FISHERY RESEARCH

ASSESSMENT OF NATIVE SALMONIDS ABOVE HELLS CANYON DAM, IDAHO

ANNUAL PROGRESS REPORT
July 1, 2006 — June 30, 2007

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IDFG Report Number 07-50
June 2007

Assessment of Native Salmonids Above Hells Canyon Dam, Idaho

Project Progress Report

2006 Annual Report

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U.S. Department of Energy
Bonneville Power Administration
Division of Fish and Wildlife
P.O. Box 3621
Portland, OR 97283-3621

Project Number 1998-002-00
Contract Number 00022947

IDFG Report Number 07-50
June 2007

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PART #1: FACTORS AFFECTING THE DISTRIBUTION, ABUNDANCE, AND POPULATION DYNAMICS OF MOUNTAIN WHITEFISH IN IDAHO

ABSTRACT

Mountain whitefish *Prosopium williamsoni* are one of four native resident salmonids in the upper Snake River basin in Idaho, but comparatively little investigation has been made regarding their population characteristics. We electrofished 2,043 study sites to assess whether physiochemical stream conditions affected mountain whitefish distribution, abundance, and population dynamics. Mountain whitefish were captured at only 106 (5.2%) sites and in only 11 of the 20 major river drainages within the study area. They were present in only 2% of the sites where width was less than 10 m, but 88% of the study sites where width was greater than 15 m. We estimated that, within the upper Snake River basin, there were approximately 5.7 million ± 1.9 million mountain whitefish, mostly in fifth- to seventh-order streams, which comprised only 3% of the total stream kilometers but constituted 67% of the total abundance. Mean annual temperature was positively correlated and site elevation was negatively correlated with mean length at age, and these variables explained 67% of the variation in mean length at age-0 and 45% of the variation in mean length at age-2. Mountain whitefish were long-lived, with 18 of 20 populations containing fish estimated to be ≥ 10 years of age. The oldest fish captured was an estimated 24 years old. Estimates of total annual survival rate, based on catch curve analysis, averaged 0.76 and ranged from 0.59 to 0.87. Whitefish transitioned from immature to mature at about 250 mm and about age 2. Males matured at a smaller size than females, but not at a younger age. Using logistic regression analyses, fish length alone explained 82 and 83% of the variation in the length at maturity models for males and females, respectively, whereas fish age alone explained 79% of the variation in the age at maturity models for both genders. The addition of other variables added little to the strength of the maturity models.

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INTRODUCTION

Like most other native salmonids in western North America, the mountain whitefish *Prosopium williamsoni* has, over the past century or more, experienced declines in abundance and distribution in portions of its historical range. However, because mountain whitefish are not as appealing to anglers as other salmonids, and thus have received less attention from fisheries managers and the angling public (Northcote and Ennis 1994), even less is known of the extent of these declines than for other salmonids. In fact, to our knowledge no broad-scale assessment of the distribution or abundance of mountain whitefish has ever been made in Idaho, or elsewhere. Declines in mountain whitefish populations may not be of the same magnitude as for other native salmonids because their historical distribution was originally much more limited than for other native salmonids, generally being restricted to mainstem rivers whereas other salmonids often occur far upstream into headwater tributaries. Mountain whitefish persist in many mainstem river reaches, despite the fact that management interventions such as population supplementation or reduced harvest regulations, which are commonplace for other salmonids, are rarely if ever used for mountain whitefish. On the contrary, from the 1950s into the 1970s, mountain whitefish removal programs were undertaken in some areas of the western United States (e.g., Corsi 1956; Jeppson 1982) because they were perceived by anglers and biologists to be in competition with trout for food and space, although this has never been substantiated (e.g., Pontius and Parker 1973; Fuller 1981; DosSantos 1985).

Mountain whitefish distribution is generally limited to larger rivers, which are more commonly located adjacent to private rather than public property. Thus, their habitat is more likely to be altered by water diversion and storage, or other anthropogenic changes, and such alterations have been shown to impact whitefish populations (Erman 1973; Bergstedt and Bergersen 1997; Paragamian 2002). Because of their sensitivity to habitat alterations, they are commonly used as an indicator species (Nener et al. 1995; Bergstedt and Bergersen 1997; McPhail and Troffe 1998; Cash et al. 2000). Therefore, a primary objective of this study was to estimate the distribution and abundance of mountain whitefish in the upper Snake River basin in Idaho, and to estimate abundance within major river drainages. By correlating whitefish distribution and abundance with stream characteristics, we attempted to ascertain what environmental factors may influence whitefish occupancy and density.

Similar to the lack of information on the status of mountain whitefish, little is known of basic population dynamics such as growth, mortality, longevity, maturity, and sex ratio. Mountain whitefish appear to grow most rapidly in their first few years of life (Pettit and Wallace 1975), and tend to mature by age 3 or 4 (Thompson and Davies 1976). Since whitefish are often virtually unexploited by anglers, survival rates may be much higher than for other salmonids, but few estimates are available in the literature (but see Thompson and Davies 1976). While stream resident trout exhibit much phenotypic plasticity in population dynamics, such as survival, growth, and length and age at sexual maturity (Jonsson and L'Abee-Lund 1993; Einum and Fleming 1999; Meyer et al. 2003), the more narrow distribution of mountain whitefish within a watershed may prevent such plasticity in this species. Our second objective was to characterize mountain whitefish population dynamics and the amount of variation among populations, and assess what factors influenced their population dynamics by collecting fish from a number of locations having a variety of environmental conditions.

OBJECTIVES

1. Determine the distribution, abundance, and population dynamics of mountain whitefish in the upper Snake River basin.

2. Assessing what environmental factors influence the distribution, abundance, and population dynamics of mountain whitefish in Idaho.

STUDY AREA

The Snake River flows through southern Idaho from east to west, flowing 1,674 km from the headwaters in Yellowstone National Park to its confluence with the Columbia River (Figure 1). The upper Snake River basin is defined herein as that portion of the Snake River drainage from Hell's Canyon Dam upstream to the headwaters of all tributaries, except (1) Pine Creek, Burnt River, Powder River, and Malheur River in Oregon, and (2) the South Fork of the Snake River and Salt River above their confluence at the Idaho-Wyoming border, except the portion of the Salt River drainage that occurs in Idaho. Discharge in most of the streams in this portion of the upper Snake River basin is heavily influenced by snowmelt and peaks between April and June. However, stream discharge in the Snake River and in a number of major tributaries is highly regulated for agricultural and hydroelectric uses by dams and diversions. Elevation within the basin ranges from 466 m at Hell's Canyon Dam to over 4,000 m at mountain peaks. The climate is semiarid with an average precipitation of about 25 cm.

The historical range of mountain whitefish in the upper Snake River basin apparently includes all major river drainages (Simpson and Wallace 1982; Behnke 2002). The Sinks drainages in eastern Idaho were not included in our analyses because (1) mountain whitefish are only found in the Big Lost River drainage within the Sinks drainages, (2) mountain whitefish in the Big Lost River are genetically distinct from whitefish in surrounding areas (Whiteley et al. 2006), and (3) a separate status assessment and subsequent management plan has been developed for mountain whitefish in the Sinks drainage by the Idaho Department of Fish and Game.

Redband trout *Oncorhynchus mykiss*, bull trout *Salvelinus confluentus*, and Yellowstone cutthroat trout *O. clarkii bouvierii* are also native, as are a number of nongame species. Nonnative trout, including rainbow trout *O. mykiss*, brook trout *Salvelinus fontinalis*, and brown trout *Salmo trutta* have been introduced throughout the basin and have widely established self-sustaining populations.

METHODS

Distribution and Abundance

Data collection occurred between 1999 and 2006 at 2,043 study sites (Table 1). We selected study sites using a standard 1:100,000 hydrography layer throughout the study area. We randomly selected study streams except where random selection was not possible due to access restrictions or river conditions that precluded sampling (e.g., no boat ramp or unsafe boat navigability). The density of sites (i.e. the sample size) across the study area was based on: (1) time constraints, considering the vastness of the study area; and (2) the limited distribution of mountain whitefish in some areas, where less sampling was needed to characterize distribution and abundance.

At each study site, unless the site was dry (*n* = 581 study sites), fish were captured using electrofishing gear. Sampling usually occurred during low to moderate flow conditions (late June to early October) to facilitate fish capture and help to standardize sampling conditions. Fish were identified, enumerated, measured to the nearest millimeter (total length, TL) and gram, and released.

Sampling in small streams (i.e. less than about 8 m wide) was conducted by depletion electrofishing (*n* = 1,356), using one or more backpack electrofishers (Smith-Root Model 15-D) with pulsed DC. Block nets were installed at the upper and lower ends of the sites to meet the population estimate modeling assumption that the fish populations were closed. Depletion sites were typically (72% of the time) between 80 and 120 m in length (depending on habitat types and ability to place block nets) and averaged 91.6 m. Maximum-likelihood abundance and variance estimates were calculated with the MicroFish software package (Van Deventer and Platts 1989). If no salmonids were captured on the first pass, no more passes were made and mountain whitefish were assumed to be absent. When all mountain whitefish were captured on the first pass, we estimated abundance to be the total catch. Because electrofishing is known to be size selective (Reynolds 1996), whitefish were separated into two length categories, <100 mm TL and ≥100 mm TL; abundance estimates were made separately for these two size groups.

At sites too large to perform backpack electrofishing (*n* = 46), mark-recapture electrofishing was conducted with a canoe- or boat-mounted unit (Coffelt Model Mark-XXII) and pulsed DC. Recapture runs were made two to seven days after marking fish, and we assumed there was no movement of marked or unmarked whitefish into or out of the study site. Site length was much longer than for depletion sites (typically 1,000–7,800 m), reducing the likelihood of fish movement. Log-likelihood estimates of whitefish abundance were made using the Mark Recapture for Windows software package (Montana Fish, Wildlife and Parks 1997). When possible, estimates were made separately by size groups (usually 25-50 mm) and summed to produce an estimate of total number of whitefish present. When the number of recaptures was very low, we increased the size groups to 100 mm and used the modified Peterson mark-recapture model to estimate abundance. We could not estimate whitefish <100 mm at the mark-recapture sites due to extremely low capture efficiencies of small fish, thus none of our analyses include whitefish of this size for the mark-recapture sites.

Where electrofishing was not possible, snorkeling was conducted (*n* = 60) following the protocol of Thurow (1994). We counted all mountain whitefish ≥ 100 mm, and total counts were used as minimal abundance estimates with no correction for any sightability bias.

We performed the following steps to approximate abundance within each stream order (Strahler 1964): 1) we summed the total length of stream in ArcGIS; 2) we standardized our estimates of abundance to the number of mountain whitefish per 100 meters of stream (our typical study site length); 3) we calculated a mean abundance and variance from all the survey sites; and 4) we multiplied mean abundance by the total number of 100 meter reaches within a particular stream order to estimate total abundance for that stream order. We then summed the mountain whitefish abundance estimates for all stream orders to obtain an overall abundance estimate (see Meyer et al. 2003). We used the stratified random sampling formulas from Scheaffer et al. (1996) to calculate population totals and variances:

$$N_{census} = \sum_{i=1}^{L} N_i \overline{y}_i$$

and for variance of N_{census} we used the formula:

$$\widehat{V}(N_{census}) = \sum_{i=1}^{L} N_i^2 \left(\frac{N_i - n_i}{N_i} \right) \left(\frac{s_i^2}{n_i} \right)$$

where s_i^2 is the variance of the observations in stratum i and n_i is the sample size within stratum i.

All sample sites, including dry and fishless sites, were included in these estimates. Below American Falls Reservoir, the mainstem of the Snake River and the minor tributaries that were lumped into this river drainage (i.e., all those tributaries not listed in Table 1) contained too few mountain whitefish to quantifiably estimate abundance. Therefore, the abundance estimate for this area was extrapolated only to seventh-order stream kilometers above American Falls Reservoir, and was based on two abundance estimates (5.3 km average reach length) obtained from this reach.

Population Dynamics

We used backpack- and boat-mounted electrofishing units to collect 1,783 mountain whitefish from 20 stream locations in 2005 and 2006. Sample streams and the study sites within the streams were selected arbitrarily, but we purposefully distributed 18 of the study sites across a broad geographic area in southern Idaho (Figure 1) in order to include a wide variety of stream conditions (Table 2). Two sample locations from northern Idaho were included to broaden our assessment. The length of stream electrofished at a site varied depending on the amount of effort needed to capture an adequate number of fish, but generally was from 200-2,000 m long. Because mountain whitefish spawn in the late fall, fish were collected in late summer to mid-fall to facilitate maturity confirmation. Captured fish were transported directly to a freezer for storage.

Sacrificed fish were thawed in the laboratory and measured for total length (TL; nearest mm) and weight (nearest g). Sagittal otoliths were removed and stored dry in vials. Age was initially estimated by viewing whole otoliths, dry or submersed in saline, with a dissecting microscope using reflected or transmitted light. The same two readers estimated the age of all fish. A subsample of otoliths were cross sectioned to (1) corroborate estimated ages throughout all age classes, (2) more thoroughly substantiate the estimated age on older fish (i.e., all fish ≥ 8 years old), and (3) resolve differences in estimated age between readers of whole otoliths. Toward this end, the subsample of otoliths were placed in epoxy and sliced with an Isomet® low speed saw, and the same readers estimated age by viewing the cross-sections with a binocular microscope. The same readers estimated age by viewing the otolith cross-sections with a compound microscope. A drop of vegetable oil was placed on the sliced sections to reduce glare from scratches caused by the sawing. Slicing increased estimated age by an average of only 1 year, or 14%, however, most of this increase occurred in fish over 8 years of age (Figure 2). Subsequently, all fish ≥ 8 years old were sliced, for a total of 718 readings of sliced otoliths. We assumed the estimated age from sliced otoliths was the correct age in all but two cases. All fish were considered one year old when they reached their first January. The index of average percent error (Beamish and Fournier 1981) for the initial readings of whole otoliths at all sites averaged 4.1% and ranged from 0.7% to 13.6%.

Gender and maturity were determined by laboratory examination of the gonads. Males were classified as immature if testes were opaque and threadlike and mature if they were large and milky white. Females were classified as immature if the ovaries were small, granular and translucent and mature if they contained well-developed eggs that filled much of the abdominal cavity (Strange 1996). Eggs were counted from 443 mature females across all sites, and a curvilinear (i.e. power function) regression equation was developed to predict fecundity (F) from fish length (TL). A length-weight relationship was similarly developed.

Growth was estimated by calculating the mean length at age (and 95% CIs) from an age-length key (DeVries and Frie 1996) developed for each sample location. Because our growth data was obtained throughout the fall, we used julian date of the sample in all subsequent growth analysis to account for this known variation instead of back-calculating growth to a standardized date, which tends to underestimate length at age (Campana 1990).

Following Robson and Chapman (1961), we estimated total annual survival rate (*S*) and 95% CIs using catch curve analyses. Catch-curve analyses have a number of assumptions, including that (1) *S* is uniform with age and does not change over time, (2) the population is sampled randomly, (3) recruitment is constant each year, and (4) all ages are equally vulnerable to the sampling gear. We assumed all sites met the first and third assumptions, but the only sites where the second assumption was met was where both abundance and population dynamics data were collected (n = 6). At these sites, to control for bias in fish size selectivity using electrofishing (assumption 4), we adjusted the catch curves by the estimated capture efficiency for each size class obtained from the mark-recapture analysis. Only age-2 and older mountain whitefish were adequately recruited to the electrofishing gear and thus useable for survival estimates. For comparison, we present both the unadjusted and adjusted estimates of *S*.

Habitat Measurements

Several physical and physiochemical stream attributes were measured to assess their effect on mountain whitefish distribution, abundance, and population dynamics (Table 2). Selection of the stream characteristics we measured was based on their ecological importance, on previous research into factors related to fish growth as well as age and length at maturity, and on their ease of collection. We generally focused on variables we felt reflected stream size or fish growing conditions.

At each collection site, we determined elevation (m) from U.S. Geological Survey (USGS) 1:24,000 topographic maps using UTM coordinates obtained at the lower end of the reach electrofished. Stream order (Strahler 1964) was determined from a 1:100,000 hydrography layer using geographic information system software. Reach gradient (%) was determined using the software package Topo! Version 2.7.3 for Windows (National Geographic Society); stream length (m) was traced between the two contour lines that bounded the lower end of the study site (average traced distance was about 2 km), and gradient was calculated as the elevational increment between the contours divided by the traced distance. Conductivity (µS/cm) was measured with a calibrated handheld conductivity meter accurate to ±2%. Stream width (m) was calculated from the average of 10 readings through the reach that was electrofished, except for large rivers (i.e. >15 m in width), where width was determined using a rangefinder accurate to ±1 m.

At the population dynamics study sites, we obtained water temperature data from several sources, including the U.S. Bureau of Reclamation, the U.S. Geological Survey, the University of Wyoming, and the Idaho Department of Environmental Quality. At some locations, we deployed electronic temperature loggers that continuously recorded water temperature. At two locations (Teton River upper site, and Fall River), data was missing for several weeks in 2005. To fill these gaps, we developed linear regressions for periods of record where data was not missing, comparing water temperature at the site to the water temperature at a nearby location that contained data for the missing period (r^2 for these comparisons was 0.97 and 0.73, respectively). We used this relationship to predict temperature for the missing period at the study site, based on data at the adjacent site. At three sites, complete data was not available for 2005, so a combination of 2005 and 2006 data was used instead to generate a complete year. From this data, mean annual water temperature was calculated, as was mean temperature throughout what we deemed to be the growing season (April-September).

Data Analyses

We used a combination of correlation analyses, logistic and multiple regression analyses, and general linear models to assess whether any of the stream attributes we measured were correlated to mountain whitefish characteristics, including their distribution, abundance, fecundity, growth, and survival. We compared the means and 95% confidence intervals (CIs) of several stream characteristics at sites with and without mountain whitefish to assess their relationship to whitefish distribution. At sites that contained mountain whitefish, we used multiple linear regression to assess the amount of variation in areal abundance (fish/m^2) that was explained by stream characteristics.

To assess the relationship between fecundity and stream conditions, we log transformed the fish length and fecundity data to create a linear relationship, and used linear regression to relate fecundity to fish length. Outliers were removed if the standardized residual values were ≥ 3.0 (Montgomery 1991). We then used multiple linear regression to assess whether any remaining variation in fecundity, not explained by fish length, could be explained by stream characteristics.

To assess whether stream attributes affected growth of juvenile mountain whitefish differently than older fish, we related mean length (mm) of age-0 and age-2 fish (the time at which most fish matured) to stream attributes with linear regression. We also assessed whether growth was different between male and female mountain whitefish by comparing von Bertalanffy growth functions, but because no differences were noted, we combined the sexes for further analyses. The correlation between survival estimates and stream attributes was also assessed using linear regression.

To evaluate sex ratio at each site, we calculated 95% CIs around the percentage of the population that was female, following Fleiss (1981); CIs not overlapping 50% indicated a statistically significant departure from a 50:50 ratio. We estimated sex ratio for all fish, and for mature fish separately in order to assess whether differential mortality or other factors skewed the sex ratio as fish got older (e.g., Greeley 1933; D.J. Schill, Idaho Fish and Game, unpublished data).

We characterized the variation in length and age at maturity across the study sites. For length at maturity, we did this by estimating at each study location the length at which the probability of being mature was 0.5 (termed ML50), using one of two methods. If there was no overlap between the largest immature and smallest mature fish, we selected the midpoint between the length of these two fish as ML50. If there was overlap, we related fish length to maturity using logistic regression, using a binary dependent variable (0 = immature, 1 = mature), and selected ML50 as the fish length at which the probability of being mature was equal to 0.5. Separate estimates were developed for males and females, since males tended to mature at a smaller size than females, and because size at maturity selection forces are different between sexes (Roff 1992). If there was overlap between immature and mature fish, and a suitable logistic regression could not be fit to the data for a site, no estimate was made at that site. These guidelines were also used for age at maturity by substituting age for length in the analyses.

We first assessed the relationship between length and age at maturity and the stream attributes we measured using simple correlation analyses between stream attributes and ML50 or MA50. We also used multiple logistic regression analyses, in which each fish was considered a sample unit. As above, a binary dependent variable was used for maturity. All independent variables were continuous. Only first order interactions were tested for significance, and were removed from the models if they were not significant. If gender could not be determined (n=123), the fish were not included in the analyses. The Hosmer and Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 1989) was used to determine whether a particular logistic regression model adequately fit the data; those models not satisfying the goodness-of-fit test were discarded. We then used the adjusted R^2 for discrete models (Nagelkerke 1991) to assess how much variation in length or age at maturity was explained by the models.

RESULTS

Distribution and Abundance

A total of 2,043 study sites were sampled across 119,996 km of stream in 20 river drainages in the upper Snake River basin (Table 1). Of these sites, mountain whitefish were captured at only 106 (5.2%) sites. Mountain whitefish were encountered most often in the Payette River (16% of sites), Boise River (16%), and Palisades/Salt drainages (12%). They were not found in 9 of the 20 river drainages, which comprised 36% of the study sites and 41% of the total stream kilometers in the upper Snake River basin. Among only the 11 river drainages where mountain whitefish were present, they were captured at 8% of the sites sampled. In comparison, at least one species of trout was captured at 1,105 (50%) of the sites surveyed. Six hundred twenty-five study sites (28%) were dry or contained too little water to contain fish.

Within the 11 river drainages where mountain whitefish were present, they were rarely caught in small tributary streams, but instead were usually found in wider, lower gradient, mainstem reaches of stream (Figure 3). In first- through third-order streams, mountain whitefish were present in only 18 of 1,142 (1.6%) study sites, whereas in fifth- through seventh-order streams, they were present in 52 of 80 (65%) study sites. Similarly, mountain whitefish were present in 65 (88%) of 74 study sites where width was greater than 15 m, but were present in only 19 (2%) of 846 study sites where width was less than 10 m. Gradient also was strongly correlated with mountain whitefish distribution, with whitefish most likely to be present when gradient was less than 1.0%. Conductivity had little apparent influence on whitefish distribution.

When considering only the 106 study sites where mountain whitefish were present, none of the stream attributes we measured were strongly correlated to whitefish areal abundance. The most strongly correlated variables were stream width (r = 0.33), stream order (r = 0.25), and conductivity (r = 0.19). However, when stream width and conductivity were combined with land ownership (public or private) in a general linear model, the model only explained 33% of the variation in mountain whitefish areal density.

We estimated that, within the upper Snake River basin, there were approximately 5.7 million ± 1.9 million mountain whitefish. Most of this abundance stems from fifth- and seventh-order streams, which comprised only 3% of the total stream kilometers but constituted 67% of the total abundance. Average abundance among all 106 study sites containing mountain whitefish was 0.022/m².

Population Dynamics

Total length (mm) and weight (g) of mountain whitefish formed an exponential relationship and were highly correlated ($g = 0.000004 \cdot TL^{3.157}$, n = 1,803, r^2 = 0.99). Fecundity also fit an exponential relationship with fish length, but there was more scatter to the data ($F = 0.000008 \cdot TL^{3.497}$, n = 479, r^2 = 0.67). Stream width also had a statistically significant relationship to fecundity, with fecundity decreasing as width increased. Adding stream width to the model increased the total amount of variation explained by the model to 72%.

Sex ratio averaged 48% female for all sites combined, and the CIs around most estimates overlapped a 1:1 ratio (Figure 4). There was no difference between the sex ratio for all fish (48 ± 3%) compared to mature fish only (45 ± 5%), as evidenced by overlapping CIs. However, in 16 of 20 comparisons, the proportion of the population that was female was lower for mature fish compared to all fish (Figure 4).

Mountain whitefish grew at a high rate in their first few years, with an average length in the fall of 134 mm at age-0 and 226 mm at age-1. Whitefish age-2 and older grew much slower, especially at age-7 and older, where growth slowed to an average of only 3.4 mm per year. Growth rates were very similar between male and female mountain whitefish, based on a comparison of mean lengths at age and von Bertalanffy growth functions (Figure 5). Mean annual temperature was positively correlated and site elevation was negatively correlated with mean length at age-0 and age-2. Inclusion of these variables alone explained 72% and 51% of the variation in mean length at age-0 and age-2, respectively, and despite the fact that our samples were collected between Julian days 193 and 312, adding Julian date to the regression models explained very little additional variation in length at age for either age class.

Mountain whitefish were long-lived relative to other salmonids, with 17 of 19 populations containing fish estimated to be at least 10 years of age or older (Table 3). Twelve percent of all aged fish were 10 years old or older. Maximum estimated age for all populations averaged 14 years, and the oldest fish captured was estimated to be 24 years old. This longevity was also evident in the estimates of total annual survival rate (S). Total annual survival rate averaged 0.76 and ranged from 0.59 to 0.87 at the six study sites where whitefish length frequency could be extrapolated to an age-length key (Table 4). Adjusting S for size selectivity produced little change in the estimates (Table 4), with correction estimates ranging from 0 to 9% lower than uncorrected estimates.

The smallest mature mountain whitefish among all 20 populations averaged 259 mm, while 7 of the 20 populations had mature fish at age 1. Typically, whitefish transitioned from immature to mature at about 250 mm and about age 2 (Table 3; Figure 6). Males matured at a statistically significantly smaller size than females, but there was no statistical difference in MA50 between genders (Figure 6). The range in ML50 was 193-298 mm for males compared to 246-299 for females, whereas for MA50 the range was 1-3 years old for males compared to 1.5-5 years old for females (Table 3).

For the logistic regression maturity models, fish length alone explained 82 and 83% of the variation in the length at maturity models for males and females, respectively. Adding mean summer temperature to the male maturity model and stream order to the female model increased the amount of variation explained by each of the models to only 84%. The addition of any other stream attributes to the model had even less impact. In comparison, fish age alone explained 79% of the variation in the age at maturity models for both males and females. As with the length at maturity model, the addition of other variables to the age at maturity model added little to the strength of the models for either gender.

DISCUSSION

We estimated there were nearly 6 million mountain whitefish in the upper Snake River basin. Despite this high abundance, their distribution was limited, having been captured in only 5% of all study sites and being completely absent from 9 of the 20 major river drainages within the study area. The limited geographic distribution of mountain whitefish in the upper Snake River basin, coupled with their overall abundance, highlights that, where they do exist in the basin, their importance in community structure is likely high.

How much their distribution has changed from historical levels is difficult if not impossible to assess. Historically, Dry, Marsh, Bannock, and Goose creeks, both Rock creeks, and the Raft River were never large rivers, and if they ever contained whitefish it was probably only in the lower reaches where stream widths were at a maximum (possibly 10-15 m), which now have been extensively altered by irrigation diversions and impoundments, sometimes resulting in complete year-round desiccation.

A surprising finding was the absence of mountain whitefish in large drainages such as the Portneuf River, Blackfoot River (except near the confluence with the Snake River), and Willow Creek drainages. To our knowledge, whitefish have never been documented in these drainages (Simpson and Wallace 1982; Thurow et al. 1988), although no barriers prevent their occurrence, at least at the lower ends of the drainages. Especially surprising was the absence of whitefish within the Owyhee River drainage. Mountain whitefish are known to exist in Battle Creek (KAM, personal observation), one of the larger tributaries (i.e., over 100 km in length) to the Owyhee River. However, in a random distribution of 230 sample sites in this drainage (134 of which were dry), 6 occurred in Battle Creek but none in the reach that is known to contain whitefish. The Owyhee River drainage is geologically and biologically similar to the Bruneau River drainage, where whitefish are sparse but broadly distributed, except for the fact that nonnative smallmouth bass Micropterus dolomieui are widespread in the Owyhee drainage but absent in the Bruneau drainage.

Perhaps a more relevant aspect of the distribution and abundance of mountain whitefish is how it currently compares with that of other native salmonids in the upper Snake River basin.

Above Shoshone Falls, we found that mountain whitefish distribution was much more limited than for Yellowstone cutthroat trout, but whitefish abundance was estimated to be 77% higher than for cutthroat trout (cf. Meyer et al. 2006). Similarly, below Shoshone Falls, mountain whitefish distribution in the Boise, Payette, and Weiser rivers was much less than for bull trout, but whitefish abundance far exceeded that for bull trout (cf. High et al. 2005).

We found that mountain whitefish were rarely found in smaller streams, but instead were located almost exclusively in larger, lower gradient mainstem rivers, where they appeared to be relatively abundant. Such a pattern of distribution and abundance is common for this species (Northcote and Ennis 1994). Few other stream conditions appeared to have much influence on mountain whitefish abundance. This suggests that only larger rivers provide adequate habitat suitability for mountain whitefish, such as cold water for metabolic function and coarse substrate for spawning and rearing. Once these basic needs are met, our results suggest that additional stream conditions we measured had little impact on the distribution and abundance of whitefish. The affiliation of mountain whitefish with wider stream segments was strong but not complete; although rare, whitefish were found in stream segments as small as 2 m wide. However, whitefish ≥ 300 mm were not found in stream segments less than 5 m wide.

A number of factors may have biased our estimates of mountain whitefish abundance in the upper Snake River basin. First, estimating abundance using snorkeling and depletion electrofishing techniques that were uncorrected for sampling efficiency biases (e.g., Riley and Fausch 1992; Peterson et al. 2004; Thurow et al. 2006) almost certainly underestimated true whitefish abundance. Second, no estimates could be made for whitefish < 100 mm at all mark-recapture and snorkel sites, which were typically done in fifth-order and higher stream segments where whitefish were most likely to be present. In addition, we assumed our one-time sample adequately portrayed the abundance of mountain whitefish at each location, but they are known to make significant seasonal movements (Pettit and Wallace 1975). Finally, mountain whitefish reside in many lentic habitats in the upper Snake River basin, such as American Falls Reservoir and Palisades Reservoirs, and in many reaches of the Snake River below American Falls, but these areas were not included in this study because we could not obtain recent reliable abundance estimates. Considering these potential sources of bias, we believe our design considerably underestimated whitefish abundance in the upper Snake River basin, and it should be viewed as a minimum estimate.

The population dynamics of mountain whitefish in our study were similar to that found in previous studies. Fecundity of mountain whitefish in Idaho (our study) was slightly but consistently higher than for whitefish in Montana (Brown 1952), Utah (Wydoski 2001), and Alberta (Thompson and Davies 1976). Growth of whitefish in our study was intermediate compared to these other studies, but our study found that growth slowed much more abruptly than has been shown previously for this species. Our use of otoliths rather than scales may partly explain this discrepancy. Sex ratio in the present study was roughly 1:1 for all mountain whitefish, and for mature fish only, whereas the sex ratio of mature mountain whitefish in Utah was 1.6:1 (Wydoski 2001). The similarity we found in growth of male and female whitefish concurs with previous findings (McHugh 1940).

Estimates of S for mountain whitefish, which averaged 0.76 among five populations, are high for stream-dwelling salmonid populations (Griffith 1999). However, exploitation within all the mountain whitefish populations was almost certainly low, and much of the total mortality of salmonid populations is typically comprised of angling mortality (Healey 1978; Braña et al. 1992; Mills et al. 2002). Estimates of survival for mountain whitefish are almost nonexistent in the literature, however, in the Sheep River in southern Alberta, S was estimated to be 0.66

(Thompson and Davies 1976). A conventional surrogate for S for unexploited or lightly exploited populations is longevity (Hoenig 1983; Quinn and Deriso 1999). Nearly all of our study populations contained fish estimated to be ≥ 10 years old, with almost half of the populations containing fish estimated to be ≥ 14 years old. In contrast, the estimated oldest mountain whitefish in previous studies has ranged from age 8 to 12 (Sigler 1951; Pettit and Wallace 1975; Thompson and Davies 1976; Wydoski 2001). The aforementioned studies used scales for age estimation, a structure that has been consistently disregarded as an accurate aging structure in long-lived fishes (e.g., Barnes and Power 1984). Our results agree with this general observation and suggest reliance on scales may lead to severe underestimation of actual age for mountain whitefish, especially for fish estimated to be age 8 or older. Because of their longevity, we suggest using otolith cross-sections for estimating the age of older mountain whitefish.

Few stream conditions appeared to be strongly related to the life history characteristics of the mountain whitefish populations in our study. Although fish length alone explained most of the variation in fecundity, we found that as stream width decreased, fecundity increased. Anderson (1985) found a similar relationship between stream width and sculpin growth, and concluded that productivity increased in a downstream manner. Such a conclusion is consistent with our finding that at lower elevation sites with higher mean water temperature, growth was higher. However, conductivity, which has been used as a measure of productivity (McFadden and Cooper 1962), showed no correlation with fecundity or growth. Meyer et al. (2003) concluded that there was little relationship between conductivity and the life history characteristics of Yellowstone cutthroat trout.

Similar to other response variables, very little variation in length or age at maturity was explained by any of the stream conditions we measured. Although ML50 ranged from 193 to 299 mm and MA50 from 1 to 5 years of age, fish length and fish age alone explained over 80% of the variation in the length and age at maturity models, respectively. Such consistency in maturity may be a reflection of the limited distribution of whitefish, such that environmental conditions were not especially variable, resulting in maturity being fairly predictable. In any event, once mountain whitefish reached mature size and age, their gonads never appeared undeveloped in the fall, suggesting that alternate year spawning may be rare in these populations. The process of spawning every year may explain why growth slowed and almost ceased for older fish.

ACKNOWLEDGMENTS

We thank Oregon Department of Fish and Wildlife, Nevada Division of Wildlife, Utah Department of Natural Resources, and Wyoming Game and Fish Department for their cooperation in data collection within their jurisdiction. Ron Roberts and Nick Gastelecutto provided invaluable assistance processing the fish samples in the lab and in aging the fish. This study was supported by funds from Federal Aid for Sport Fish Restoration and from the Bonneville Power Administration.

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Table 1. Summary of mountain whitefish distribution in 21 river drainages in the upper Snake River basin, Idaho.

River drainages	Total kilometers	Number of sites sampled	Dry or nearly dry sites	Sites containing MWF	Population abundance Estimate	Population abundance 90% CI
Weiser River	3,146	84	12	4	992	845
Payette River	6,795	254	12	40	1,499,216	1,616,939
Boise River	7,823	152	12	24	322,691	171,763
Owyhee River	15,024	230	136	0	0	-
Bruneau River	6,422	118	46	10	8,664	7,757
Big Wood River	6,351	121	64	3	2,876	2,870
Salmon Falls Creek	3,965	75	33	0	0	-
Rock Creek	1,388	19	11	0	0	-
Dry/Marsh/Rock	1,221	33	20	0	0	-
Goose Creek	2,529	87	30	0	0	-
Raft River	3,821	99	29	0	0	-
Bannock Creek	640	7	2	0	0	-
Portneuf River	2,233	88	10	0	0	-
Blackfoot River	2,183	83	13	1	1,642	2,739
Willow Creek	1,700	95	25	0	0	-
South Fork Snake River	1,830	84	27	3	1,566,431	971,267
Palisades/Salt River	1,390	65	6	8	17,768	11,776
Teton River	2,383	94	23	4	279,378	219,044
Henry's Fork Snake River	3,562	93	15	7	588,478	423,487
Snake River mainstem and tributaries	45,590	162	55	2	1,441,312	587,437
Total	119,996	2,043	581	106	5,729,449	1,859,583

Table 2. Stream characteristics at study sites used to estimate mountain whitefish population dynamics in Idaho. Site location numbers correspond to Figure 1. Blank spaces indicate missing data.

	Site Location	Date	UTM coordinates East	North	Zone	Elev-ation (m)	Stream order (1:100,000 scale)	Conduct-ivity (µS/cm)	Grad-ient (%)	Mean width (m)	Number of fish sampled	Mean water temperature (°C) Annual	Apr-Sep
1	Kootenai River	9/26/06	560016	5395725	11	549		230	< 0.01	128.0	91	7.7[a]	9.7[a]
2	Pahsimeroi River	10/12/06	737203	4948134	11	1,447	4		0.33	10.2	81	9.0[b]	12.7[b]
3	Payette River	10/13/06	543654	4861406	11	722	6	62	0.21	48.2	71	11.9	17.7
4	SF Payette River	10/17/06	584473	4880005	11	937	4	71	0.37	43.7	124	7.7	11.9
5	Boise River (lower)	11/9/05	516423	4840758	11	700	5	459	0.12	32.9	64	13.2	18.4
6	Boise River (upper)	10/31/05	566658	4827288	11	830	5	90	0.16	36.1	79	8.8	12.0
7	MF Boise River	8/29/06	627042	4850112	11	1,277	5	55	0.70	27.9	77	8.7	13.8
8	SF Boise River (upper)	9/1/05	665159	4828902	11	1,618	5	113	0.61	25.2	104	8.5	13.4
9	SF Boise River (lower)	10/19/06	618232	4801725	11	1,046	5		0.30	31.8	81	7.2	10.3
10	Big Wood River	11/3/05	714026	4829359	11	1,616	5	172	0.64	23.3	62		13.5
11	Snake River (lower)	9/30/05	391056	4786226	12	1,368	7	328	0.10	70.5	93	10.4	14.8
12	Snake River (upper)	9/28/05	418778	4845382	12	1,460	7	333	0.25	84.8	120	8.7	13.9
13	SF Snake River (lower)	9/27/05	440507	4834936	12	1,515	6	365	0.16	42.8	97	8.3	12.3
14	SF Snake River (upper)	9/29/05	483104	4798938	12	1,640	6	327	0.14	96.4	80	7.5	10.3
15	Stump Creek	10/13/05	493958	4737673	12	1,887	3	835	0.42	6.9	69	7.2[b]	12[b]
16	Crow Creek	10/11/05	489676	4715833	12	1,985	3	502	0.86	5.3	75		
17	Teton River (lower)	10/17/05	451132	4864709	12	1,522	5	350	0.18	32.2	113	9.4	15.3
18	Teton River (upper)	10/18/05	484921	4840977	12	1,825	4	350	0.07	25.0	96	8.1[c]	12.0[c]
19	Fall River	10/23/06	468141	4877084	12	1,610	5	67	0.50	48.5	99	7.4[c]	13.2[c]
20	Henry's Fork Snake River	9/19/05	473014	4883874	12	1,604	5	143	0.29	62.3	107	9.4	15.3

[a] Data from 2006

[b] Data from mid-2005 to mid-2006

[c] Calculated in part from regression analysis (see methods)

Table 3. Variation in length and age at maturity and longevity for male and female mountain whitefish in Idaho. ML50 and MA50 refer to the length and age, respectively, at which the probability of a mountain whitefish being mature at a particular site is 50%. Blank spaces indicate where data was inadequate to make estimates.

			Length at maturity (mm)			Age at maturity			Oldest
			Largest	Smallest		Oldest	Youngest		aged
Site location	Sex	n	immature	mature	ML50	immature	mature	MA50	fish
Kootenai River	M	52	255	204	235	3	1	2.0	10
	F	39	342	250	261	5	2	3.3	9
Pahsimeroi River	M	44	234	267	251	1	2	1.5	11
	F	37	285	282	270	3	2	2.3	9
Payette River	M	39	166	220	193				
	F	30	266	230	247				
SF Payette River	M	57	278	265	266	3	2	2.2	24
	F	61	290	258	262	3	2	2.1	17
Boise River (lower)	M	34	240	237	240	1	1	1.2	8
	F	29	235	257	246	1	2	1.5	9
Boise River (upper)	M	44	272	333	298	2	4	3.0	15
	F	29	286	296	291	3	3	3.0	12
MF Boise River	M	34	232	215	217	1	1	3.0	10
	F	32	235	260	248	2	2	2.0	13
SF Boise River (upper)	M	41	228	253	241	2	3	2.5	13
	F	48	262	264	263	3	2		13
SF Boise River (lower)	M	33	263	287	275	1	1	1.0	17
	F	46	311	292	289	2	2	2.0	18
Big Wood River	M	33	144	226		0	1		9
	F	21	228	328		1	3		9
Snake River (lower)	M	47	238	235	235	2	2	2.0	9
	F	38	312	243	251	2	2	2.0	10
Snake River (upper)	M	40	292	255	263	3	2	1.8	16
	F	65	348	272	290	4	2	1.9	12
SF Snake River (lower)	M	44	263	262	264	2	2	2.0	10
	F	47	315	299	296	5	5	5.0	11
SF Snake River (upper)	M	39	140	270		0	2		19
	F	34	299	299	299	4	4	4.0	16
Stump Creek	M	35	247	219	225	3	2	2.0	9
	F	26	253	237	252	3	2	2.8	10
Crow Creek	M	30	236	265	251	1	2	1.5	11
	F	29	280	273	275	3	3	3.0	14
Teton River (lower)	M	54	311	220	232	3	1	1.3	14
	F	50	278	278	278	2	2	2.0	16
Teton River (upper)	M	37	270	282	276	3	3	3.0	16
	F	55	305	270	278	4	3	3.1	14
Henry's Fork Snake River	M	53	230	205	230	2	1	1.5	17
	F	49	286	250	263	3	2	2.7	14
Falls River	M	55	321	238	245	7	2		11
	F	40	300	254	261	4	3	2.5	12

Table 4. Estimates of total annual survival rate uncorrected (S) and corrected (S_c) for size selectivity for age-1 and older mountain whitefish at selected study sites in Idaho.

Site location	S	S_c
Boise River (lower)	0.64	0.59
SF Boise River (lower)	0.89	0.87
SF Boise River (upper)	0.80	0.80
MF Boise River	0.75	0.68
Teton River (lower)	0.85	0.79
Teton River (upper)	0.87	0.85

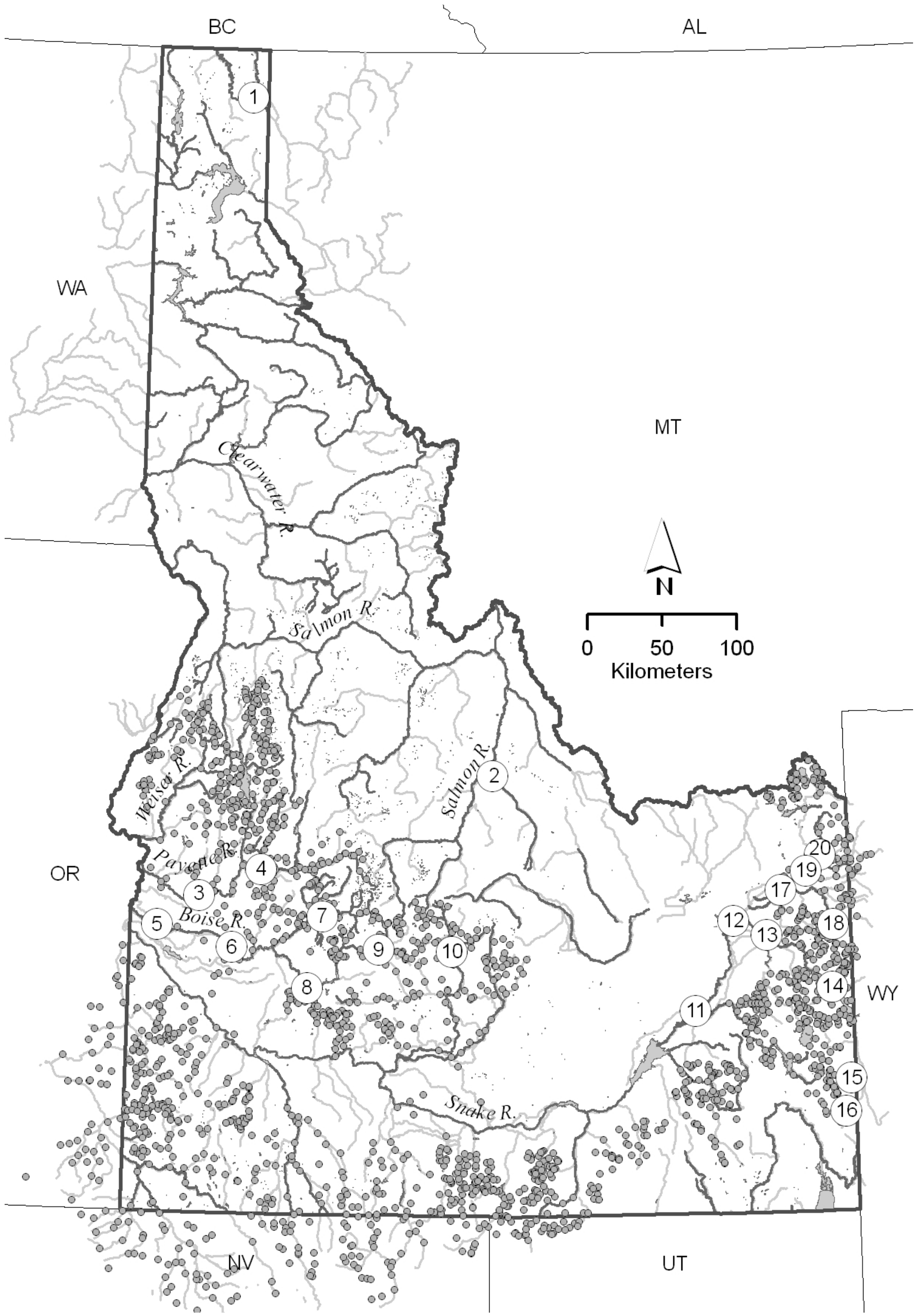

Figure 1. Distribution of mountain whitefish study sites used to determine abundance (dots) and population dynamics (numbered dots) in Idaho. Site numbs correspond to Table 2.

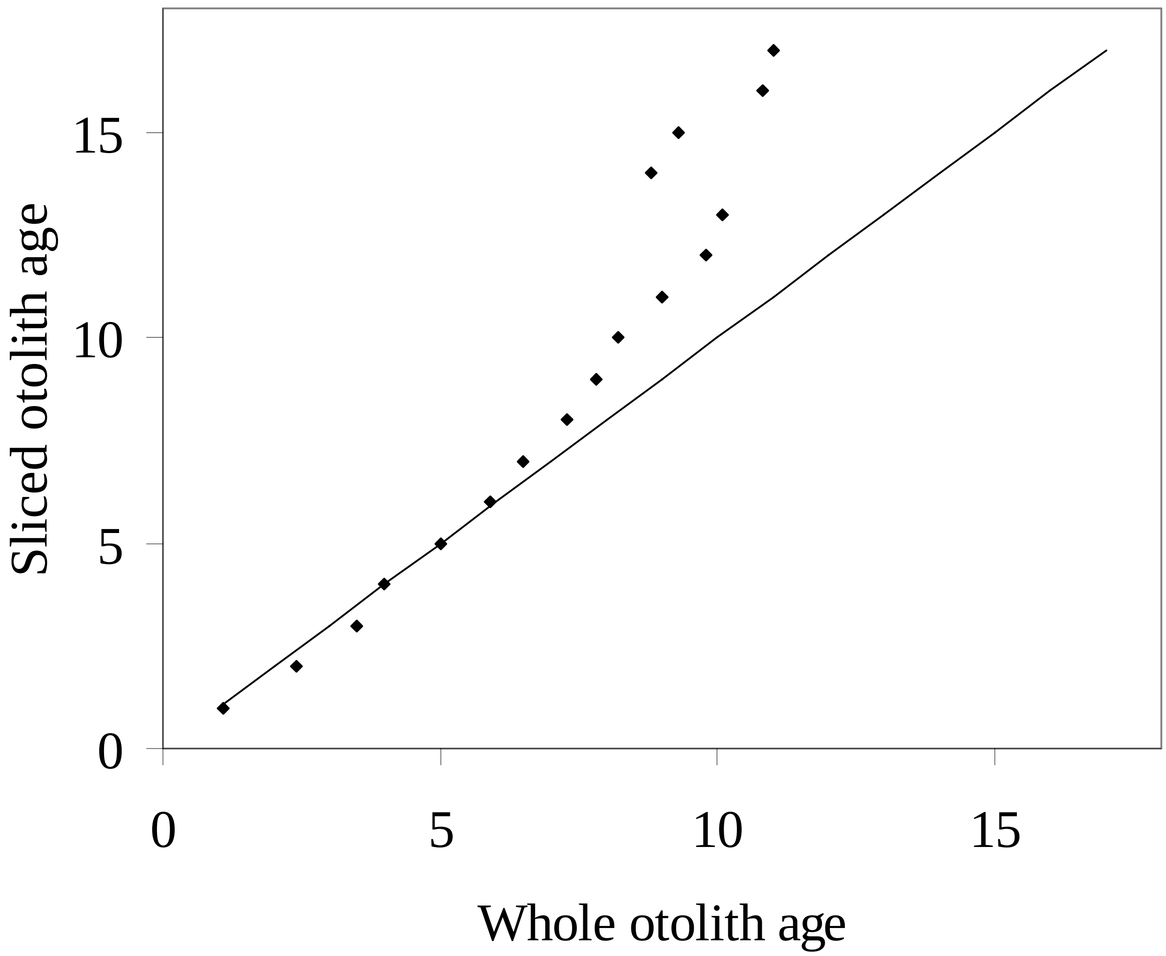

Figure 2. Relationship between estimates of mountain whitefish age using whole and sliced otoliths from 20 populations in Idaho. Line represents a 1:1 relationship.

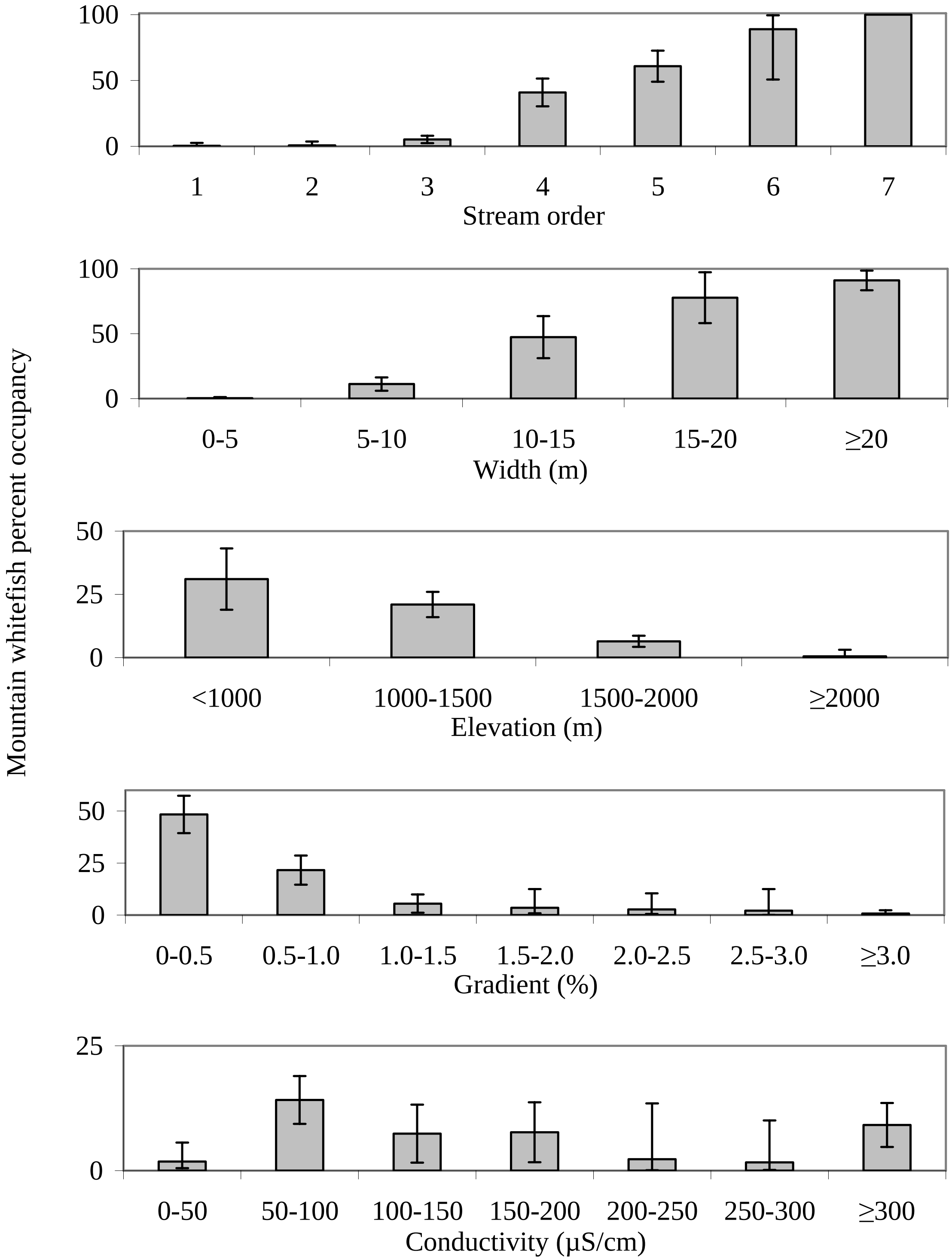

Figure 3. Observed frequency of occurrence (and 95% confidence intervals) for mountain whitefish relative to several stream characteristics in the upper Snake River basin in Idaho.

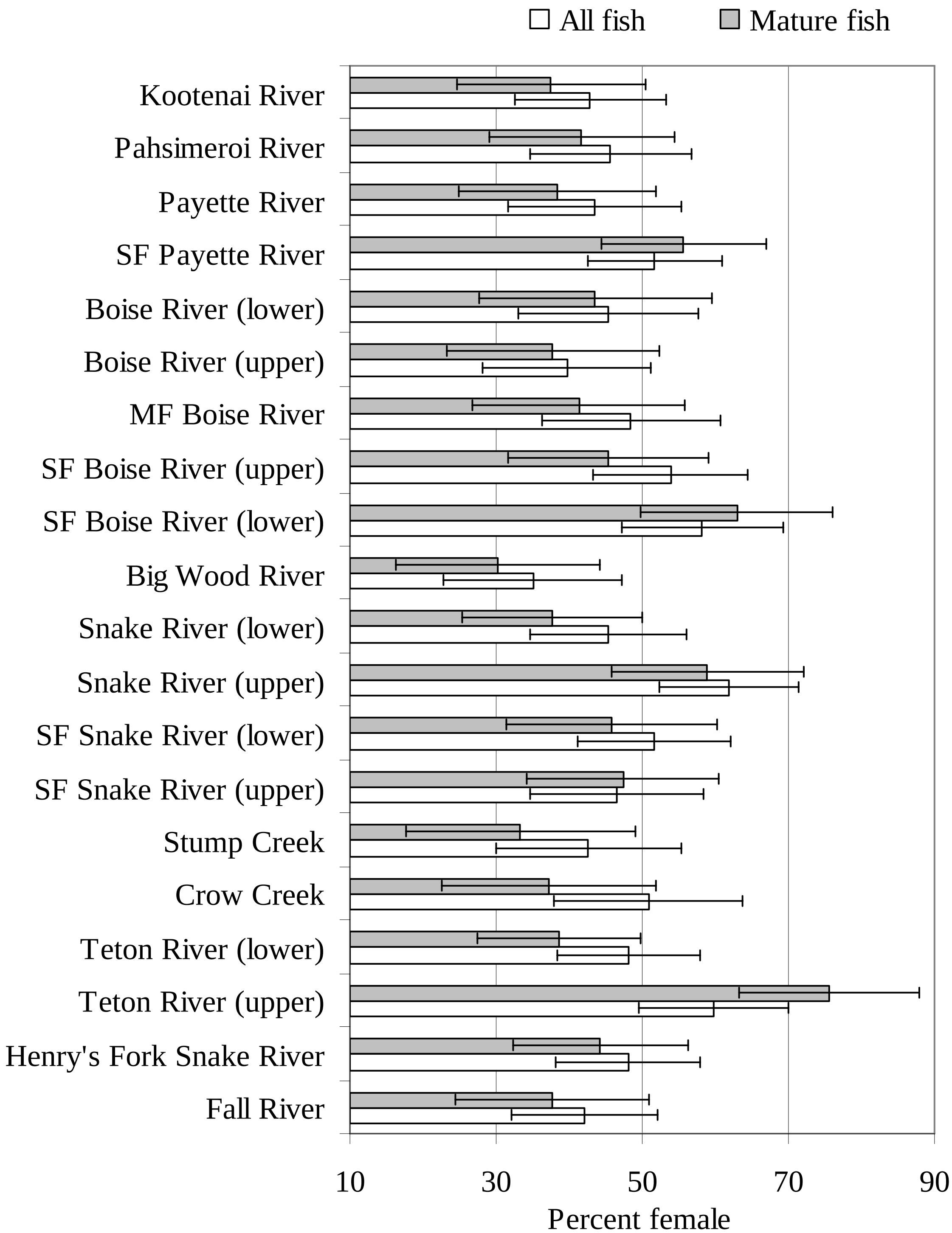

Figure 4. Estimates of sex ratio for mountain whitefish at study sites throughout Idaho.

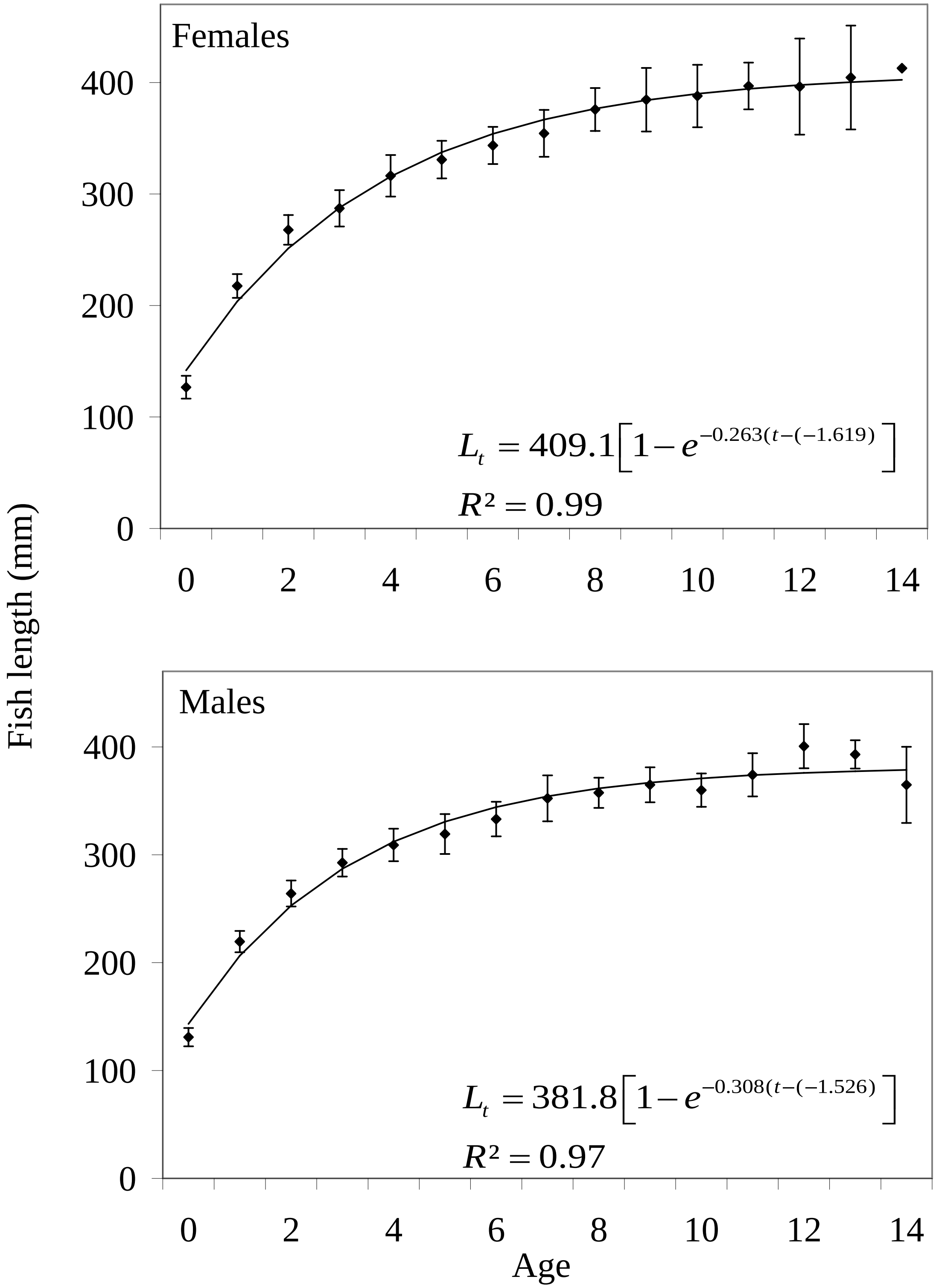

Figure 5. Mean length at age (and 95% confidence intervals) for female and male mountain whitefish from 20 study sites in Idaho. The equations and curves are for von Bertalanffy growth curves calculated from the means.

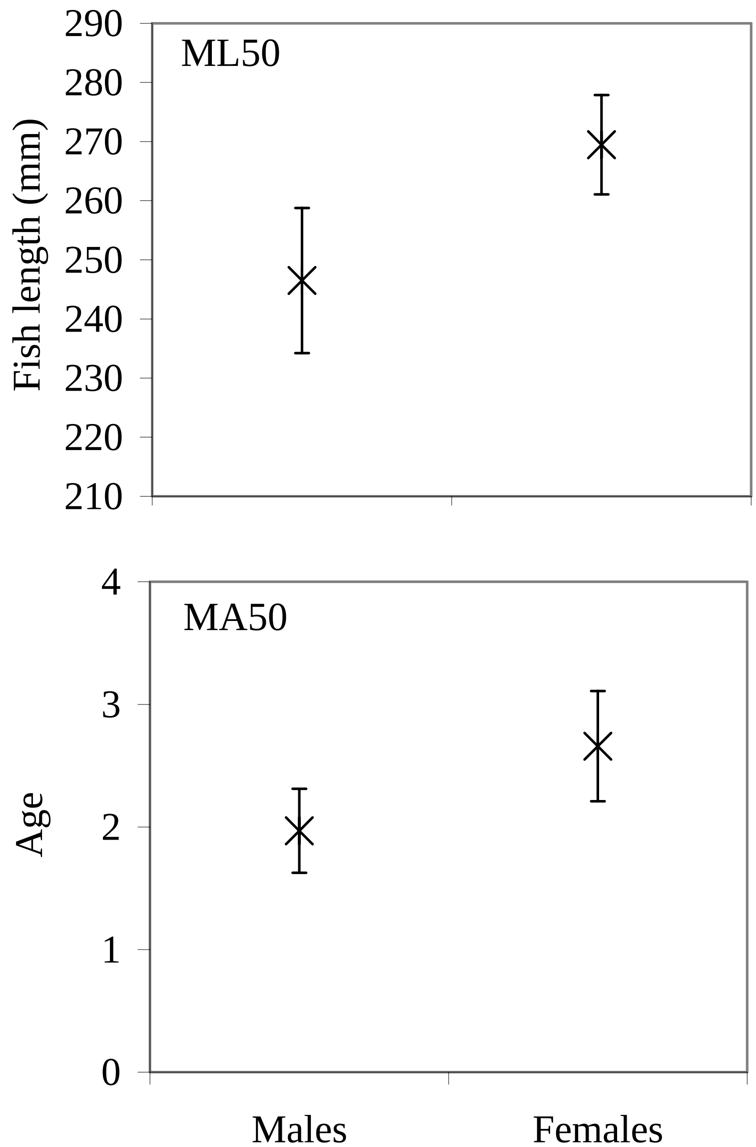

Figure 6. Mean length and age at which the probability of being mature was 0.5 (ML50 and MA50, respectively) for female and male mountain whitefish from 20 study sites in Idaho. Error bars are 95% confidence intervals for the means.

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