainage began in the late 1890s and continued in Glacier National Park until the mid-twentieth century. Today, stocking of nonnative species continues in some waters on tribal lands. Nonnative fishes that have established self-sustaining stocks within the Saint Mary River drainage include Yellowstone cutthroat trout (*O. clarki bouvieri*), rainbow trout (*O. mykiss*), and the hybrids of those two fishes, as well as brook trout (*S. fontinalis*), kokanee (*O. nerka*), and lake whitefish (*Coregonus clupeaformis*). Brook, rainbow, and Yellowstone cutthroat trout (and their hybrids) inhabit Gunsight lake (Fredenberg 1996; Michels 1996); Yellowstone cutthroat trout occur in Flattop Lake, located at the head of a small nameless tributary to Boulder Creek (R. Wagner, Service, personal communication), and in Slide Lake, where they have apparently interbred with rainbow trout (Fredenberg 1996; Michels 1996); and rainbow trout, brook trout, and kokanee occur in Lake Sherburne, along with native mountain whitefish, burbot, northern pike, and suckers (Wagner and Fitzgerald 1995; Fredenberg 1996). Self-sustaining stocks of native fishes have also been established in formerly fishless waters in the Saint Mary River drainage.

METHODS

Capture Methods

Electrofishing was used to collect bull trout from representative reaches of Boulder, Kennedy, Otatso, and Lee creeks and a Lee Creek tributary, Jule Creek. Sampling was conducted between mid-July and late August 1998 and 1999, when stream flows were generally low and waters clear. Fish were captured using a Smith-Root battery-powered backpack electrofisher (Model 15-B) operated at 500-800 V and 25-30 Hz DC, depending on the influence of stream temperature and conductivity on our ability to capture fish. Single electrofishing passes (moving upstream) were made through each stream reach, and all cover types were sampled.

Between about late August and mid-October, 1997-1999, fish traps and associated weirs were operated near the mouths of Boulder, Kennedy, and Otatso creeks, and in Lee Creek (1999 only) near the international boundary, to collect downstream-migrating bull trout that spawned in these tributary streams. Throughout the trapping period, all traps were cleaned and checked at least daily. Traps were removed after the downstream migration of bull trout appeared to have ended or weather and related conditions precluded further sampling.

Traps, designed to capture adult bull trout and other downstream-moving fishes, consisted of boxes with weir wings that spanned the entire stream width (5-12 m). Boxes (1.0 m long, 1.0 m wide, and 1.0 m high) had frames made of steel tubing, 1.3-cm mesh galvanized hardware screen walls and bottoms, and hinged plywood lids secured with

padlocks. Vexar mesh funnels were fastened to the trap entrances. Weir wings, attached at the funnel entrances and angled upstream to opposing streambanks, directed fish into the boxes and prevented fish passage around the traps. Wings consisted of 1.2-m lengths of 1.3-cm metal conduit, spaced at 2.5-cm intervals, and cabled together to form a "picket fence." Steel fence posts driven into the stream bottom supported the wings. The 2.5-cm interval between pickets was chosen to minimize the collection of debris while prohibiting the passage of large fish.

Processing of Captured Bull Trout

Total length (TL, mm) and weight (g) were measured and recorded for each fish captured. Bull trout longer than 200 mm TL were uniquely tagged. In 1997, visual implant (VI) tags were injected subcutaneously, immediately posterior to the left eye; in 1998-1999, passive integrated transponder (PIT) tags were injected into the dorsal musculature, directly below the dorsal fin. Recapture of tagged fish provided an opportunity to compare scales from fish that were known to have aged 1 or 2 years since initial capture. Back-calculated lengths at times of annulus formation were used to estimate annual growth rates. The direct proportion method was used because the relationship between the body length and hard-part radius was strongly linear (Devries and Frie 1996).

Scales from each bull trout were taken from an area posterior to the dorsal fin and above the lateral line. Scale samples were impressed on cellulose acetate sheets and examined using a Bioscope (model 60-A) projector at X 143 or X 176.

All incidental mortalities, as well as intentionally sacrificed bull trout (a few fish from each stream) and five bull trout that died in gill nets set in the Saint Mary canal (Mogen and Kaeding 2000), were weighed, measured and frozen. Both pelvic fins, sagittal otoliths, cleithra, and opercular bones, as well as several vertebrae were removed from the thawed bull trout in the lab. Before removal of the hard parts from the bull trout, procedures were practiced on thawed hatchery rainbow trout of similar size supplied by the Bozeman Fish Technology Center.

Sagittal otoliths were removed by making an incision perpendicular to the horizontal axis of the fish's body, immediately posterior to the eyes and extending downward to the base of the orbit. After the brain was removed, the otoliths usually were evident ventral and caudal to the midbrain and easily removed with forceps. The otoliths were cleaned for 2 minutes with diluted (10%) bleach (sodium hypochlorite), rinsed with distilled water, wiped with tissue paper, and placed in numbered vials. Otoliths were later embedded in epoxy resin (EPO-KWICK fast-cure epoxy). Thin transverse sections (0.25 mm thickness) were cut on equal sides of the nucleus, at right angles to the long axis of the embedded otoliths, with a Buehler Isomet low-speed saw. Sections were then hand-polished with 2000-grit sand paper on both sides until the nucleus and annuli were visible. Polished sections were then mounted on glass microscope slides with thermoplastic glue (Crystal Bond). The transverse sections were placed under a cover slip and viewed with transmitted light under a compound microscope at X 100.

Whole pelvic fins were removed as close to the body as possible, cut perpendicular to the fin ray, and dried in numbered scale envelops. The trimmed fins

were imbedded in epoxy in a manner similar to the otoliths. Two or three thin sections (0.25 mm thick) were cut from the proximal end of the embedded fin rays with the Isomet saw. Sections were hand-polished thin enough to allow adequate light transmission for identification of annuli. Polished sections were mounted on a glass slide with thermoplastic glue. The samples were placed under a cover slip and viewed with transmitted light under a compound microscope at X 40 to X 100.

Thoracic vertebrae were removed from the spine below the anterior margin of the dorsal fin. Five vertebrae were brushed free of all muscle and connective tissue, washed with hot water and dilute bleach, rinsed with distilled water, dried, and placed in numbered vials. The vertebrae, imbedded in epoxy similar to the otoliths and fin rays, were viewed as a longitudinal section. The longitudinal section (0.25 to 0.50 mm thick) was cut at the focus of the centrum with the Isomet saw, hand-polished until the annuli were visible, mounted on a glass slide with thermoplastic glue, and placed under a cover slip. The sections were viewed with transmitted light on a compound microscope at X 40 to X 100.

Opercular bones were extracted by cutting the surrounding muscles at the anterior border and separating the opercule joints from the skull at the top of the gill covers. After separating the opercular bones and exposing the cleithrum (which forms most of the pectoral girdle), an incision was made between the posterior edge of the cleithrum and the muscle and connective tissue. The incision separated the inner surface of the cleithrum from the underlying soft tissue. The cleithrum was then separated from the post-temporal bones (dorsally) and the pectoral fins (ventrally). The opercular bones and cleithra were

cleaned, dried, and placed in numbered coin envelopes. The right operculum bone and cleithrum were each viewed using a dissecting microscope at low magnification with reflected light and against a black background. In instances when the translucent bands were indistinct against the black background, the structure was held up against a light source and examined using transmitted light.

The Petersen method was used to analyze the length-frequency of captured bull trout. Length-frequency analysis involves comparisons of a large number of fish in a population and it is based on the assumption that the lengths of fish in some year-classes, particularly those for younger fish, will distribute normally around a mean length (Mackay et al. 1990).

Reading and Interpretation of Marks on Hard Parts

All of the hard parts were examined without reference to the fish size, location, or any other information that may cause examiner biases in age estimates. After all of the samples were examined and the resulting data analyzed preliminarily, a second reading of all materials was preformed. Age estimates from the second estimation were assumed to be more accurate than the first because of the experience gained by the examiner. Apart from the initial comparisons of estimated ages between readings, only the age estimates from the second reading of all hard parts were used in my analyses.

Scale annuli were identified as series of partial or broken circuli crowded together. The annuli were counted, and the distances to the outer edge of each annulus and to the scale margin were measured along the maximum anterior radius. To identify and correct

for possible missing first-year annuli, the number of circuli through the first annulus was counted for each scale.

Thin sections from otoliths, fin rays, and vertebrae, and the whole opercules and cleithra, all show alternating translucent and opaque bands. In otoliths, fin rays, and vertebrae, translucent bands represented periods of slow growth and opaque bands represented periods of active growth (Devries and Frie 1996). Taken together, one opaque and adjacent translucent band composed 1 year of growth; translucent bands in otoliths, fin rays, and vertebrae were counted to age the fish. However, with opercules and cleithra, the translucent bands represent periods of active growth, whereas opaque bands represent periods of slow growth (Devries and Frie 1996). Taken together, one translucent and adjacent opaque band composed 1 year of growth; opaque bands were counted in opercules and cleithra to age the fish. The direction for aging the otolith section was from the nucleus outward along the ventral radius. For opercular bones, aging began with the first distinct opaque band and proceeded diagonally towards the posterior radius of the bone. For cleithra, aging began from the origin (V-shaped notch in the bone) out towards the ventral edge of the anterior blade. For vertebrae, aging began at the focus of the centrum and proceeded out to the edge. For fin rays, aging began at the focus and proceeded outward along the anteromedial axis.

Comparisons of Estimated Ages Between Readings

Differences between the first and second readings (i.e. Delta Hard Part [HP]) were calculated for each sample by subtracting age estimated during the first readings (HP1)

from the estimated age from the second (HP2). Delta HP was then used to make comparisons across all ages (second readings) within individual hard parts, as well as among all the hard parts examined.

Because I also collected scales from recaptured bull trout, I was able to compare the estimated age at recapture to the estimated age at initial capture. That provided an estimated delta age for each recaptured fish, which could in turn be compared to the known delta age (i.e. the year of recapture minus the year of initial capture) for each recaptured fish. The difference in delta ages (DDA) was then calculated by subtracting the known delta age from the estimated delta age. Differences in delta ages were compared to the estimated age from the second scale readings.

Statistical Applications

All statistical analyses were conducted using Number Cruncher Statistical System (NCSS 1999). For comparisons among hard parts, correlation matrix and simple linear regression procedures were used. Second-order polynomial fits were constructed to visually estimate whether linear or curvilinear relations best fit the data. One-way ANOVA, followed by Bonferroni (All-Pairwise) Multiple Comparison Tests, were used to compare mean back-calculated lengths at annuli for each age class and each stream. All statistical test were performed with $\alpha = 0.05$.

RESULTS

Length-Frequency Distributions for Captured Bull Trout

From 1997 to 1999, 825 bull trout were captured by electrofishing and fish traps in Boulder, Kennedy, Otatso, and Lee creeks (Table 1). Total length of the smallest bull trout captured during electrofishing was 52 mm in Lee Creek and the largest was 725 mm in Kennedy Creek (Figure 2). The smallest bull trout captured by traps was 76 mm in Otatso Creek and the largest was 720 mm in Kennedy Creek (Figure 3). Overall, most large bull trout (600 – 700 mm) were caught in Boulder and Kennedy creeks. No bull trout that large were caught from Lee Creek, and only four large fish were caught in Otatso Creek.

Table 1. Numbers of bull trout collected by electrofishing (1998-1999) and traps (1997-1999) from which scale samples were taken, Saint Mary River drainage, Montana.

			Electrofishing		
Year	Boulder Creek	Kennedy Creek	Otatso Creek	Lee Creek	Total
1998	26	38	95	46	205
1999	17	44	116	42	219
Total	43	82	211	88	424

			Fish Traps		
Year	Boulder Creek	Kennedy Creek	Otatso Creek	Lee Creek	Total
1997	46	33	17	----	96
1998	70	34	33	----	137
1999	55	28	16	69	168
Total	171	95	66	69	401

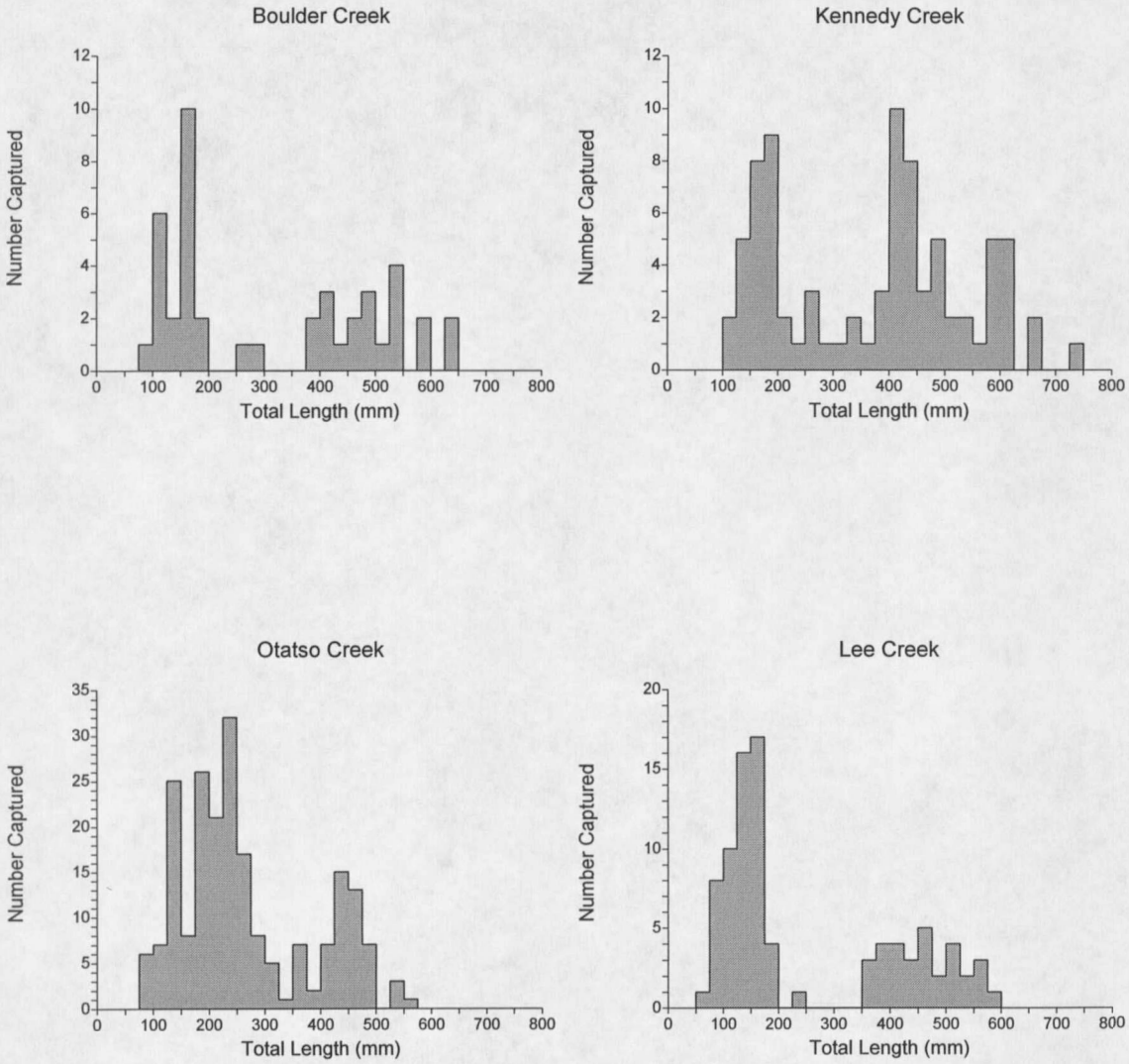

Figure 2. Length-frequency distributions for all bull trout captured during electrofishing surveys in Boulder, Kennedy, and Lee creeks, Saint Mary River drainage, Montana, 1998-1999.

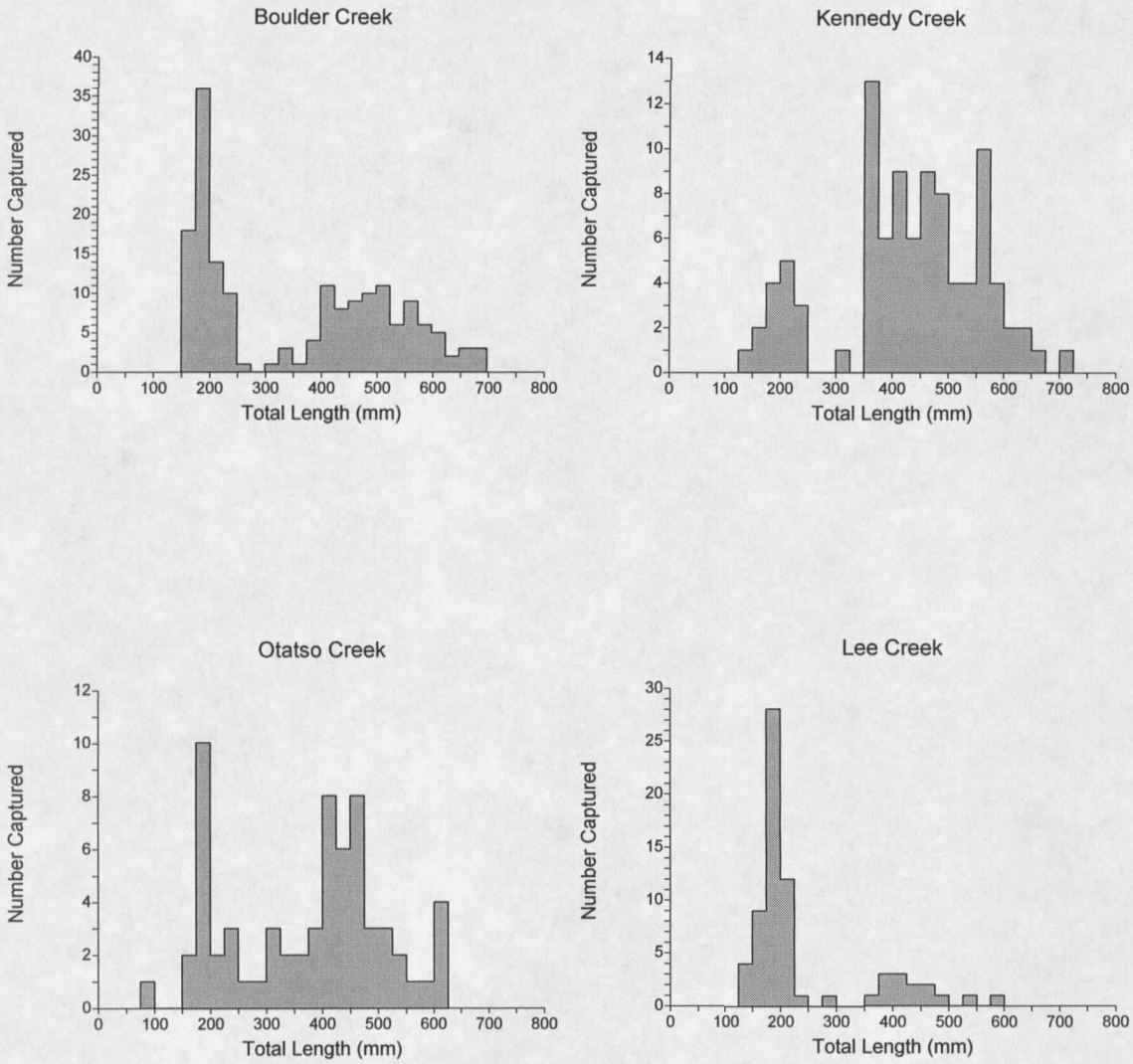

Figure 3. Length-frequency distributions for all bull trout captured in fish traps in Boulder and Kennedy creeks (1997-1999), and Lee Creek (1999 only), Saint Mary River drainage, Montana.

Length-frequency distribution of bull trout sampled by electrofishing and traps was not useful in distinguishing age classes, except perhaps, for a possible age-class of fish 100 to 250 mm TL (Figures 2 and 3). In addition, there appeared to be segregation between probable juvenile (i.e., generally < 250 mm TL) and probable adult (i.e., generally > 350 mm TL) bull trout. Few bull trout 250 to 350 mm long were captured.

Comparisons of Ages Between Readings of Hard Parts

In addition to the 825 scale samples obtained from bull trout (Table 1), 47 sets of all six hard parts were obtained from bull trout in 1999 (Table 2). Relations between estimated age and differences between the first and second readings (Delta HP) for each of the hard parts (Figure 4) were highly significant for both scales and vertebrae. These two relations had positive slopes (β_1), although there was considerable scatter in the scale data. A single influential point was responsible for the significant relationship for vertebrae, however. When that data point was discounted, the relation was not significant. The relation for cleithra was also significant and had a positive slope (Figure 4). Therefore, four of the six hard parts did not show significant relations between Delta HP and estimated age.

Table 2. Numbers and capture location of bull trout from which 47 sets of six hard parts were analyzed, Saint Mary River drainage, Montana (1999).

Capture Technique	Boulder Creek	Kennedy Creek	Otatso Creek	Lee Creek	Saint Mary Canal	Total
Electrofishing	3	3	13	3	----	22
Fish Traps	7	2	1	10	----	20
Gill Nets	----	----	----	----	5	5

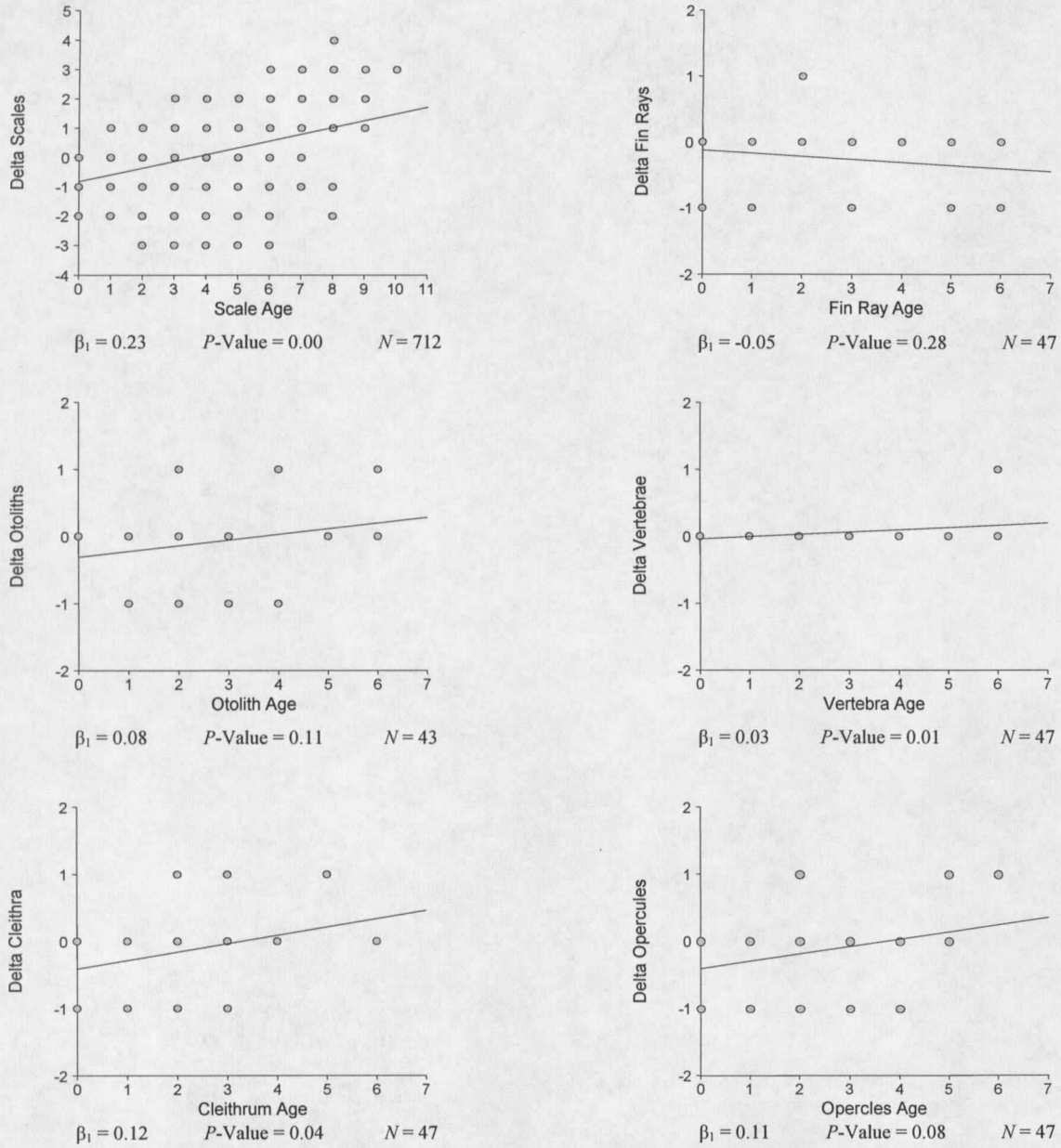

Figure 4. Correlation between the delta hard part and age from the second reading for each of the bull trout hard parts examined. Lines represent the linear regression line through the data. Differences between the first and second readings (Delta Hard Part [HP]) were calculated for each sample by subtracting age estimated with the first readings (HP1) from the estimated age from the second (HP2).

The significant, positive relations for scales and cleithra suggest age of young bull trout was over-estimated in the first age estimation, whereas that of older fish was under-estimated. Furthermore, results from vertebrae were most reproducible between readings, whereas results from scales were least reproducible.

Comparisons of Age Estimates Among Hard Parts

Pair-wise associations between ages estimated (second readings only) from the various hard parts were highly significant (Table 3). Three of the four strongest associations ($r > 0.90$) involved vertebrae; the fourth was between opercules and cleithra.

Table 3. Associations between ages from the second reading of paired hard parts of bull trout, Saint Mary River drainage, Montana (1999).

	Hard Parts				
	Fin rays	Otoliths	Vertebrae	Opercules	Cleithra
Scales $N = 711$	$r = 0.84$ $P = 0.00$ $N = 44.0$	0.80 0.00 40.0	0.85 0.00 44.0	0.81 0.00 44.0	0.83 0.00 44.0
Fin rays $N = 47$		$r = 0.82$ $P = 0.00$ $N = 43.0$	0.92 0.00 47.0	0.87 0.00 47.0	0.86 0.00 47.0
Otoliths $N = 43$			$r = 0.85$ $P = 0.00$ $N = 43.0$	0.85 0.00 43.0	0.89 0.00 43.0
Vertebrae $N = 47$				$r = 0.92$ $P = 0.00$ $N = 47.0$	0.91 0.00 47.0
Opercules $N = 47$					$r = 0.93$ $P = 0.00$ $N = 47.0$

Growth Rates Based on Total Length and Estimated Age at Capture

Relations between bull trout TL at capture and estimated age from scales, fin rays, sagittal otoliths, opercular bones, vertebrae, and cleithra for fish younger than age 7 and shorter than 600 mm, based on a second-order polynomial line fitted to these data, were essentially linear (Figure 5). The relation for otoliths had an increasing slope, however.

When all of the data for scales were examined (i.e. fish estimated to be as old as 10 years and as large as 725 mm at capture), the annual increment in growth rate from the second-order polynomial fit showed a decreasing trend toward an apparent asymptote near 650 mm TL (Figure 6). Thus, as bull trout get older, they grow more slowly in length.

Estimated Maximum Bull Trout Size

Plotting length of recaptured bull trout against their length at initial capture 1 year earlier allowed me to estimate the theoretical maximum length of bull trout in Saint Mary River drainage (Figure 7). The theoretical maximum TL was calculated as 688 $\pm$ 48 mm (95% C.I.).

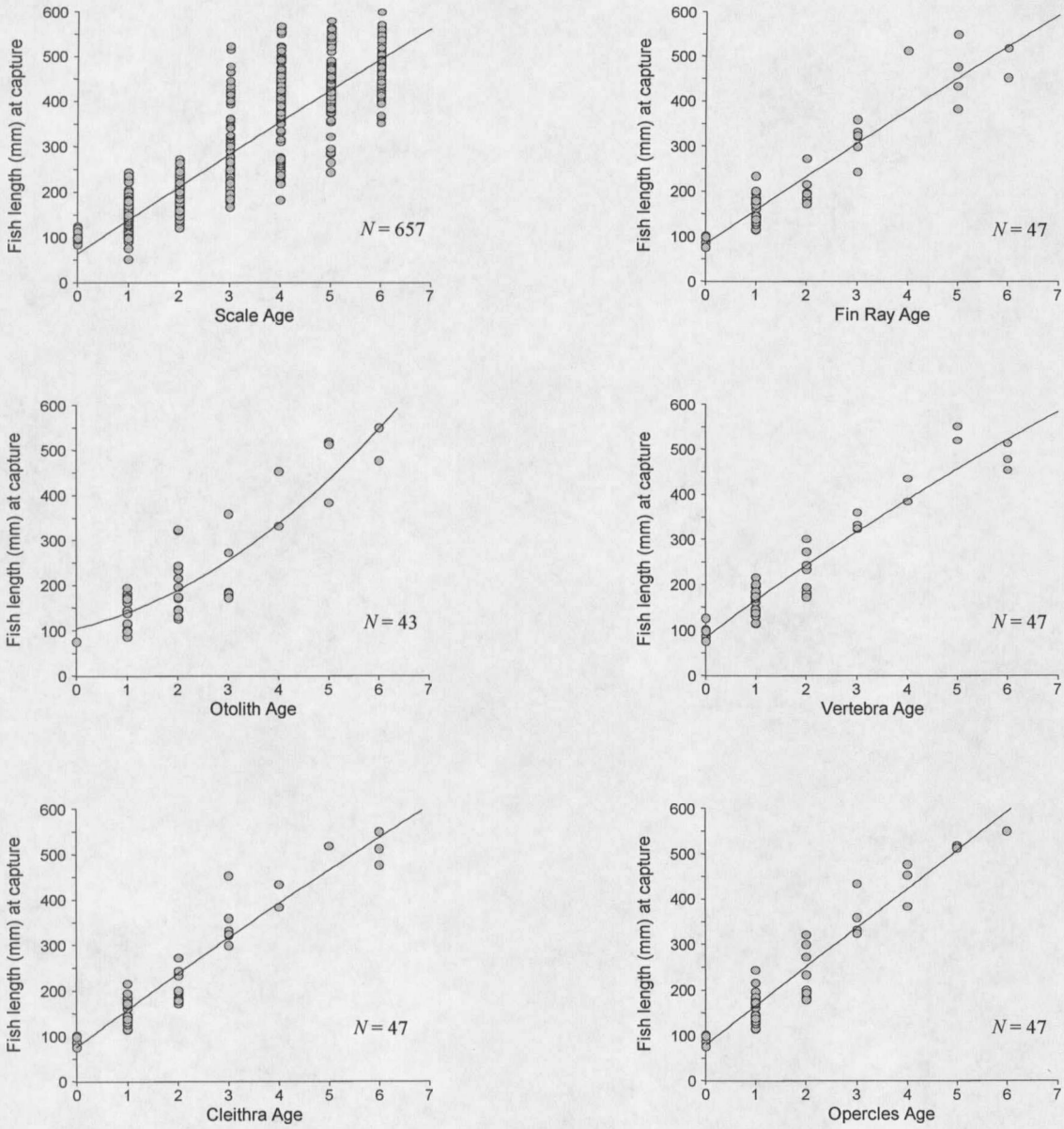

Figure 5. Relation between bull trout length at capture and estimated age obtained using six hard parts. The line represents the 2nd order polynomial fit of the data.

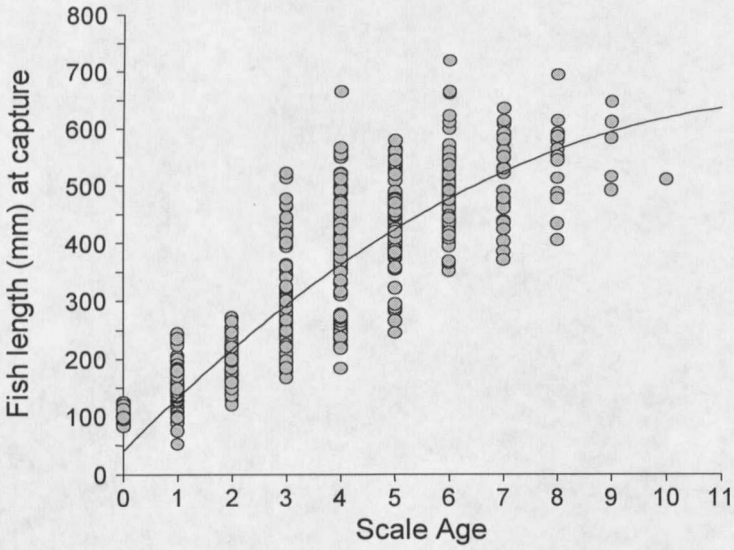

Figure 6. Relation between bull trout length at capture and estimated age obtained using scales ($N = 711$). The line represents the 2nd order polynomial fit of the data.

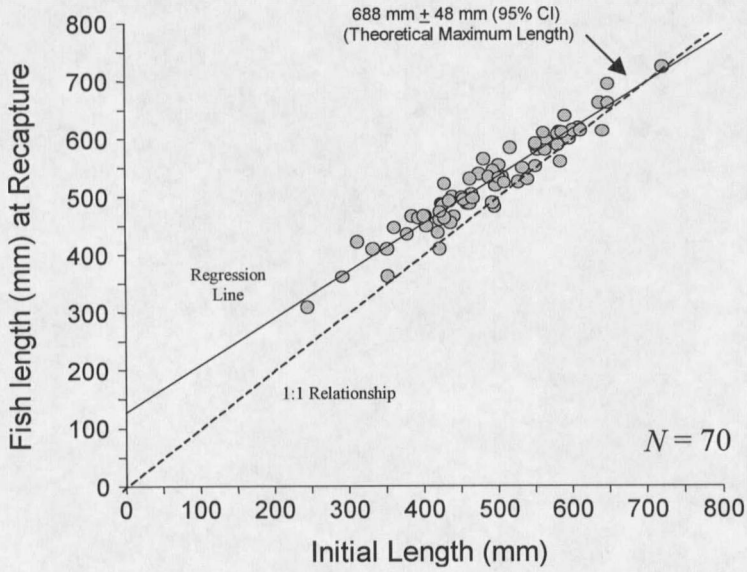

Figure 7. Relation between bull trout length at recapture and length at initial capture one year earlier. Dashed line shows agreement (1:1 relationship). Solid line represents the best-fit linear regression line through the data.

Differences in Delta Age Comparisons

Thirty-three pairs of scale samples from recaptured bull trout were available for comparing DDA and estimated age. Estimated ages for these bull trout ranged from 3 to 8 years. If DDA equaled zero, the estimated increase in bull trout age equaled the known increase in age. If the DDA was less than zero, either the age at recapture was under-estimated or age at initial capture was over-estimated. Conversely, if the DDA was greater than zero, either the age at recapture was over-estimated or age at initial capture was under-estimated.

In general, DDA for fish estimated as less than 5 years old was less than 0; DDA for fish 5 years old equaled 0; and DDA for fish older than 5 was greater than 0 (Figure 8). Bull trout estimated as 6 or 7 year old showed the greatest variation in DDA.

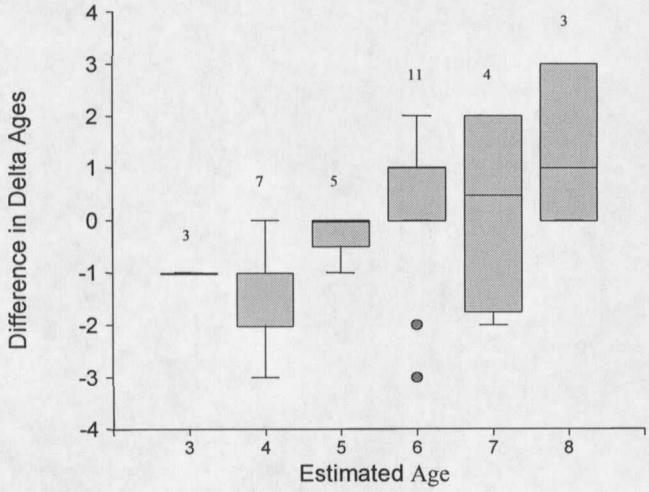

Figure 8. Box plot comparisons between the differences in delta age (DDA) with the 2nd age estimation of scales from 33 recaptured bull trout. Sample size is indicated above each box. Box plot represents a 5 number summary of a distribution consisting of the median M, the quartiles Q_1 and Q_3, and the smallest and largest individual observations. Data represented by circles are outliers.

Back-Calculated Lengths at Annuli

The number of circuli through the first annulus was approximately normally distributed, with slight right-skewing (Figure 9). The absence of a bimodal distribution in circuli suggested that "retarded" scales (Laakso 1955) were not present in my sample. Had a bimodal distribution been evident, it would have suggested that some bull trout formed their first annulus during the first year of life, whereas other bull trout formed their first annulus during the second year. Bull trout in the Saint Mary River drainage formed their first annulus as age-class 2 fish.

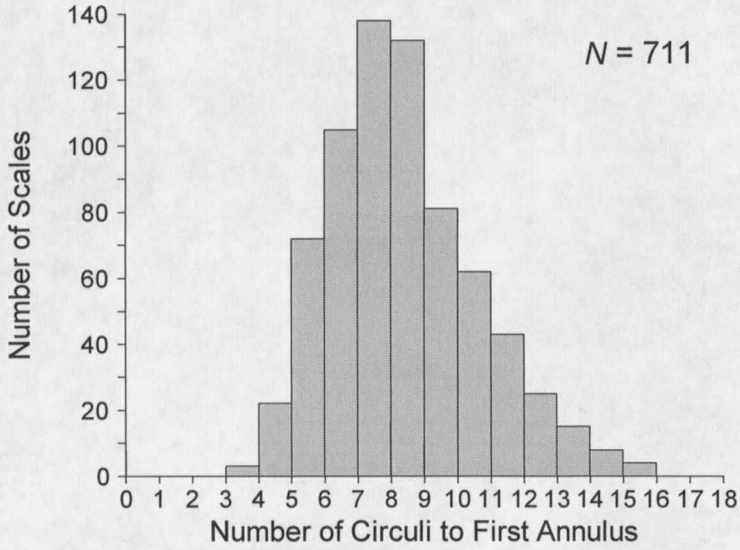

Figure 9. Number of circuli through the first annulus for all bull trout scales ($N = 711$), Saint Mary River drainage, Montana, 1997–1999.

There were no statistical differences in mean back-calculated lengths among age-classes of bull trout within any of the individual annuli for Boulder Creek (Appendix,

Table 4). For bull trout from Kennedy Creek, mean lengths at annulus II for age-class 3 were significantly shorter than for age-class 4 (Appendix, Table 5). For bull trout in Otatso Creek below the falls, there were no statistical differences in mean back-calculated lengths among age-classes within any of the individual annuli (Appendix, Table 6). However, bull trout in Otatso Creek above the falls had significant differences in mean length among age-classes for annuli I, II, III, and IV (Appendix, Table 7). Mean lengths for age-class 4 were shorter than for age-class 7 at annulus I and II. Mean lengths for age-class 5 were shorter than for age-class 7 at annulus III and IV. For bull trout in Lee Creek, significant differences occurred at annulus II and III (Appendix, Table 8). Mean length for age-class 4 was significantly shorter than for age-class 6 at annulus II. Age-class 4 was also shorter than both age-class 5 and 6 at annulus III. The back-calculated mean lengths at annuli for bull trout did not indicate Lee's phenomenon, which would otherwise result in shorter lengths at annuli for older fish than for younger fish.

I also compared overall mean back-calculated length for bull trout in each creek at each annulus (Appendix, Table 9). Overall mean lengths in Otatso Creek above the falls were significantly shorter than bull trout in Kennedy Creek at annulus I and IV. Mean lengths in Boulder Creek were significantly shorter than both Kennedy Creek and Otatso Creek, below the falls, at annulus II. Mean lengths in both Otatso Creek above the falls and Lee Creek were significantly shorter than Kennedy Creek at annulus II and III. In general, bull trout in Kennedy Creek appear to grow faster than in the other creeks.

DISCUSSION

This study compared ages estimated from scales, pelvic fin rays, sagittal otoliths, opercular bones, vertebrae, cleithra, and length frequency. Each aging method had advantages and disadvantages in preparation and interpretation. Scales and fin rays were easy to collect and did not require sacrifice of the fish, although fin rays were taken only from dead bull trout in this study. Another advantage of using scales was that it was possible to collect scales from the same fish in consecutive years, and their preparation for reading did not require excessive time or equipment. Age estimation using scales was difficult, however. In older fishes it was difficult to distinguish the later scale annuli, which become quite closely packed (Sharp and Bernard 1988; Baker and Timmons1991; Casselman and Gunn 1992; Hining et al. 2000). In addition, for each of the six 100-mm intervals of TL between 101 and 700 mm, the percentage of bull trout that had regenerated, damaged, or otherwise unusable scales increased with fish size (5, 4, 13, 20, 34, and 57 percent, respectively).

The main disadvantage of fin rays was the time required for preparation. Fin rays had to be extracted, imbedded, and sectioned. Hand polishing was especially tedious and time consuming since it was necessary to repeatedly check the sample and make sure that it was being adequately polished but not over-polished. Another problem with the preparation of fin rays was keeping the smallest samples oriented properly while embedding them in epoxy molds. Also, small black spots on fin-ray sections made it difficult to differentiate among some annuli and sometimes resulted in over-polishing.

An obvious disadvantage of using sagittal otoliths, vertebrae, opercules, and cleithra for age estimation was that it required sacrificing the fish. Although otoliths were easily removed from large fish and could have been removed in the field, removal from small fish was best accomplished under a dissecting microscope in the lab. Otoliths also required considerable equipment and polishing, similar to fin rays. Some otoliths were difficult or impossible to interpret. My data support the findings of Baker and Timmons (1991) who reported that distinguishing between the later annuli and possible spawning checks was difficult in older fish. Furthermore, freezing specimens before otolith removal is not recommended since otoliths sometimes fracture. Fractures reflected transmitted light and made age interpretation difficult. Another difficulty encountered was aberrant otoliths that had blocks of crystalline material of various sizes that piled up irregularly. Aberrant otoliths show no alternating patterns of translucent and opaque zones and are therefore unreadable (Mugiya 1972).

Vertebrae were easily removed, but that needed to be done in the lab. Disadvantages for vertebrae were similar to those for fin rays and otoliths. Additional problems with the vertebrae came from bubbles in the glue that formed during mounting. Air bubbles that adhered to the vertebrae caused buoyancy and made it difficult to keep the vertebrae properly oriented as the glue hardened. However, vertebrae were the easiest to age of the structures examined, and age estimates from vertebrae were most reproducible. There were a few exceptions with vertebrae that were difficult to read near the core, similar to problems described by Baker and Timmons (1991).

For cleithra and opercules, the advantage was that once cleaned, they were ready

to be aged. The principal disadvantage for both the cleithra and opercules occurred mainly in older fish, which had thick bones that obscured the first annulus, similar to findings of Schmitt and Hubert (1981), Sharp and Bernard (1988), and Baker and Timmons (1991).

Length-frequency distributions are sometimes used to help distinguish age classes of fish populations, but the accuracy of this technique relies on similar growth rates of fish within each age-class (Devries and Frie 1996). Whitworth and Strange (1983) and Hining et al. (2000) were able to distinguish the different age classes of young rainbow trout in the Appalachian streams. However, in my study, lengths overlapped greatly among age classes. Bull trout 250 to 350 mm in range were conspicuously scarce, in both electrofishing and fish traps (Figure 2 and 3). The only clear distinction that could be made based on length-frequency was between the probable juvenile (i.e. generally < 250 mm TL) and probable adult bull trout (i.e. generally > 350 mm TL). Bull trout in the 250 to 350 mm range, largely absent from my samples, are most likely maturing in the main stem of the Saint Mary River or in Lower Saint Mary Lake (Mogen and Kaeding 2000).

Of the six hard parts examined in my study, vertebrae appeared to be the best for determining bull trout ages because the first and second readings were identical in 98% of the cases (Figure 4). Otoliths and fin rays were the next best in reproducibility (74%), followed by opercular bones and cleithra (62% and 57%, respectively). Scales had the poorest reproducibility (37%), after discounting the regenerated and damaged scales (Figure 4). This finding is similar to that of Allen et al. (1990), who reported that scales generally are not suitable for aging bull trout.

The best agreements among aging methods, comparing the second, more-accurate readings of the estimated ages, occurred for opercular bones and cleithra ($r = 0.93$) (Table 3). This agreement in estimated ages was strong despite the low reproducibility between first and second readings of both opercular bones and cleithra. The next three highest associations involved vertebrae. Vertebrae had good agreements with fin rays ($r = 0.92$), opercles ($r = 0.91$), and cleithra ($r = 0.91$).

Reading of sectioned vertebrae, as done in my study, led to highly reproducible estimates of ages. This contrasts with other studies in which unsectioned vertebrae were examined. Sharp and Bernard (1988) and Baker and Timmons (1991) examined whole vertebrae of lake trout and Arctic char (*S. alpinus*), respectively, and concluded that mean estimated age from vertebrae was similar to that from scales and thus was too low. Sharp and Bernard (1988) noted that if annuli are more detectable on sectioned vertebrae, this structure still has promise as a means of accurately determining the age.

Allen et al. (1990) recommend otoliths as the best method for bull trout age determination, particularly for younger fish. I, however, did not find this to be the case because I had difficulties in recognizing the translucent bands associated with the first few annuli.

Fin rays, a potentially non-lethal aging structure, have been validated for aging brown trout (*Salmo trutta*) (Burnett 1969; Shirvell 1980). In my study, fin rays were similar to otoliths in the percent agreement between the first and second readings of estimated ages. Nordeng (1961) and Barber and McFarlane (1987) rejected fin rays for aging Arctic char because of the difficulty in distinguishing the first two or three annuli.

However, Williamson and Macdonald (1997) found evidence to support the use of fin rays, rather than scales, to age northern populations of bull trout.

The cause of the poor reproduce of aging opercular bones most likely arose from my inexperience in reading these structures. However, McConnell (1952), Neuhold (1956), and Sharp and Bernard (1988) also reported problems reading opercular bones of carp (*Cyprinus carpio*), Utah chub (*Gila atraria*), and lake trout, respectively.

Poor reproduce of age determination from cleithra probably resulted from slow growth of bull trout in my study. Translucent bands on the cleithra were more visible in transmitted light than reflective light, which is consistent with estimates using cleithra from slower-growing fish (Casselman 1974; Sharp and Bernard 1988). Sharp and Bernard (1988) disregarded cleithra altogether because of the large measurement errors in the replicated counts from cleithra.

One of the major assumptions of all aging techniques is that growth of bony structures is directly proportional to body growth throughout the life of a fish (Devries and Frie 1996). Therefore, formation of annuli is related to changes in growth during alternating periods of relatively fast (i.e. spring and summer) and slow (e.g., fall and winter) growth (Devries and Frie 1996). One problem with aging fish in northern waters is their higher longevity and slower growth rate that results in annuli that become particularly crowded and indistinguishable in adult fish (Johnson 1976).

Slow growth may also occur after a fish reaches sexual maturity because more energy is devoted to the maturation of gametes than to somatic growth, or simply because physical stream conditions are not conducive to rapid growth (Erickson 1983; Niewinski

and Ferreri 1999). Simkiss (1974) and Casselman (1990) established that bones and otoliths in many fishes have priority over scales in calcium deposition and, on some occasions, calcium may be reabsorbed from scales. Furthermore, although distinguishable, scales may become regenerated or damaged and will not accurately reflect an individual's age or growth.

Comparison of aging methods, as done in my study, does not establish the absolute accuracy of any techniques (Mills and Beamish 1980), so a true age validation experiment still needs to be conducted for bull trout in the Saint Mary River drainage. The recommended validation method by Mills and Beamish (1980) was a mark-recapture study. The results from my study show, as do others (Sikstrom 1983; Sharp and Bernard 1988; Baker and Timmons1991; Casselman and Gunn 1992; Hining et al. 2000), that the use of scales for aging some northern fishes may be a poor choice. However, based on other studies (Williamson and Macdonald 1997; Braaten et al. 1999; Niewinski and Ferreri 1999), scales can be used to estimate the age of immature fish.

Although vertebrae appeared to be best for determining age of bull trout, back-calculations of length from vertebrae would not have been reliable because producing sections of vertebrae with consistent orientation would have been nearly impossible. Because of the much larger sample size and the ability to perform back-calculations, scales were used instead.

Based on the analysis of 711 scale samples (after discounting the regenerated and damaged scales), the mean back-calculated lengths of bull trout from the Saint Mary River drainage appear to show that bull trout in the Kennedy Creek population grow

significantly faster during the first 4 years than populations in other creeks sampled (Appendix, Table 9). Two major external factors controlling fish growth are water temperature and food availability (Weatherly and Gill 1987), factors I did not measure. However, Mogen and Kaeding (2000) reported that from late August through October 1997–1999, the mean-daily water temperatures were 1 to 4 °C higher in Kennedy Creek than in the other streams.

The Saint Mary River drainage bull trout population, presumably a mixture of river- and lake-dwelling fish, exhibits growth rates (after age 5) intermediate to adfluvial and fluvial bull trout populations studied elsewhere (Figure 10). In the first 4–5 years of life, growth rates of Saint Mary River drainage bull trout were similar to neighboring adfluvial populations from Flathead Lake (Fraley and Shepard 1989), Hungry Horse Reservoir, and Lake Koocanusa (Goetz 1989) as well as others (Bjornn 1961; Conner et al.1997; Riehle et al. 1997). However, fluvial populations from the Clearwater and Muskeg rivers (Alberta) exhibited higher growth in these younger age-classes (Figure 10). By age III, most bull trout have emigrated from less productive natal streams and have switched to a piscivorous diet, resulting in increased growth rates (Rieman and McIntyre 1993; Mogen and Kaeding 2000). After emigration, the adfluvial populations inhabiting Flathead Lake, Hungry Horse Reservoir, and Lake Koocanusa exhibited faster growth than the Saint Mary population, as well as the Clearwater and Muskeg river populations (Figure 10).

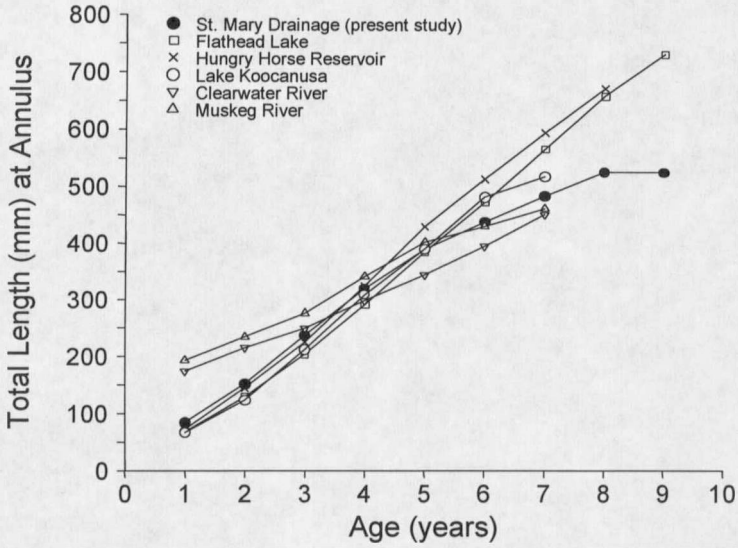

Figure 10. Growth of bull trout in the Saint Mary River drainage, Flathead Lake, Hungry Horse Reservoir, and Lake Koocanusa, northwestern Montana, and the Clearwater and Muskeg rivers, western Alberta.

My ability as the reader of the hard parts in this study undoubtedly affected the variation in estimates of ages, as has been noted elsewhere for estimated ages (Martin 1966; Sharp and Bernard 1988). Because aging fish from hard parts is both art and science, consistency in interpretation is critical. Vertebrae were easily analyzed and were the preferred structure in my study. Use of vertebrae requires that fish be sacrificed, which is a substantial disadvantage when working with a threatened species. Scales and fin rays produced less accurate and less reproducible ages, but have the advantage of being obtainable through non-lethal sampling. Selection of aging methods for bull trout should depend on the specific objectives of the intended study, and the advantages and disadvantages of using structures obtainable from non-lethal versus lethal sampling.

REFERENCES CITED

Allan, J., R. Hawryluk, and Don Hildebrandt. 1990. Bull trout (*Salvelinus confluentus*). Page 55 *in* MacKay, W.C., G.R. Ash, and H.J. Horris (eds.). Fish aging methods for Alberta. R.L. & L. Environmental Services Ltd. in association with Alberta Fish and Wildlife Division and University of Alberta, Edmonton.

Baker, T.T. and L.S. Timmons. 1991. Precision of ages estimated from five bony structures of arctic char (*Salvelinus alpinus*) from the Wood River System, Alaska. Canadian Journal of Fisheries and Aquatic Science 48:1007-1014.

Barber, W.E. and G.A. McFarlane. 1987. Evaluation of three techniques to age artic char from Alaskan and Canadian waters. Transactions of the American Fisheries Society 116:874-881.

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

Bjornn, T.C. 1961. Harvest, age structure, and growth of game fish populations from Priest and Upper Priest lakes. Transactions of the American Fisheries Society 100:423 – 438.

Braaten, P.J., M.R. Doeringsfeld, and C.S. Guy. 1999. Comparison of age and growth estimates for river carpsuckers using scales and dorsal fin ray sections. North American Journal of Fisheries Management 19:786-792.

Brown, C.J.D. 1971. Fishes of Montana. Big Sky Books. Montana State University Bozeman, Montana.

Burnett, A.M.R. 1969. An examination of the use of scales and fin rays for age determination of brown trout (*Salmo trutta* L.). New Zealand Journal of Marine and Freshwater Resources 3:147-151.

Casselman, J.M. 1974. Analysis of hard tissue of pike *Esox lucius* L. with special reference to age and growth. Pages 13-27 *in* T.B. Bagenal, editor. Aging of fish. The Gresham Press, Old Woking, Surrey, England.

Casselman, J.M. 1990. Growth and relative size of calcified structures of fish. Transactions of the American Fisheries Society 119:673-688.

Casselman, J.M. and J.M. Gunn. 1992. Dynamics in year-class strength, growth, and calcified-structure size of native lake trout (*Salvelinus namaycush*) exposed to moderate acidification and whole-lake neutralization. Canadian Journal of Fisheries and Aquatic Science 49:102-113.

Conner, E., D. Reiser, K. Binkley, D. Paige, and K. Lynch. 1997. Abundance and distribution of an unexploited bull trout population in the Cedar River Watershed, Washington. Pages 403 – 411 *in* Mackey, W.C., M.K. Brewin, and M. Monita, editors. Friends of the bull trout conference proceedings. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary.

Devries, D.R. and R.V. Frie. 1996. Determination of age and growth. Pages 483-512. *in* B.R. Murphy and D.W. Willis, editor. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Donald, D.B. and D.J. Alger. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.

Erickson, C.M. 1983. Age determination of Manitoban walleyes using otoliths, dorsal spines, and scales. North American Journal of Fisheries Management 3:176-181.

Federal Register. 1999. Determination of threatened status for bull trout in the coterminous United States. U.S. Federal Register 64(210): 58909-58936.

Fraley, J.J. 1994. Bull trout, further adventures of a travelin' fish. Montana Outdoors Magazine, Montana Department Fish, Wildlife, and Parks, May/June.

Fraley, J.J. and B.B. Sheperd. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead lake and river system, Montana. Northwest Science 63:133-143.

Fredenberg, W. 1996. Bull trout status report for the international headwaters of the Oldman River Drainage: St. Mary, Belly, and Waterton rivers. U.S. Fish and Wildlife Service, Kalispell, Montana.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. U.S. Department of Agriculture, Forest Service, Willamette National Forest, Eugene, Oregon.

Hining, K.J., J.L. West, M.A. Kulp, and A.D. Neubauer. 2000. Validation of scales and otoliths for estimating age of rainbow trout from southern Appalachian streams. North American Journal of Fisheries Management 20:978-985.

Johnson, L. 1976. Ecology of arctic populations of lake trout, (*Salvelinus namaycush*), lake whitefish, (*Coregonus clupeaformis*), Artic char, (*S. alpinus*), and associated species in unexploited lakes of the Canadian Northwest Territories. Journal of the Fisheries Research Board of Canada 33:2459-2488.

Laakso, M. 1955. Variability in scales of cutthroat trout in mountain lakes. Proceedings of the Utah Academy of Science, Arts, and Letters 32:81-87.

MacKay, W.C., G.R. Ash, and H.J. Horris (eds.). 1990. Fish aging methods for Alberta. R.L. & L. Environmental Services Ltd. in association with Alberta Fish and Wildlife Division and University of Alberta, Edmonton.

Martin, N.V. 1966. The significance of food habits in the biology, exploitation and management of Algonquin Park, Ontario, lake trout. Transactions of the American Fisheries Society 95:415-422.

McConnell, W.J. 1952. The opercular bone as an indicator of age and growth in carp. *Cyprinus carpio Linnaeus*. Transactions of the American Fisheries Society 81:138-149.

Michels, W.R. 1996. St. Mary drainage angling report. Glacier National Park. Unpublished Report.

Mills, K.H. and R.J. Beamish. 1980. Comparison of fin-ray and scale age determinations for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. Canadian Journal of Fisheries and Aquatic Science 37:534-544.

Mogen, J.M. and L.R. Kaeding. 2000. Ecology of bull trout (*Salvelinus confluentus*) in the Saint Mary River drainage, a progress report. Prepared for U.S. Bureau of Reclamation.

Mugiya, Y. 1972. On aberrant sagittas of teleostean fishes. Japanese Journal of Ichthyology 19:11-14.

NCSS. 1999. Number cruncher statistical system 2000. Kaysville, Utah.

Nelson, J.S. and M.J. Paetz. 1992. The fishes of Alberta. 2nd Edition. The University of Alberta Press, Edmonton, Alberta.

Neuhold, J.M. 1956. Age and growth of the Utah chub, *Gila atraria* (Girard), in Panguitch Lake and Navajo Lake, Utah, from scales and opercular bones. Transactions of the American Fisheries Society 85:217-233.

Niewinski, B.C. and C.P. Ferreri. 1999. A comparison of three structures for estimating the age of yellow perch. North American Journal of Fisheries Management 19:872-877.

Nordeng, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, north Norway. 1. Age and spawning frequency determined from scales and otoliths. Nytt Magasin foer Zoology. (Oslo) 10:67-123.

Riehle, M., W. Weber, A.M. Stuart, S. L. Thiesfeld, and D. E. Ratliff. 1997. Progress report of the multi-agency study of bull trout in the Metolius River System, Oregon. Pages 137–144 *in* Mackey, W.C., M.K. Brewin, and M. Monita, editors. Friends of the bull trout conference proceedings. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary.

Rieman, B.E. and J.D. McIntyre. 1993. Demographic and habitat requirements for the conservation of bull trout. General technical report, INT-302. U.S. Forest Service, Intermountain Research Station, Ogden, Utah.

Schmitt, D.N. and W.A. Hubert. 1982. Comparison of cleithra and scales for age and growth analysis of yellow perch. Progressive Fish-Culture 44:87-88.

Sharp, D. and D.R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management 8:367-372.

Shirvell, C.S. 1980. Validity of fin-ray aging for brown trout. Journal of Fisheries Biology 18:377-383.

Sikstrom, C.B. 1983. Otolith, pectoral fin ray, and scale age determinations for arctic grayling. Progressive Fish-Culture 45:220-223.

Simkiss, K. 1974. Calcium metabolism of fish in relation to aging. Pages 1-12 *in* T.B. Bagenal, editor. Aging of Fish. The Gresham Press, Old Woking, Surrey, England.

Wagner, R. and G.W. Fitzgerald. 1995. Fisheries status report: St. Mary storage unit. Final Report 1995. U.S. Fish and Wildlife Service, Lewistown, Montana.

Weatherly, A.H. and H.S. Gill. 1987. The biology of fish growth. Academic Press Incorporated. (London) Ltd.

Whitworth, W.E. and R.J. Strange. 1983. Growth and production of sympatric brook and rainbow trout in an Appalachian stream. Transactions of the American Fisheries Society 112:469-475.

Williamson, C.J. and J.S. Macdonald. 1997. The use of three aging techniques to estimates the growth rates for rainbow trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) from selected locations near Takla Lake B.C. Canadian Technical Report of Fisheries and Aquatic Sciences 2191.

APPENDIX A

MEAN BACK-CALCULATED LENGTHS FROM DISTANCE BETWEEN THE FOCUS AND EACH ANNULUS ON SCALES FOR BULL TROUT IN BOULDER, KENNEDY, OTATSO, AND LEE CREEKS

Table 4. Mean back-calculated length from distance between the focus and each annulus on scales for bull trout in Boulder Creek. Among age-classes within individual annuli, data that do not have a letter superscript in common have mean values that are significantly different (One-Way ANOVA, $P < 0.05$; Bonferroni (All-Pairwise) Multiple Comparison Test, $P < 0.05$). If no superscript appears, there are no significant differences among age-classes within that annulus.

Age-Class	Annulus									
	I	II	III	IV	V	VI	VII	VIII	IX	X
2	**Mean** = 86.69 **S. D.** = 25.06 ***N*** = **26**									
3	**Mean** = 72.59 **S. D.** = 15.07 ***N*** = **54**	131.91 24.17								
4	**Mean** = 85.33 **S. D.** = 25.47 ***N*** = **15**	155.13 49.09	228.2 72.1							
5	**Mean** = 83.75 **S. D.** = 24.55 ***N*** = **12**	151.33 37.63	238.92 57.83	307.92 73.46						
6	**Mean** = 90.82 **S. D.** = 16.26 ***N*** = **11**	161.36 24.3	248 35.13	337.64 44.23	405.64 60.82					
7	**Mean** = 89.72 **S. D.** = 24.69 ***N*** = **18**	158.11 33.66	242.56 39.22	327.06 50.46	390.83 57.5	434 62.74				
8	**Mean** = 87.36 **S. D.** = 29.57 ***N*** = **11**	151.73 35.09	236.55 45.4	317.09 46.52	388.45 55.71	438.27 56.65	477.73 58.04			
9	**Mean** = 91.43 **S. D.** = 18.34 ***N*** = **7**	157.14 24.88	244.57 36.55	336 42.58	410.57 54.34	465.86 61.56	510.57 67.79	543.29 71.95		
10	**Mean** = 71.8 **S. D.** = 19.99 ***N*** = **5**	133 27.25	205 33.65	295.4 36.03	357.4 33.89	410.8 42.15	451.8 46.39	486 51.22	517.8 55.08	
11	**Mean** = 81 **S. D.** = **0** ***N*** = **1**	154	272	325	380	430	483	518	558	589
Total	**Mean** = 81.96 **S. D.** = 22.11 ***N*** = 160	145.34 32.91 134	237.44 49.17 80	322.12 51.63 65	392.66 54.99 53	437.57 58.09 42	482.13 59.1 24	519.31 65.28 13	524.5 51.93 6	589 0 1

Table 5. Mean back-calculated length from distance between the focus and each annulus on scales for bull trout in Kennedy Creek. Among age-classes within individual annuli, data that do not have a letter superscript in common have mean values that are significantly different (One-Way ANOVA, $P < 0.05$; Bonferroni (All-Pairwise) Multiple Comparison Test, $P < 0.05$). If no superscript appears, there are no significant differences among age-classes within that annulus.

Age-Class	Annulus							
	I	II	III	IV	V	VI	VII	VIII
2	**Mean** = 75.92 **S. D.** = 14.42 ***N*** = **13**							
3	**Mean** = 77.5 **S. D.** = 23.09 ***N*** = **22**	145.23[a] 23.78						
4	**Mean** = 99.26 **S. D.** = 29.37 ***N*** = **19**	181.21[b] 46.16	256.79 50.58					
5	**Mean** = 94.18 **S. D.** = 24.36 ***N*** = **33**	172.06[ab] 35.95	268.33 47.74	341.51 48.73				
6	**Mean** = 89.77 **S. D.** = 25.95 ***N*** = **30**	160.33[ab] 37.94	244.37 52.49	325 56.19	385.07 52.9			
7	**Mean** = 86.33 **S. D.** = 20.17 ***N*** = **18**	159.89[ab] 29.53	245.33 27.3	336.61 36.77	401.78 38.99	445.83 41.21		
8	**Mean** = 98.71 **S. D.** = 15.73 ***N*** = **7**	162.86[ab] 30.94	238.71 29.56	336.29 39.62	407 56.49	461.71 61.96	497.14 70.74	
9	**Mean** = 77.2 **S. D.** = 9.36 ***N*** = **5**	147.8[ab] 21.53	227.8 38.78	314.8 48.94	386.2 55.47	460.8 54.56	520.8 47.23	559 47.77
Total	**Mean** = 88.5 **S. D.** = 24.27 ***N*** = 147	163.3 36.09 134	252.6 46.37 112	333.41 48.43 93	392.73 49.29 60	452.03 47.54 30	507 60.73 12	559 47.77 5

Table 6. Mean back-calculated length from distance between the focus and each annulus on scales for bull trout in Otatso Creek (below the falls). Among age-classes within individual annuli, data that do not have a letter superscript in common have mean values that are significantly different (One-Way ANOVA, $\underline{P} < 0.05$; Bonferroni (All-Pairwise) Multiple Comparison Test, $\underline{P} < 0.05$). If no superscript appears, there are no significant differences among age-classes within that annulus.

Age-Class	Annulus						
	I	II	III	IV	V	VI	VII
2	**Mean** = 111 **S. D.** = 0 *N* = 1						
3	**Mean** = 84.14 **S. D.** = 13.99 *N* = 14	151.36 28.54					
4	**Mean** = 78.83 **S. D.** = 30.77 *N* = 12	155.42 37.46	229.92 48.75				
5	**Mean** = 91.2 **S. D.** = 13.85 *N* = 10	167.5 29.43	248.4 47.35	314.2 55.71			
6	**Mean** = 85.5 **S. D.** = 20.15 *N* = 10	158.5 25.37	249 30.01	335.3 28.96	390.3 33.82		
7	**Mean** = 106 **S. D.** = 22.35 *N* = 7	177.43 38.41	252.86 40.83	337.71 31.75	397 23.22	434.29 22.25	
8	**Mean** = 96 **S. D.** = 0 *N* = 1	174	239	312	383	428	471
Total	**Mean** = 88 **S. D.** = 21.76 *N* = 55	160.37 31.52 54	243.55 41.7 40	327.54 40.77 28	392.5 28.5 18	433.5 20.72 8	471 0 1

Table 7. Mean back-calculated length from distance between the focus and each annulus on scales for bull trout in Otatso Creek (above the falls). Among age-classes within individual annuli, data that do not have a letter superscript in common have mean values that are significantly different (One-Way ANOVA, $\underline{P} < 0.05$; Bonferroni (All-Pairwise) Multiple Comparison Test, $\underline{P} < 0.05$). If no superscript appears, there are no significant differences among age-classes within that annulus.

Age-Class	Annulus							
	I	II	III	IV	V	VI	VII	VIII
2	**Mean** = 76.85[ab] **S. D.** = 18.29 ***N*** **= 41**							
3	**Mean** = 82.11[ab] **S. D.** = 16.83 ***N*** **= 38**	147.47[ab] 20.87						
4	**Mean** = 74.76[a] **S. D.** = 14.88 ***N*** **= 38**	139.37[a] 29.78	211.61[ab] 42.23					
5	**Mean** = 82.1[ab] **S. D.** = 29.52 ***N*** **= 29**	140.28[ab] 38.1	206.69[a] 47.02	271.97[a] 52.81				
6	**Mean** = 87.95[ab] **S. D.** = 35.5 ***N*** **= 21**	156.76[ab] 49.56	238.71[ab] 62.17	313.29[ab] 64.01	371.95 68.16			
7	**Mean** = 96.44[b] **S. D.** = 18.69 ***N*** **= 16**	170.31[b] 31.38	253.75[b] 43.12	335.06[b] 48.64	400.5 53.98	439.75 55.42		
8	**Mean** = 111[ab] **S. D.** = **0** ***N*** **= 1**	204[ab]	282[ab]	363[ab]	430	486	536	
9	**Mean** = 88.5[ab] **S. D.** = 10.61 ***N*** **= 2**	170.5[ab] 16.26	236.5[ab] 10.61	293.5[ab] 9.19	353.5 2.12	401.5 9.19	451.5 12.02	487 12.73
Total	**Mean** = 81.56 **S. D.** = 22.67 ***N*** = 186	148.48 34.56 145	223.02 50.47 107	301.12 60.12 69	383.9 61.6 40	438.16 53.32 19	479.67 49.52 3	487 12.73 2

Table 8. Mean back-calculated length from distance between the focus and each annulus on scales for bull trout in Lee Creek. Among age-classes within individual annuli, data that do not have a letter superscript in common have mean values that are significantly different (One-Way ANOVA, $\underline{P} < 0.05$; Bonferroni (All-Pairwise) Multiple Comparison Test, $\underline{P} < 0.05$). If no superscript appears, there are no significant differences among age-classes within that annulus.

Age-Class	Annulus						
	I	II	III	IV	V	VI	VII
2	**Mean** = 82.15 **S. D.** = 18.4 ***N*** = **41**						
3	**Mean** = 82.69 **S. D.** = 15.13 ***N*** = **52**	145.06[ab] 20.22					
4	**Mean** = 75.09 **S. D.** = 17.69 ***N*** = **11**	131.45[a] 25.74	192.55[a] 31.6				
5	**Mean** = 81.71 **S. D.** = 17.79 ***N*** = **14**	152.93[ab] 24.68	239.21[b] 34.56	316.64 44.65			
6	**Mean** = 89 **S. D.** = 15.25 ***N*** = **13**	165.08[b] 22.11	252.08[b] 37.54	336.23 53.75	401.54 50.46		
7	**Mean** = 80 **S. D.** = 8.22 ***N*** = **5**	142.2[ab] 9.42	208.4[ab] 18.7	279 42.07	341 50.44	379.4 59.01	
8	**Mean** = 87.13 **S. D.** = 15.29 ***N*** = **8**	153.5[ab] 25.81	223.5[ab] 42.75	300.75 44.98	367.25 51.59	420.5 53.33	459.88 54.26
Total	**Mean** = 82.58 **S. D.** = 16.42 ***N*** = 144	147.72 23.07 103	226.94 40.44 51	315.13 49.57 40	379.35 54.51 26	404.69 57.03 13	459.88 54.26 8

Table 9. Overall mean back-calculated length from distance between the focus and each annulus on scales for bull trout in the Saint Mary River drainage. Among age-classes within individual annuli, data that do not have a letter superscript in common have mean values that are significantly different (One-Way ANOVA, $\underline{P} < 0.05$; Bonferroni (All-Pairwise) Multiple Comparison Test, $\underline{P} < 0.05$). If no superscript appears, there are no significant differences among age-classes within that annulus.

Stream	Annulus									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Boulder Creek	**Mean** = 81.96[a,b]	145.34[a]	237.44[a,b]	322.12[a,b]	392.66	437.57	482.13	519.31	524.5	589
	S. D. = 22.11	32.91	49.17	51.63	54.99	58.09	59.1	65.28	51.93	0
	N = 160	134	80	65	53	42	24	13	6	1
Kennedy Creek	**Mean** = 88.5[a]	163.3[c]	252.6[a]	333.41[a]	392.73	452.03	507	559		
	S. D. = 24.27	36.09	46.37	48.43	49.29	47.54	60.73	47.77		
	N = 147	134	112	93	60	30	12	5		
Otatso Creek (below the falls)	**Mean** = 88[a,b]	160.37[b,c]	243.55[a,b]	327.54[a,b]	392.5	433.5	471			
	S. D. = 21.76	31.52	41.7	40.77	28.5	20.72	0			
	N = 55	54	40	28	18	8	1			
Otatso Creek (above the falls)	**Mean** = 81.56[b]	148.48[a,b]	223.02[b]	301.12[b]	383.9	438.16	479.67	487		
	S. D. = 22.67	34.56	50.47	60.12	61.6	53.32	49.52	12.73		
	N = 186	145	107	69	40	19	3	2		
Lee Creek	**Mean** = 82.58[a,b]	147.72[a,b]	226.94[b]	315.13[a,b]	379.35	404.69	459.88			
	S. D. = 16.42	23.07	40.44	49.57	54.51	57.03	54.26			
	N = 144	103	51	40	26	13	8			
Grand Total	**Mean** = 83.85	152.22	237.09	320.33	389.13	437.44	484.25	526	524.5	589
	S. D. = 21.81	33.19	48.22	52.72	52.58	53.49	57.93	60.48	51.93	0
	N = 692	570	390	295	197	112	48	20	6	1