Environmental Factors Related to the Distribution, Abundance, and Life History Characteristics of Mountain Whitefish in Idaho

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Abstract.—Mountain whitefish *Prosopium williamsoni* are a broadly distributed native salmonid in western North America, but comparatively little investigation has been made regarding their population characteristics. We surveyed 2,043 study sites to assess whether physiochemical stream conditions affected mountain whitefish distribution and abundance in southern Idaho, and at 20 of these sites life history characteristics were also estimated. A total of 581 sites were dry or contained too little water to support any fish species. Mountain whitefish were captured at 106 sites; for these sites only, mean abundance was 2.2/100 m^2. They were rarely present when mean wetted width was less than 10 m but were almost always present when wetted width was greater than 15 m. We estimated that within the study area there were approximately 4.7 ± 1.8 million mountain whitefish, mostly in fifth- to seventh-order streams, which comprised only 13% of the total stream kilometers but accounted for 93% of the total abundance of whitefish. Growth was positively related to mean annual water temperature and negatively related to site elevation. Mountain whitefish were long lived, most (90%) populations containing fish estimated to be at least 10 years old. This longevity produced total annual survival rates averaging 0.82 (range = 0.63–0.91). In general, the growth, fecundity, and survival of mountain whitefish were higher in the upper Snake River basin than in other areas for which data have been reported. Whitefish matured at about 250 mm and about age 2, with little variation in length and age at maturity between sites; males matured at a smaller size and younger age than females. The disproportionate use of larger (i.e., >15-m-wide) streams by mountain whitefish in southern Idaho differs from the situation in more northerly locations, where they apparently are more common in smaller streams.

Mountain whitefish *Prosopium williamsoni* are a widely distributed species of salmonid in western North American rivers, ranging from the Colorado River basin in the south to the MacKenzie River basin in northwestern Canada (Behnke 2002). While the status, life history characteristics, and habitat requirements of most native salmonids in western North America have been the subject of much research, comparatively little is known of the mountain whitefish, in large part because they are less appealing to anglers and have therefore received far less attention from fisheries managers and researchers (Northcote and Ennis 1994). In fact, from the 1950s into the 1970s, mountain whitefish removal programs were undertaken by government agencies in some areas of the western United States (Corsi 1956; Erickson 1971; Jeppson 1982) because they were perceived by anglers and biologists to limit trout production via competition for food and space, an assertion that has not been substantiated (Pontius and Parker 1973; Fuller 1981; DosSantos 1985).

Mountain whitefish in general are distributed lower in watersheds in larger rivers compared with other stream-dwelling salmonids (Gard and Flittner 1974; Platts 1979; Maret et al. 1997), presumably because smaller headwater streams do not provide suitable habitat such as adequate pool size (Sigler 1951). Habitat alterations such as channelization, impoundments, and changes in flow regime are common in larger rivers (Sheehan and Rasmussen 1999) and have been shown to negatively affect local mountain whitefish populations (e.g., Erman 1973; Northcote and Ennis 1994; Paragamian 2002). Because mountain whitefish are sensitive to these and other habitat alterations, they are sometimes used as an indicator species for local environmental assessments (Nener et al. 1995; Bergstedt and Bergersen 1997; McPhail and Troffe 1998; Cash et al. 2000), but broad-scale assessments of their status have rarely been made. Similarly, little is known of the basic life history characteristics for mountain whitefish, such as rates of growth and mortality, longevity, maturity, and sex ratio of populations. 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 mountain 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). Specific habitat requirements for mountain whitefish are also not well defined, impeding predic-

tions of (1) where occupancy is likely in a drainage or (2) the impacts of further habitat alterations on populations. Although regression analysis is often considered overly simplistic for determining fish–habitat relationships because it assumes, often incorrectly, that rearing habitat is saturated and populations are limited by the habitat features being measured (Platts and Nelson 1988), it can be useful for exploring potential factors that may limit the distribution and abundance of animal populations (Scott et al. 2002).

To help fill the above-mentioned information gaps, we used broad-scale sampling to estimate the distribution and abundance of mountain whitefish in the upper Snake River basin in Idaho. Concomitantly, we retained fish from a small subsample of locations in the upper Snake River basin and two outside the basin to characterize mountain whitefish life history characteristics in Idaho and the amount of variation in these characteristics among populations. To ascertain what environmental factors may influence mountain whitefish population characteristics, we correlated their distribution, abundance, and life history characteristics to stream habitat conditions that we felt reflected stream size or fish growing conditions, and that previously have been shown to be related to salmonid population characteristics in western North America (e.g., Dunham et al. 1999; Meyer et al. 2003; Zoellick and Cade 2006).

Study Area

The Snake River flows for 1,674 km from the headwaters in Yellowstone National Park to its confluence with the Columbia River. The historical range of mountain whitefish in the upper Snake River basin (i.e., the Snake River upstream of Hell's Canyon Dam at the Idaho–Oregon border) is not well defined but apparently included most major river drainages (Simpson and Wallace 1982; Behnke 2002). We surveyed fish and habitat from Hell's Canyon Dam upstream to the Wyoming border (Figure 1). Stream surveys were conducted mostly in Idaho but also within the state boundaries of Oregon, Nevada, Utah, and Wyoming, where portions of the headwaters of river drainages lay outside the state of Idaho. The Sinks drainages in eastern Idaho were not included because mountain whitefish are not native to these drainages except for the Big Lost River, where mountain whitefish are the subject of a separate assessment and management plan.

Discharge in most of the streams in this portion of the Snake River basin is heavily influenced by snowmelt and peaks between April and June. However, streamflow in the Snake River and in a number of major tributaries is highly regulated for agricultural and
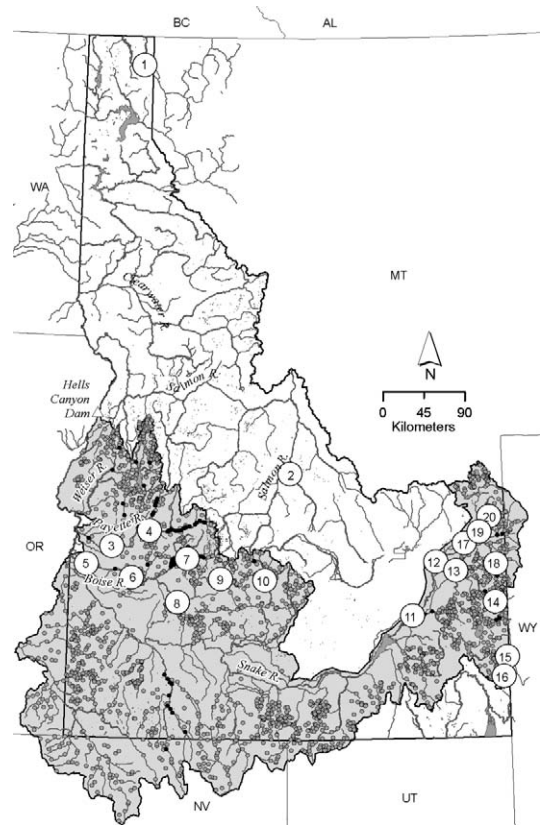

FIGURE 1.—Distribution of mountain whitefish study sites used to determine abundance (dots) and life history characteristics (numbered dots) in the upper Snake River basin (shaded area). Site numbers correspond to those in Table 2. Black and numbered dots indicate sites where mountain whitefish were captured.

hydroelectric uses by dams and diversions, which alters natural flow patterns. Elevation within the basin ranges from over 4,000 m at mountain peaks to 466 m at Hell's Canyon Dam. The climate is semiarid, with an average precipitation of about 25–30 cm annually.

Redband trout *Oncorhynchus mykiss gairdneri*, bull trout *Salvelinus confluentus*, and Yellowstone cutthroat trout *O. clarkii bouvieri* are native to the upper Snake River basin, as are a number of sucker, sculpin, and minnow species (Simpson and Wallace 1982). Nonnative trout (including rainbow trout *O. mykiss*, brook trout *S. fontinalis*, and brown trout *Salmo trutta*) have been introduced throughout the basin and are widely established and self sustaining.

Methods

Distribution and abundance.—Data were collected between 1999 and 2006. Spatially balanced randomly

TABLE 1.—Summary of mountain whitefish distribution and abundance in 21 major river drainages in the upper Snake River basin, Idaho; CI = confidence interval; NA = not applicable.

River drainage	Total kilometers	Number of sites sampled	Dry or nearly dry sites	Sites containing mountain whitefish	Mean density per		Population abundance	
					100 m^2	100 m	Estimate	90% CI
Weiser River	3,146	84	12	4	0.1	1.1	992	845
Payette River	6,795	254	12	40	1.4	45.2	1,499,216	1,616,939
Boise River	7,823	152	12	24	1.9	63.0	322,691	171,763
Owyhee River	15,024	230	136	0			0	
Bruneau River	6,422	118	46	10	0.5	5.4	8,664	7,757
Big Wood River	6,351	121	64	3	0.3	6.4	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	NA	4.1	1,642	2,739
Willow Creek	1,700	95	25	0			0	
South Fork Snake River	1,830	84	27	3	9.3	613.9	1,566,431	971,267
Palisades–Salt River	1,390	65	6	8	2.3	14.8	17,768	11,776
Teton River	2,383	94	23	4	4.1	101.5	279,378	219,044
Henry's Fork Snake River	3,562	93	15	7	5.3	285.5	588,478	423,487
Snake River above American Falls Reservoir	165	2	0	2	3.5	265.7	438,321	178,571
Remaining Snake River tributaries	44,883	160	55	0			0	
Total	119,453	2,043	581	106	2.2	78.3	4,726,457	1,818,848

selected study sites were generated with the help of the Environmental Protection Agency's Environmental Monitoring and Assessment Program. The technique maps two-dimensional space (in our study, a 1:100,000 scale hydrography layer) into one-dimensional space with defined, ordered spatial addresses, and uses restricted randomization to randomly order the spaces, which when systematically sampled results in a spatially balanced sample (Stevens and Olsen 2004). The generation of study sites was stratified by stream order (Strahler 1964). This technique was followed except where access restrictions or river conditions precluded sampling; at these locations, which constituted less than 1% of the surveys conducted, study sites were selected to be representative of the entire reach. A total of 2,043 study sites were thus surveyed (Table 1; Figure 1). At each study site, unless the site was dry ($n = 581$ sites), fish were surveyed using either electrofishing or snorkeling gear at or near base flow conditions (late June to early October) to facilitate fish capture and to help standardize fish and habitat sampling conditions.

Sampling in small streams (i.e., less than about 8-m wetted width; $n = 1,356$) was conducted by depletion electrofishing with one or more backpack electrofishers (Smith-Root Model 15-D) with pulsed direct current (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. Between two and four passes were made, and

sites were typically (72% of the time) between 80 and 120 m in length (depending on breaks in habitat types and ability to place block nets), and averaged 92 m (range = 40–190 m). Fish were identified, enumerated, measured to the nearest millimeter (total length [TL]) and gram, and released. All salmonids we encountered were captured, whereas qualitative assessments of relative abundance for all other species were made but quantitative estimates of abundance were not made. Estimates of fish abundance and variance for salmonids were made with the maximum likelihood model in 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), depletion data and subsequent abundance estimates were separated into two length categories (<100 and ≥100 mm TL).

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. All salmonids were marked with a caudal fin clip during the marking run, and marked and unmarked salmonids were captured during a single recapture run usually 2 but sometimes up to 7 d later. We assumed there was no movement of marked or unmarked fish into or out of the study site,

and attempted to reduce the likelihood of movement by lengthening the reaches to 1–7.8 km long and releasing all marked fish at least 100 m inside the study reach. Estimates of salmonid abundance and variance were made separately for each species using the log-likelihood model in the Fisheries Analysis + software package (Montana Fish, Wildlife and Parks 2004). Estimates were made separately by size-groups (25–50 mm) and summed to produce an estimate of total number of fish present. When the number of recaptures was low, we increased size-groups to 100 mm or more and used the modified Petersen model to estimate abundance and variance. At all but two sites, we were able to create size-groups meeting the criteria that (1) the number of mountain whitefish marked in the marking run multiplied by the catch in the recapture run was at least four times the estimated population size and (2) at least three recaptures occurred per size-group; meeting these criteria creates modified Petersen estimates that are less than 2% biased (Robson and Regier 1964). As a result of low capture efficiencies, we could not estimate fish smaller than 100 mm TL at the mark–recapture sites.

When electrofishing was not possible due to access constraints or because streams were too large for backpack electrofishing and too small for boat electrofishing, daytime snorkeling was conducted ($n = 60$) following the protocol of Thurow (1994). Wetted width at the snorkel sites was typically 10–40 m wide (average width = 18 m; range = 2–92 m). Snorkeling was not conducted unless visibility was 2 m or more. From one to three snorkelers were used depending on stream width, and we attempted to count all salmonids larger than 100 mm TL and binned them into 25-mm size-classes; no other fish species were enumerated. In general, in streams of less than 0.7 m average depth, upstream snorkeling was conducted, whereas for deeper streams, snorkeling was conducted in a downstream manner. Total counts were used as minimal abundance estimates with no correction for any sight-ability bias.

Mountain whitefish distribution and abundance was summarized separately for each of 21 major river drainages in the upper Snake River basin (Table 1). The dozens of minor tributaries to the Snake River from American Falls Dam to Hell's Canyon Dam were compiled together into one major river drainage; abundance estimates could not be obtained for the main stem of the Snake River in this section, although mountain whitefish occupy some portions of this reach.

Abundance estimates were stratified by stream order and were developed using the following steps: (1) we summed the total length of stream by stream order in ArcGIS; (2) we standardized our estimates of abun-

dance to the number of mountain whitefish/100 m of stream (our typical study site length); (3) we calculated a mean abundance and variance, stratified by stream order, from all the survey sites; and (4) we multiplied mean abundance by the total number of 100-m 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. 2006). We used the stratified-random-sampling formula from Scheaffer et al. (1996) to calculate population totals as

$$N_{\text{census}} = \sum_{i=1}^{L} N_i \bar{y}_i,$$

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

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

where N_i is the number of 100-m sections in stream order i, $\bar{y}_i$ is the average number of mountain whitefish from samples obtained from stream order i, L is the number of stream orders, s_i^2 is the standard deviation in stream order i, and n_i is the sample size for stream order i. All sample sites, including dry and fishless sites, were included in these estimates.

Life history characteristics.—We used backpack and boat-mounted electrofishing units to collect 1,783 mountain whitefish from 20 stream locations in 2005 and 2006 to estimate mountain whitefish life history characteristics. Most of the study sites were selected arbitrarily from among the above-mentioned locations where population estimates were already being made, but we purposefully distributed the sites across a broad geographic area in the upper Snake River basin (Figure 1) in order to include a variety of stream habitat conditions (Table 2). Two sample locations from central and northern Idaho, outside the upper Snake River basin, were added to broaden our assessment of life history characteristics. Fish were retained during the recapture run so the population estimates were not affected by their removal. Because mountain whitefish spawn in October and November, fish were collected in late August to early October to facilitate maturity confirmation. Captured fish were transported directly to a freezer for storage.

Sacrificed fish were thawed in the laboratory and measured for length (TL, mm) and weight (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 and reread to (1) corroborate estimated ages throughout all age-classes, (2) substantiate the estimated age of fish 8-years-old or older, and (3) resolve differences in estimated age between readers of whole otoliths. The subsampled 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. A drop of vegetable oil was placed on the sliced sections to reduce glare from scratches caused by cross-sectioning. All fish were considered 1-year-old when they reached their first January. The index of average percent error (Beamish and Fournier 1981) was calculated as a measure of reader precision.

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 479 mature females across all sites, and a curvilinear (i.e., power function) regression equation was developed to predict fecundity (F, eggs per female) from fish length (TL). A length–weight relationship was similarly developed.

We estimated growth by calculating the mean length at age and 95% confidence intervals (CIs) from an age–length key (DeVries and Frie 1996) developed for each sample location. We assumed all fish captured at the site were representative of that site, but admittedly we may have captured some migrant fish that were present at a particular location for only a portion of the year. Our growth data were obtained throughout the fall, so we used Julian date of the sample in all subsequent growth analyses to account for this known variation instead of back-calculating growth to a standardized date, which tends to underestimate length at age (Campana 1990).

Only age-2 and older mountain whitefish were adequately recruited to the electrofishing gear and thus useable for survival estimates. Following Quinn and Deriso (1999), we estimated total annual survival rate (S) and 95% CIs using catch-curve analysis, which requires that (1) survival 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. The only sites where the second assumption was met was where both abundance and demographic data were collected ($n = 15$). At these sites, catch curves could be adjusted to remove bias in fish size selectivity only at

six sites where capture efficiency for several size-classes could be estimated from the mark–recapture analyses (Beamesderfer and Rieman 1988); we present both the unadjusted and adjusted estimates of S for comparison. We assumed these sites reasonably met the first and third assumptions because the coefficient of determination resulting from simple linear regression of the $\log_e$ of catch at age as a function of age was fairly high (mean $r^2 = 0.61$; Isermann et al. 2002).

Habitat measurements.—Several stream habitat conditions were measured at all survey sites to assess their relationship with mountain whitefish distribution, abundance, and life history characteristics. 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 was determined from a 1:100,000 hydrography layer using geographic information system software. Reach gradient (%) was determined using the software package Topo! for Windows, version 2.7.3 (National Geographic Society); the distance between the contour lines that bounded the study site was traced (average traced distance was usually 1–2 km depending on the length of the fish sampling reach), and gradient was calculated as the elevational increment between the contours divided by the traced distance. Conductivity (μS/cm) was measured using a calibrated handheld conductivity meter accurate to ±2%. Stream wetted width (m) was calculated from the average of 10 measurements through the reach using a tape measure, except for large rivers (i.e., > 15 m in width), where width was calculated from the average of 10 measurements using a rangefinder accurate to ±1 m.

At the 20 study sites where demographic data were collected, we obtained water temperature data (hourly or daily values) from several sources, including the U.S. Bureau of Reclamation, the USGS, 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 hourly intervals. At two locations (Teton River upper site and Fall River), data were missing for several weeks in 2005. To fill these data gaps, we developed linear regressions comparing water temperatures at the study sites to nearby locations (with a complete record of data) for periods of record where data were available at both locations ($r^2 = 0.97$ for Teton River upper site and 0.73 for Fall River). We used these relationships to predict temperature for the missing period of record at the study sites, based on data at the nearby site. At three additional sites, complete data were not available for 2005 and no nearby locations were available, so a combination of

TABLE 2.—Stream characteristics at study sites used to estimate mountain whitefish life history characteristics in Idaho. Site location numbers correspond to those in Figure 1. Blank spaces indicate missing data; UTM = Universal Transverse Mercator; SF = South Fork; MF = Middle Fork.

| Site | Location | Date | UTM coordinates | | | Elevation (m) |
			East	North	Zone	
1	Kootenai River	Sep 26, 2006	560016	5395725	11	549
2	Pahsimeroi River	Oct 12, 2006	737203	4948134	11	1,447
3	Payette River	Oct 13, 2006	543654	4861406	11	722
4	SF Payette River	Oct 17, 2006	584473	4880005	11	937
5	Boise River (lower)	Nov 9, 2005	516423	4840758	11	700
6	Boise River (upper)	Oct 31, 2005	566658	4827288	11	830
7	MF Boise River	Aug 29, 2006	627042	4850112	11	1,277
8	SF Boise River (upper)	Sep 1, 2005	665159	4828902	11	1,618
9	SF Boise River (lower)	Oct 19, 2006	618232	4801725	11	1,046
10	Big Wood River	Nov 3, 2005	714026	4829359	11	1,616
11	Snake River (lower)	Sep 30, 2005	391056	4786226	12	1,368
12	Snake River (upper)	Sep 28, 2005	418778	4845382	12	1,460
13	SF Snake River (lower)	Sep 27, 2005	440507	4834936	12	1,515
14	SF Snake River (upper)	Sep 29, 2005	483104	4798938	12	1,640
15	Stump Creek	Oct 13, 2005	493958	4737673	12	1,887
16	Crow Creek	Oct 11, 2005	489676	4715833	12	1,985
17	Teton River (lower)	Oct 17, 2005	451132	4864709	12	1,522
18	Teton River (upper)	Oct 18, 2005	484921	4840977	12	1,825
19	Fall River	Oct 23, 2006	468141	4877084	12	1,610
20	Henry's Fork Snake River	Sep 19, 2005	473014	4883874	12	1,604

[a] Data from 2006.
[b] Data from mid-2005 to mid-2006.
[c] Calculated in part from regression analysis (see Methods).

2005 and 2006 data at each site were used to generate a complete year of temperature data. Mean annual water temperature was calculated for each site, as was mean temperature throughout what we deemed to be the growing season (April–September). Because hourly values were not available for all sites, daily maximum or minimum temperatures were not available metrics for analyses.

Data analyses.—We used a combination of correlation analyses, logistic and multiple regression analyses, and general linear models to assess whether the stream characteristics we measured were correlated to mountain whitefish distribution, abundance, fecundity, growth, survival, and length and age at maturity. For the 1,462 sites surveyed that were not dry or nearly dry, we compared the means and 95% 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 ($n = 106$), we used multiple linear regression to assess the amount of variation in areal density (fish/m^2) that could be explained by the stream characteristics we measured.

The remaining analyses were for the sites with mountain whitefish demographics data ($n = 20$). To assess the relationship between fecundity and the stream characteristics we measured, 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 or greater (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 the stream characteristics we measured.

To assess whether stream characteristics we measured were related to 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 characteristics with linear regression. We assessed whether growth was different between male and female mountain whitefish by comparing von Bertalanffy growth functions, but because no statistically significant differences were noted, we combined the sexes for further analyses. We also assessed whether fish density affected growth (i.e., density dependence) using correlation analysis.

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 mountain whitefish, and for mature fish only, to assess whether differential mortality or other factors skewed the sex ratio as fish aged (e.g., Greeley 1933).

We characterized the variation in length and age at maturity across the study sites. For each study location, we estimated the length at which the probability of

TABLE 2.—Extended.

Site	Stream order (1:100,000 scale)	Conductivity (μS/cm)	Gradient (%)	Mean width (m)	Number of fish sampled	Mean water temperature (°C)	
						Annual	Apr–Sep
1		230	<0.01	128.0	91	7.7[a]	9.7[a]
2	4		0.33	10.2	81	9.0[b]	12.7[b]
3	6	62	0.21	48.2	71	11.9	17.7
4	4	71	0.37	43.7	124	7.7	11.9
5	5	459	0.12	32.9	64	13.2	18.4
6	5	90	0.16	36.1	79	8.8	12.0
7	5	55	0.70	27.9	77	8.7	13.8
8	5	113	0.61	25.2	104	8.5	13.4
9	5		0.30	31.8	81	7.2	10.3
10	5	172	0.64	23.3	62		13.5
11	7	328	0.10	70.5	93	10.4	14.8
12	7	333	0.25	84.8	120	8.7	13.9
13	6	365	0.16	42.8	97	8.3	12.3
14	6	327	0.14	96.4	80	7.5	10.3
15	3	835	0.42	6.9	69	7.2[b]	12.0[b]
16	3	502	0.86	5.3	75		
17	5	350	0.18	32.2	113	9.4	15.3
18	4	350	0.07	25.0	96	8.1[c]	12.0[c]
19	5	67	0.50	48.5	99	7.4[c]	13.2[c]
20	5	143	0.29	62.3	107	9.4	15.3

being mature was 0.5 (termed ML50), using one of two methods (see Meyer et al. 2003). If there was no overlap between the largest immature and smallest mature fish, we selected the midpoint between the
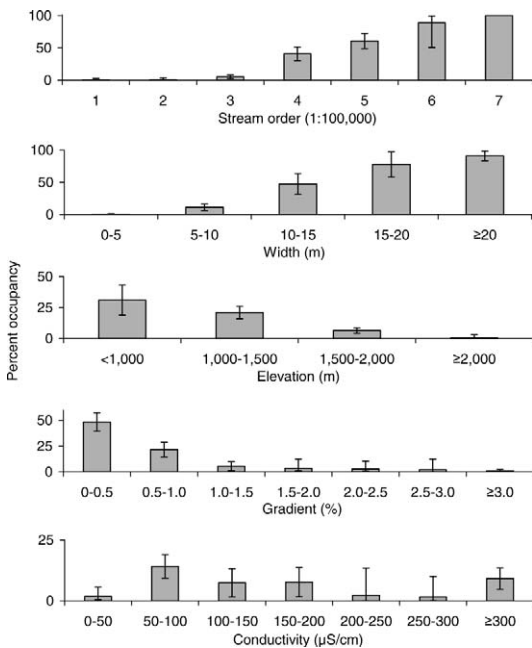

FIGURE 2.—Observed frequency of occurrence (and 95% CIs) for mountain whitefish relative to several stream characteristics in the upper Snake River basin in Idaho.

lengths 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 equaled 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). We characterized age at maturity (MA50) in a similar fashion by substituting age for length in the analyses.

We related length and age at maturity to the stream characteristics we measured using multiple logistic regression analyses; each fish was considered a sample unit. As above, a binary dependent variable was used for maturity, and 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 a fish was too small to visually determine gender based on examination of the gonads ($n = 123$), it was not included in the analyses. The Hosmer–Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 1989) was used to determine whether a particular logistic regression model adequately fit the data, and models not satisfying the test were discarded. We 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 surveyed across 119,453 km of stream in 21 major river drainages in the upper Snake River basin (Table 1). Five hundred eighty-one study sites (28%) were dry or had insufficient water to support any fish species. Mountain whitefish were captured at only 106 (7%) of the 1,462 remaining sites and were encountered most often in the Payette River (16% of sites), Boise River (16%), and Palisades–Salt drainages (12%). They were not found in 10 of the 21 major river drainages, including all of the smaller tributaries of the Snake River. Together these 10 drainages comprised 44% of the study sites and 65% of the total stream kilometers in the study area (Table 1). Among only those 11 drainages where mountain whitefish were present, they were captured at 12% of the sites that were not dry. In contrast, at least one species of trout was captured at 1,105 (76%) of the 1,462 non-dry sites surveyed. At the 86 sites where both whitefish and trout were present, mountain whitefish, on average, comprised 39% of the salmonid population.

Within the 920 sites that were not dry and that were within the drainages where mountain whitefish were present, they were rarely caught in small tributary streams, but instead were usually found in wider, lower-gradient, main-stem reaches of stream (Figure 2). Considering only the non-dry sites, mountain whitefish were present in first- through third-order streams in only 18 of 767 (2%) study sites, whereas in fifth- through seventh-order streams, they were present in 52 of 72 (72%) study sites. Similarly, mountain whitefish were present in 65 (88%) of 74 study sites where width was greater than 15 m, but only 23 (3%) of 808 study sites where width was less than 10 m. Gradient was also strongly correlated with mountain whitefish distribution, as whitefish were most likely to be present when gradient was less than 1.0%. We did not detect an influence of conductivity on whitefish distribution.

In the 106 study sites where mountain whitefish were present, none of the stream characteristics we measured were strongly correlated to whitefish areal density. The most strongly correlated variables were stream width ($r = 0.33$), stream order ($r = 0.25$), and conductivity ($r = 0.19$). Stream width and conductivity were statistically significant variables in a multiple regression model that explained 21% of the variation in mountain whitefish areal density.

We estimated that there were approximately 4.7 ± 1.8 million mountain whitefish within the reaches of the upper Snake River basin where we could produce estimates (Table 1). Most of this abundance stems from fifth- through seventh-order streams, which comprised only 13% of the total stream kilometers but accounted for 93% of the total abundance. Average abundance among all 106 study sites containing mountain whitefish was 2.2/100 m^2 (range = 0.03–25.9) or 78.3/100 m of stream (range = 0.4–1,257.3).

Life History Characteristics

Total length and weight of mountain whitefish formed an exponential relationship and were highly correlated (weight = $0.000004 \cdot TL^{3.157}$, $n = 1,803$, $r^2 = 0.99$). Fecundity also fit an exponential relationship with fish length, but data were more scattered ($F = 0.000008 \cdot TL^{3.497}$, $n = 479$, $r^2 = 0.67$). Stream wetted width was significantly correlated with the log of fecundity, which decreased as wetted width increased, though the relationship was weak ($r = -0.22$). A model including stream width and the log of fish length explained 72% of the variation in the log of fecundity.

Sex ratio averaged 48% female for all 20 sites combined (Table 3), and the CIs around the estimates at 19 of 20 study sites overlapped a 1:1 ratio. There was no difference between the sex ratio for all fish (48 ± 3%) compared with mature fish only (45 ± 5%) as evidenced by overlapping CIs. However, in 16 comparisons, the proportion of the population that was female was lower for mature fish compared with all fish.

Using sectioned otoliths 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 3). Subsequently, otoliths from all fish 8-years-old or older were sectioned, for a total of 718 readings of sectioned otoliths. We assumed the estimated age from sectioned otoliths was the correct age in all but two cases. The index of average percent error for the initial readings of whole otoliths at all sites averaged 4.1% (range = 0.7–13.6%).

Mountain whitefish grew quickly in their first few years as average fall length was 134 mm at age 0 and 226 mm at age 1. Age-2 and older whitefish grew more slowly, especially past age 6 when growth decreased to an average of 3 mm/year. Growth rates were similar between male and female mountain whitefish, based on a comparison of mean lengths at age and von Bertalanffy growth functions (Figure 4). 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 adding Julian date to the regression models explained little additional variation in length at age for either age-class. Density of

TABLE 3.—Variation in length and age at maturity and longevity for male (M) and female (F) mountain whitefish in Idaho. The terms ML50 and MA50 refer to the length and age, respectively, at which the probability of a mountain whitefish's being mature at a particular site is 50%. Blank spaces indicate where estimates could not be made due to small sample size. The sex ratio calculations in the text were based on samples sizes of each sex at each site.

| Site | Sex | n | Length at maturity (mm) | | | Age at maturity (years) | | | Oldest aged fish (years) |
			Largest immature	Smallest mature	ML50	Oldest immature	Youngest mature	MA50	
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

mountain whitefish was not correlated with growth for any age-class ($r < 0.30$), suggesting density dependence was not evident in the data.

Mountain whitefish were long lived; 17 of 19 sites contained fish estimated to be at least 10 years of age (Table 3). Twelve percent of all aged fish were 10 years old or older. Maximum estimated age for all sites 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). When adjusted for size selectivity, S averaged 0.82 and ranged from 0.63 to 0.91 at six study sites (Table 4). Adjusting S for size selectivity produced some change in the estimates (Table 4), corrected estimates of S

ranging from 0% to 34% (mean = 8%) lower than uncorrected estimates.

Male mountain whitefish matured at a smaller size and younger age than females (Table 3; Figure 5). Males reached maturity at a mean length of 247 ± 12 mm (range = 193–298 mm), compared with 270 ± 8 mm for females (range = 246–299 mm). The smallest mature mountain whitefish averaged 259 mm among all 20 sites. They matured at a mean age of 2.0 ± 0.3 for males (range = 1–3) and 2.7 ± 0.5 for females (range = 1.5–5). Seven of the 20 populations contained fish that had matured by age 1, but in all cases those fish were males.

Fish length alone explained 82% and 83% of the variation in the length at maturity logistic regression
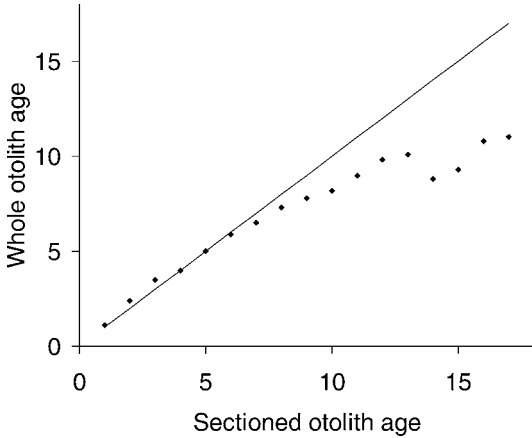
FIGURE 3.—Relationship between estimates of mountain whitefish age using whole and sectioned otoliths from 20 populations in Idaho. Data points are the mean whole otolith ages for each sectioned otolith age. The line depicts a 1:1 relationship.

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 by only one to two percentage points. The addition of any other stream characteristic to the model had even less effect. 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

TABLE 4.—Estimates of mountain whitefish total annual survival rate based on catch curves that were uncorrected (S) and corrected (S_c) for size selectivity for age-2 and older fish at selected study sites in Idaho.

Site	S	S_c
Boise River (lower)	0.78	0.77
SF Boise River (lower)	0.96	0.63
SF Boise River (upper)	0.88	0.88
MF Boise River	0.92	0.89
Teton River (lower)	0.93	0.91
Teton River (upper)	0.91	0.86

maturity model added little predictive value for either gender.

Discussion

Our results suggest that stream size was the most important factor influencing both the distribution and abundance of mountain whitefish in the upper Snake River basin. Indeed, they were rarely found in smaller streams (<10 m wetted width) but instead were located almost exclusively in larger (>10–15 m wetted width), lower-gradient, main-stem rivers, where they were abundant. This concurs with Maret et al. (1997), who concluded that one of the most important environmental factors affecting the distribution of mountain whitefish in the upper Snake River basin was upstream watershed size. Although the mechanism behind this relationship has not been established, Sigler (1951)

FIGURE 4.—Mean length at age (and 95% CIs) for female and male mountain whitefish for 20 populations in Idaho. The equations and curves are for von Bertalanffy growth curves calculated from the mean lengths at age.
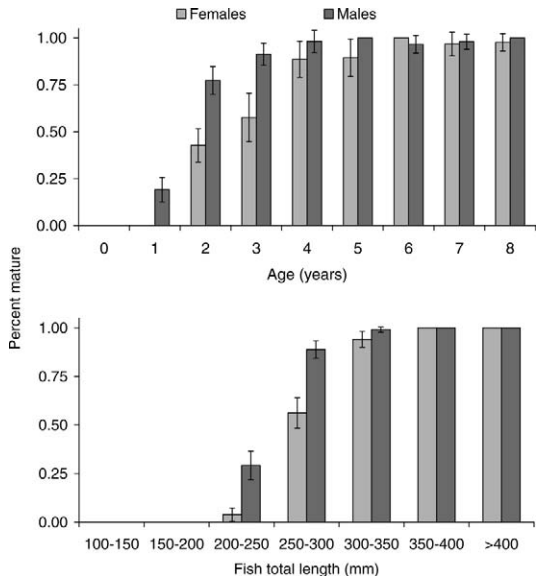

FIGURE 5.—Proportions of male and female mountain whitefish mature at age and at size for 20 populations in Idaho. Error bars show 95% CIs.

speculated that smaller streams do not provide adequate cover for mountain whitefish and concluded that their upstream distribution in the Logan River in Utah ceased where pools were less than 5 m wetted width. Similarly, Platts (1979) found that mountain whitefish in central Idaho were present only in streams of more than 6 m wetted width. However, the argument that fish cover or pool size is inadequate for mountain whitefish in small streams is contradicted by snorkel surveys conducted annually in central and northern Idaho, where mountain whitefish were found in 13 of 30 (43%) and 117 of 164 (71%) study sites that were less than 5 and 5–10 m wetted width, respectively (Idaho Department of Fish and Game, unpublished data). Mountain whitefish also occupy smaller streams in Canada (e.g., McPhail and Troffe 1998). We speculate that, in general, there is a latitudinal shift in occupancy of small streams by mountain whitefish. Future research comparing habitat availability for and utilization by mountain whitefish in southern versus northern populations in a variety of habitats and stream sizes may reveal whether this shift is caused by differences in channel geomorphology, water temperature, migratory life history patterns, or other physiochemical or behavioral factors.

Mountain whitefish in the upper Snake River basin were captured at only 7% of all survey sites that contained enough water to support fish, and were completely absent from 10 of the 21 major river drainages within the basin. How much this distribution has changed from historical levels is difficult to assess. Historically, their presence in several of the drainages may have been limited because they 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 (10–15 m); today, these lower reaches have been extensively altered by irrigation diversions and impoundments, sometimes resulting in year-round desiccation. Mountain whitefish have never been documented in the Portneuf River, Blackfoot River (except near the confluence with the Snake River), or Willow Creek drainages (Simpson and Wallace 1982; Thurow et al. 1988), and our surveys confirmed this. The Owyhee River drainage was the only drainage known to be historically occupied by mountain whitefish (Saul et al. 2001) where we failed to detect them, and although they currently exist in one tributary in the drainage (K.A.M., personal observation), none of the six surveys we conducted occurred in the reach occupied. The Owyhee River drainage is similar to the adjacent Bruneau River drainage (where mountain whitefish are sparse but broadly distributed) except that nonnative smallmouth bass *Micropterus dolomieu* have become widespread in

the Owyhee River drainage but are absent in the Bruneau River drainage. We hypothesize that predation by this nonnative invader (Fritts and Pearsons 2008), coupled with habitat alterations resulting from grazing and agricultural land use (Hann et al. 1997), largely explains the near absence of mountain whitefish in the Owyhee River drainage in recent decades.

Not only was mountain whitefish occupancy and abundance higher in lower-elevation, larger rivers, but the fish also grew faster in these reaches due in large part to warmer stream temperatures. In fact, growth, fecundity, and survival of mountain whitefish were higher in the upper Snake River basin than in other areas for which data have been reported, suggesting that southern Idaho streams provide comparatively better habitat for this species. For example, mean growth of 218, 290, and 325 mm TL toward the end of the growing season in our study for ages 1, 3, and 5, respectively, was higher than that reported by Wydoski (2001), who summarized mountain whitefish growth data from several studies across western North America and reported an average of 169, 260, and 328 mm TL at annulus formation for ages 2, 4, and 6, respectively. Fecundity was also higher in our study compared with the slower-growing populations summarized by Wydoski (2001); a similar correspondence between higher growth and higher fecundity (but smaller egg size) has been shown in brown trout populations (Lobon-Cervia et al. 2003). Although growth of older fish appeared to have slowed in our study compared with studies reported in Wydoski (2001), this convergence may also be due to our use of cross-sectioned otoliths rather than scales (all the other studies) since scales tend to underestimate age in long-lived fishes (e.g., Barnes and Power 1984).

Similar to growth and fecundity, estimates of S for mountain whitefish in our study (mean = 0.82) was higher than reported elsewhere (e.g., Thompson and Davies 1976; $S = 0.66$). Unfortunately, only one estimate of S for mountain whitefish could be found in the literature, but 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 or older (almost half of the populations contained fish estimated to be 14 years old or older), whereas the estimated oldest mountain whitefish in previous studies ranged from age 8–12 (Sigler 1951; Pettit and Wallace 1975; Thompson and Davies 1976; Wydoski 2001).

Direct comparisons we made between whole and cross-sectioned otoliths suggest that reliance on whole otoliths may lead to considerable underestimation of actual age for mountain whitefish, especially for fish

estimated to be age 8 or older (Figure 4). Because of their longevity, we suggest using cross-sectioned otoliths for estimating the age of older mountain whitefish and for subsequent calculations of S. We observed a smaller change in S after correcting for gear selectivity (0–34%) than an earlier study by Beamesderfer and Rieman (1988) on several coolwater and warmwater species (17–69%). The smaller amount of change in our estimates is surprising considering that capture efficiency varied substantially, from an average of 9% for 100–200-mm mountain whitefish to 25% for fish larger than 400 mm. However, because mountain whitefish were very long lived, this difference in capture efficiency was distributed across many age-classes, which reduced the magnitude of the bias in uncorrected estimates of S.

The percent of the mature population that was female was lower in our study (45 ± 5%) compared with that reported for Utah (62%; Wydoski 2001). The balanced sex ratios we found probably indicate that mortality between sexes was similar over time. Unequal mortality between genders can be caused by angling mortality (McFadden 1961), which was minimal for mountain whitefish in our study, or by a shorter life span for one gender (usually males) resulting from earlier attainment of sexual maturity (Hoar 1957). Although we found that males matured at a smaller size and younger age than females, this did not skew the sex ratio.

Fish length and age explained most of the variation in the length- and age-at-maturity models we developed for mountain whitefish in Idaho, and little additional variation was explained by the stream habitat conditions we measured. In contrast, stream habitat conditions such as site elevation, stream gradient, and stream size explained much of the variation in length- and age-at-maturity models developed for Yellowstone cutthroat trout (Meyer et al. 2003, 2006), a species that exhibited a wider range in length and age at maturity among populations. While stream resident trout often exhibit much phenotypic plasticity in life history characteristics such as length and age at maturity, survival, and growth (e.g., Jonsson and L'Abee-Lund 1993; Einum and Fleming 1999; Meyer et al. 2003), the more narrow distribution of mountain whitefish within the upper Snake River basin may have prevented such plasticity from being displayed by this species. Alternatively, mountain whitefish may inherently be less capable of exhibiting substantial plasticity in life history characteristics, which may have partly contributed to the restricted spatial distribution we observed. Regardless, 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 the populations we studied. The process of spawning every year may partially explain why growth slowed and almost ceased for older fish in our study.

Fish length also explained most of the variation in fecundity, but we found that as stream width decreased, fecundity increased. This relationship, although statistically significant, was weak ($r = -0.22$), possibly unimportant biologically, and certainly counterintuitive. Indeed, Anderson (1985) found an opposite relationship between stream width and sculpin fecundity and concluded the relationship stemmed from increased productivity in a downstream direction.

A number of factors may have biased our estimates of mountain whitefish distribution and abundance in the upper Snake River basin. First, estimating distribution and abundance using snorkeling and depletion electrofishing techniques that were uncorrected for sampling efficiency probably led to an underestimation of both parameters (e.g., Riley and Fausch 1992; Mullner et al. 1998; Peterson et al. 2004; Thurow et al. 2006), although this may have been slight since most of the distribution and abundance occurred in larger rivers where the less-biased methods of mark–recapture were used. Second, no estimates could be made for fish smaller than 100 mm TL at sites where mark–recapture and snorkel surveys were conducted (i.e., at sites in larger rivers), although this omission may have been minor considering that even age-0 fish were larger than 100 mm TL by late summer (Figure 4). In addition, we assumed our one-time sample adequately portrayed the distribution and abundance of mountain whitefish at each location, but they are known to make significant seasonal movements (Pettit and Wallace 1975; Thompson and Davies 1976). Finally, mountain whitefish reside in many lentic habitats in the upper Snake River basin 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. Despite these limitations, our density estimates at the 106 occupied sites (mean = 2.2/ 100 m^2) were similar to estimates from previous studies employing the same sampling methods, fish size cutoffs, and density estimation procedures; such estimates have included snorkeling estimates of 27.6/ 100 m (Ham and Pearsons 2000), 1.4/100 m^2 (DuPont et al. 2004), and 2.7/100 m^2 (LRK Communications 2004), and a mark–recapture electrofishing estimate of 3,200/100 m (Paragamian 2002).

In summary, our results indicate that mountain whitefish in southern Idaho were typically located in streams wider than 15 m, where they were abundant, long lived, and fast growing (especially at warmer water temperatures) until they reached sexual maturity

at age 2 or 3. Although their total abundance (over 4.7 million at a minimum) suggests that mountain whitefish are relatively secure in the upper Snake River basin, much remains unknown for this species in Idaho and elsewhere. Most notably, data on trends in distribution and abundance are scarce, and we hope that our study will serve as a baseline for future evaluations of mountain whitefish in southern Idaho. In addition, factors limiting the distribution and abundance of mountain whitefish have rarely been studied; we admittedly measured few physiochemical characteristics, and future research that incorporates additional characteristics, such as stream and pool depth (Sigler 1951; Platts 1979), may more fully describe the factors limiting mountain whitefish populations. Even basic estimates of population abundance are lacking except in localized areas. Such information gaps exist in part because mountain whitefish continue to remain an afterthought for most fisheries research and management programs in western North America. Only through more focused efforts will we gain sufficient knowledge of the status, limiting factors, and life history characteristics of the mountain whitefish to effectively manage this species.

Acknowledgments

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