ABUNDANCE, PRODUCTION, AND TISSUE STOICHIOMETRY OF MOUNTAIN WHITEFISH (*PROSOPIUM WILLIAMSONI*) IN A CENTRAL IDAHO WILDERNESS STREAM

Michael J. Lance [1,2] and Colden V. Baxter [1]

[1] Stream Ecology Center, Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209 USA

[2] E-mail: michael.j.lance@gmail.com

Abstract. Mountain whitefish (*Prosopium williamsoni*) are among the most abundant native fishes in western North America, yet their ecological role is largely unknown because they have not been considered a valuable game fish. This study investigated the ecological importance of mountain whitefish in Big Creek, a wilderness watershed in central Idaho. Using underwater visual counts, hook and line surveys, and stoichiometric analysis we estimated distribution, abundance, total biomass, production, and nutrient and energy contributions within main stem Big Creek. Similar to other studies, when compared to four other common fish species in the watershed (juvenile rainbow/steelhead trout (*Oncorhynchus mykiss*), juvenile Chinook salmon (*Oncorhynchus tshawytscha*), bull trout (*Salvelinus confluentus*), and westslope cutthroat trout (*Oncorhynchus clarki lewisi*)), mountain whitefish were the dominant fish species in Big Creek both in abundance and biomass. Mountain whitefish whole body percent values for N, P, and the resulting N:P ratio were similar to values observed in other salmonids. In light of their abundance and relative composition, it is likely that mountain whitefish constitute a large, important pool of nutrients and energy in the Big Creek watershed, and they probably are a major ecological link between Big Creek and the greater Salmon River Watershed.

Key words: Big Creek, Idaho; mountain whitefish; *Prosopium williamsoni*; biomass; production; nutrient and energy composition

INTRODUCTION

Mountain whitefish (*Prosopium williamsoni*) are frequently among the most abundant fish in rivers and lakes of the Pacific Northwest (Scott 1973, Northcote and Ennis 1994), but have not received research or conservation attention proportionate to their probable ecological importance. This has been due, in part, to their historic status as a non-game fish; they have often been viewed by the public and fisheries managers as undesirable, perceived as competitors with other members of the family Salmonidae, and in some cases even targeted for extirpation (Erickson 1966; Dufek et al. 1999). Mountain whitefish have often been described as relatively abundant (see Northcote and Ennis 1994 for review), and a modest number of studies have described their food habits and life history (e.g., Brown 1952, Pontius and Parker 1973, Pettit and Wallace 1975, Davies and Thompson 1976, Overton et al. 1978). However, there are few published estimates of their population size or their contributions to fish biomass or production (c.f., Goodnight and Bjornn, 1971, Bergerson 1973). They often appear most abundant in mid-sized rivers, and the challenges of estimating fish demographics and production in such habitats (usually not amenable to traditional electro-fishing techniques) has probably contributed to this lack of information.

Because they likely comprise a major component of fish biomass and production, mountain whitefish may serve as important reservoirs and transport vectors for energy and nutrients in Pacific Northwest watershed ecosystems. If so, placing this species in the context of ecosystem budgets or food web models requires not only estimates of their production, but information on the energy and elemental composition of their tissues. Some eco-toxicological studies have reported characteristics of mountain whitefish tissues (e.g., Campbell et al. 2000), but these have typically focused on bioaccumulation of pollutants and indices such as muscle lipid content rather than the whole organism analysis needed for assessing their possible role in ecosystems. We are aware of no study that has combined estimates of mountain whitefish population characteristics with those of their tissue composition in order to begin to place this species in its broader ecological context.

Here we report the results of a study aimed at quantifying and combining population and tissue composition characteristics of mountain whitefish to address some of the gaps in understanding described above. We chose to study mountain whitefish and make comparisons to other fishes in Big Creek, a mid-sized (7th order) tributary to the Middle Fork of the Salmon River located within the Frank Church-River of No Return Wilderness in central Idaho. This watershed is the site of ongoing ecosystem studies, and its wilderness character and unregulated connectivity to larger rivers provides an excellent context within which to investigate mountain whitefish and their ecological role.

MATERIALS AND METHODS

Abundance of mountain whitefish in Big Creek was estimated using underwater survey methods similar to those used in other recent studies in Pacific Northwest rivers (Baxter, 2002; Torgersen et al. 2006). Snorkel surveys have been shown to be an accurate method for estimating fish populations (Northcote and Wilkie, 1963; Thurow, 1994) and are especially useful in several ways: in mid-sized streams where traditional electrofishing techniques are not possible, where the presence of sensitive species may limit the use of electrofishing, and in circumstances where more intensive mark-recapture efforts are not feasible. Our study had to deal with all three of these factors, and as such snorkeling was the best and most feasible means of surveying fish populations. In this study we used both single and multiple pass snorkel surveys to estimate the abundance of mountain whitefish, as well as the other water column dwelling fishes in this system which included westslope cutthroat trout (*Oncorhynchus clarki lewisi*), steelhead/rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*), bull trout (*Salvelinus confluentus*), northern pikeminnow (*Ptychocheilus oregonensis*), and suckers (*Catostomus spp.*). Suckers were only identified to genus because of the difficulties in identifying inland suckers without close examination though it is likely that all suckers observed were either largescale suckers (*Catostomus macrocheilus*) or bridgelip suckers (*Catostomus columbianus*). We also counted sculpin (*Cottus spp.*), longnose dace (*Rhinichthys cataractae*), and speckled dace (*Rhinichthys osculus*), though underwater surveys of these species are not likely to be as reliable as other survey methods due to the cryptic, benthic nature of these fish. Thus we did not use the numbers of these fish observed for estimating abundance.

To estimate total abundance for the water column dwelling taxa, single pass snorkel surveys were conducted in daylight hours from the confluence with the Middle Fork of the Salmon River to a point approximately 60 km upstream in the headwaters of Big Creek. Snorkel surveys were conducted during the summer low flow period from late July through mid August 2006 because low flow conditions corresponded to the period of greatest water clarity. Water clarity was not quantified but during the survey period there was never an instance when the entire stream bottom could not be observed by one surveyor. Along the surveyed stream segment, single pass snorkel counts were conducted in every pool and every third riffle provided that the combined length of the two un-surveyed riffles was not greater than 500 m. Snorkel surveys were also conducted in the major tributaries of Big Creek, but mountain whitefish were only observed in the lower sections of Monumental Creek, Cabin Creek, and Rush Creek in densities much smaller than what was observed in the mainstem of Big Creek. Therefore we did not include tributaries in our estimates or analyses of the mountain whitefish population.

While completing the extensive, single-pass snorkel surveys, we also measured the length and width of each habitat unit including the un-surveyed riffles. We later used the dimensional measurements of each habitat to scale our fish abundance estimates (per square area) to the entire surveyed length of Big Creek, including the un-surveyed riffles. The latter was accomplished by multiplying the surface area of the un-surveyed riffle habitat by the mean density of fish observed in riffles of the corresponding stream segments used in the multi-pass underwater surveys (see below). Total fish abundance of each species was then estimated by summing the total number of fish observed in surveyed habitats with abundance estimates for the un-surveyed riffles. Similar to methods described by Thurow (1994), a 95% confidence interval around fish counts from the single pass snorkel surveys was derived from the standard deviation of fish observed in three pass snorkel counts. This was possible in pool habitats, but in riffles there were not enough fish observed to statistically develop a separate confidence interval; we therefore assume that since the same methods and efforts were applied to the two habitats, the precision of our estimates was similar in both habitats.

To compare biomass among fish species, species abundance (as determined from the single pass surveys) was multiplied by the mean fish weight of each respective species. Mean weight values for juvenile Chinook salmon and juvenile rainbow trout/steelhead were determined from parallel studies that were conducted in Big Creek (Holocek, Dean and Brian Kennedy, University of Idaho, personal communication). Estimates of weight for adult Chinook salmon were obtained from local fish biologists (IDFG, personal communication). Weight values for bull trout and west slope cutthroat trout were calculated from representative mean length values consistent with our observations from the snorkel surveys (300 mm for cutthroat trout and 350 mm for bull trout) using the same length/weight regression equation developed for whitefish (see below). Because bull trout, cutthroat trout, and mountain whitefish all have a similar body form, we assumed that their length weight regressions would be similar enough to allow us to make course comparisons of total biomass using only one regression for all three species. It was desirable to estimate weights of bull trout and cutthroat trout this way because we wanted to avoid unnecessary handling or angling mortality.

In order to characterize mountain whitefish size structure and estimate the precision of our underwater surveys, we conducted multi-pass snorkel surveys at twelve sites. These sites were positioned every 4-8 km along the 60 km of Big Creek that was surveyed during the single pass survey. Each unit was located in habitat representative of the surrounding stream segment and consisted of a pool and an adjacent riffle. Counting only mountain whitefish, three snorkel passes were made in both the pool and riffle segments during which mountain whitefish were classified into five different size classes: 0-100 mm, 100-200 mm, 200-300 mm, 300-400 mm, and 400 + mm.

To estimate mountain whitefish length, weight, and age, we collected fish using hook and line surveys along the length of the study segment of Big Creek. Angling allowed us to selectively target mountain whitefish with almost all of our incidental by-catch consisting of west slope cutthroat trout; very few of the federally protected fish species (Chinook salmon, steelhead trout, and bull trout) were encountered during the hook and line survey and those that were incidentally captured were immediately released unharmed. From these angling surveys, 64 mountain whitefish were measured (total length in mm), weighed (g), and 4 scales were collected from each fish above the lateral line and posterior to the dorsal fin. Scale annuli were counted using a microscope to determine age. Scales that were either blank or deformed were discarded and were not analyzed.

For analysis of tissue composition, fifteen mountain whitefish captured from throughout Big Creek during the hook and line survey were euthanized, frozen, and sent to the University of Idaho's Hagerman Fish Culture Experiment Station. Fish collected for tissue analysis were 244 to 512 g in mass and 311 to 402 mm in length. Tissue samples were processed as described by Green et al. (2002). Briefly, fish tissues were ground, dried, and homogenized. Once the tissue powder was dry, tissue dry weight was determined. Nitrogen content was determined using a LECO nitrogen determinator, and protein estimates were derived by multiplying the nitrogen value by 6.25. Mineral ash values for Ca, K, Mg, Na, P, and S were determined using standard methods (AOAC, 1984). Tissue lipid content was determined by methylene chloride extraction using a Goldfisch Extractor and energetic values were determined using a bomb calorimeter.

We calculated whitefish length at weight, mean fish weight of each size class, and growth by combining data from the angling and snorkel surveys. By plotting fish length at weight and fitting a logistical curve to the data, we derived the following length/weight regression: $y = 0.0094x + 2.5217$, $r^2 = 0.9347$ (y = ln fish mass [g], x = length [mm]). We estimated growth of fish at age by averaging the weight of fish that were the same age and then subtracting the average weight of fish that were one year younger than the respective age being analyzed. This process was repeated for all ages observed (3-7 yrs), and an overall average annual growth rate of mountain whitefish in Big Creek was estimated by averaging the values across ages.

Mean fish weight for each size class in the multi-pass snorkel survey was calculated in two different ways. For the three largest size classes, representative fish weights for each size class were estimated using the average weight of mountain whitefish captured during the angling survey whose total length fell between the respective size classes (200-300 mm, 300-400 mm, and 400+ mm). Because we rarely observed and never captured fish belonging to the two smaller size classes, we estimated their weights by using representative lengths for each size class (based on snorkel observations; lengths used were 75 mm and 175 mm respectively) and referencing those lengths to corresponding weight values derived from the length/weight equation. In order to calculate biomass of mountain whitefish we had to account for the fact that the size structure of fish captured during the hook and line survey was different than the actual size structure of fish observed during the multi-pass snorkel survey. To do this for each stream segment and habitat type, we multiplied the mean mass of fish in each size class by the proportional abundance of fish in each size class observed during the multi-pass surveys and summed all five individual size class values together. This weighted mass per fish estimate was then multiplied by our estimate of total mountain whitefish abundance in Big Creek to generate an estimate of total mountain whitefish biomass. Production for mountain whitefish in Big Creek was estimated by multiplying our estimate of average proportional growth by the total estimated abundance, and despite the fact that our estimates were based on only a small timeframe, we believe that our estimates, although course, were representative of the actual production rates of mountain whitefish tissues in Big Creek. Tissue nutrient, lipid, energy, and mineral content values were multiplied by both the production and total biomass estimates for mountain whitefish to generate estimates of standing stocks and flows of nutrients and energy associated with mountain whitefish tissue elaboration in Big Creek.

RESULTS

Mountain whitefish were the most abundant fish observed in Big Creek with a total of 3,678 (95% confidence interval = ± 683) fish observed. Numerically they comprised 33% of fish observed during summer snorkel surveys of Big Creek. Mountain whitefish were observed in

Big Creek from the confluence with the Middle Fork of the Salmon River to an uppermost location 53 km upstream, with a general trend of decreasing abundance with distance upstream.

Of the mountain whitefish observed during the multipass snorkel surveys, 93% were larger than 200 mm in total length, 6.4% were between 100 and 200 mm, and only 0.4% of fish observed were less than 100 mm (Fig 2 a.). Few juveniles (still showing parr marks) were observed, though searches were rigorously conducted in shallow areas, near woody debris, near habitat structure, and in many side channels. During the extensive snorkel survey, in addition to mountain whitefish we observed 2275 (± 423) juvenile Chinook salmon, 2257 (± 419) juvenile steelhead/rainbow trout, 1368 (± 254) west slope cutthroat trout, 384 (± 71) northern pikeminnow, 72 (± 13) bull trout, 36 (± 7) adult Chinook salmon, and a smaller number of suckers (Fig 1 a.). As we expected, few sculpin, longnose dace, or speckled dace were observed.

We estimated the total biomass of mountain whitefish in Big Creek during the time frame of our study was 1.48 g/m^2 (1250 kg) which was 59% of the total estimated salmonid biomass of 2.50 g/m^2 (2107 kg). Other salmonid biomass values were as follows (Fig 1 b.; in parentheses is total biomass and percent of salmonid biomass): west slope cutthroat 0.34 g/m^2 (283 kg; 13%), juvenile steelhead/rainbow trout 0.30 g/m^2 (255 kg; 12%), adult Chinook salmon 0.26 g/m^2 (216 kg; 10%), juvenile Chinook salmon 0.09 g/m^2 (77 kg; 4%), and bull trout 0.03 g/m^2 (24 kg; 1%).

Based on scale analysis, whitefish ages ranged from 3-7 years, and the majority of fish we observed were 4 or 5 years old (median age was 4 yrs). Based on mass at age data, mountain whitefish in Big Creek exhibited an average growth of 48 g/yr and increased in body mass 18% per year. Mountain whitefish displayed a growth curve of $y = 322.32\ln(x) - 134.01$ (y = weight in grams, x = age in years, $r^2 = 0.9206$). Based on growth rates and the observed age structure, we estimated an annual whitefish production to biomass ratio of 0.35. We estimated mountain whitefish production by applying this production to biomass ratio (0.35 per year) to our estimates of mountain whitefish biomass. Because of the clumped distribution of mountain whitefish, there was a large amount of variation in fish production between pools and riffles as well as with distance from the confluence with the Middle Fork of the Salmon River. Production in pools ranged from 6.8 g/m^2 near the confluence with the Middle Fork of the Salmon River to 0.4 g/m^2 in the headwaters, and production in riffles along that same reach varied from 0.87 g/m^2 to 0.02 g/m^2, though unlike pools, riffles had no discernable pattern with regards to distance from the mouth. Taking into account the variability of abundance and biomass across all habitats, we estimated mean annual production of mountain whitefish tissue in Big Creek to be 0.51 g/m^2 (433.4 kg).

Using the 15 fish euthanized, we estimated mountain whitefish tissue composition (in parentheses is listed the standard deviation of the values). Whitefish mean tissue moisture content was 72.1% (1.94); whitefish dry weight tissue composition was 65.3% (4.80) proteins, 19.5% (5.48) lipids, and 15.2% (2.85) ash weight. Dry tissue energy content was equal to 5.3 Kcal/g and dry weight elemental content by percent was: 10.5% N, 3.0% Ca, 2.3% P, 1.2% K, 0.7% S, 0.3% Na, and 0.1% Mg. This resulted in a molar N:P ratio of 10.0:1 (N:P by weight was equal to 4.5:1).

Biomass estimates for mountain whitefish composition and energy were 269 mg/m^2 (227.3 kg) of protein, 82 mg/m^2 (68.9 kg) of lipids, and 1.9 x 10^9 Kcal of energy. From tissue elemental composition data we estimated that Big Creek's whitefish biomass contained 43 mg/m^2 (36.5 kg) of N, 13 mg/m^2 (10.6 kg) of Ca, 10 mg/m^2 (8.1 kg) of P, and 5.2 mg/m^2 (4.4 kg) of K. Based on production rates whitefish annually produced 94 mg/m^2 (78.6 kg) of protein, 29 mg/m^2 (23.8 kg) of lipids, and 6.4 x 10^8 Kcal of energy. Likewise, we estimated that mountain whitefish annual tissue elaboration was associated with 15 mg/m^2 (12.6 kg) of N, 4.3 mg/m^2 (3.7 kg) of Ca, 3.3 mg/m^2 (2.8 kg) of P, and 1.8 mg/m2 (1.5 kg) of K.

DISCUSSION

Mountain whitefish likely comprise a large portion of the fish biomass and production in watersheds throughout their entire range. Mountain whitefish were the most abundant fish species we observed in Big Creek. They comprised 32% of all fish observed and accounted for the largest portion of fish biomass. Whitefish made up 36 % of the salmonid abundance, 59 % of the salmonid biomass, and in Big Creek mountain whitefish contributed the largest component of fish biomass and production. These results are similar to those reported by Goodnight and Bjornn (1971) whose study of another tributary to the Salmon River, the Lemhi River, generated one of the only other estimates of mountain whitefish biomass and production that we are aware of. In the Lemhi River, mountain whitefish made up 60-80% of the biomass, and 52% of the total fish production. Their estimate of overall mountain whitefish production in the Lemhi River is similar to what we observed in pools in the lower portion of Big Creek (6.8 g/m^2) however it was quite a bit greater than our estimate for mountain whitefish production in the entire length of Big Creek (7.1 g/m^2 in the Lemhi and 0.51 g/m^2 in Big Creek). This large difference could be due to differences in habitat or stream productivity but likely the largest factor affecting the difference in total fish production estimates is that we estimated production based upon all habitats along the entire length of Big Creek. The study in the Lemhi River only made estimates based upon select 30-60 m segments of stream and likely did not account for the large variation in whitefish abundance, biomass, and production in relation to habitat type and distance from a larger river. It is also possible that our estimates may be smaller because underwater fish counts often underestimate fish populations. In smaller streams, snorkel surveys have been shown to produce population estimates that are 35% lower than depletion type electrofishing population estimates (Mullner et al., 1998). While snorkel surveys generally produce conservative estimates of water column dwelling stream fishes, it is likely that our estimates of benthic, cryptic fish species (sculpins, dace, etc) are not representative of their actual abundance in Big Creek. For the reasons listed above, it is likely that our population, biomass, and production estimates for all of the fish species we observed in Big Creek are quite conservative.

Mountain whitefish population structure and ecological contributions are probably dynamic throughout the year; in multiple studies it has been shown that mountain whitefish are generally a migratory fish species (Davies and Thompson, 1976; Rockhold and Berg, 1995; Baxter, 2002), and since we only sampled during the months of June, July, and August our estimates represent a snapshot based on the distribution and tissue composition of whitefish at that time. The absence of juvenile mountain whitefish in Big Creek suggests that rearing occurs in larger river habitats downstream, though it is likely that some spawning does occur in Big Creek, and that mountain whitefish are present all year at some level (Baxter, unpublished data). Mountain whitefish movements probably represent a substantial form of ecological connectivity between Big Creek, the Middle Fork of the Salmon River, the mainstem Salmon River, and the lower Snake River. In eastern deciduous watersheds, upstream fish movements have been shown to counteract half of the nutrient loss due to leaf litter export (Hall, 1972). In Big Creek, which is a larger watershed with a steep gradient and small riparian zone confined to the valley bottom (thus limiting the amount of leaf litter entering and being retained in the stream), it may be that mountain whitefish migration into the watershed could have a larger contribution to the ecosystem than what was observed by Hall (1972). If our estimates of abundance, biomass, production, tissue composition, and energy contributions were extended to include the larger river segments of the network, mountain whitefish ecological contributions might appear even greater.

Another measure of fish composition that may affect the role of mountain whitefish in a food web setting is body protein and lipid content, though these measures of salmonid tissue composition have rarely been obtained outside of aquaculture settings. Of the fish found in Big Creek, we were only able to find values of wild fish tissue lipids and proteins for bull trout and juvenile Chinook salmon. Bull trout tissue composition was 15.82 percent protein and 6.05 % lipids (Selong et al. 2001); juvenile Chinook tissue composition was 6.0 % lipids (Beckman et al. 2000). We observed that mountain whitefish lipid content was very similar to these values, and whitefish protein content was about 3% higher than for bull trout. It is likely that these patterns of protein and lipid content are similar to other native salmonids in Big Creek and as such mountain whitefish likely constitute a very large, nutritious prey population in Big Creek for predators like otters, bears and piscivorous birds.

Fish can be a very important component in aquatic nutrient cycling regimes in that they can store large amounts of necessary nutrients in their tissues (particularly N and P), they can transport those nutrients large distances in relatively short time periods, and they excrete nutrients in forms that are easy for primary producers to manifest (mainly phosphate [PO_3^-], ammonium [NH_4^+], and urea [$(NH_2)_2CO$]) (Schindler and Eby, 1997; McIntyre et al., 2007). The amount of nutrients elaborated into tissue can be affected by multiple factors including diet, size, and taxonomy (Schindler and Eby, 1997; Hendrixson et al. 2007; McIntyre and Flecker, 2009), and these same factors can impact excretion of nutrients by fish. Ecological stoichiometry can be used as an indicator of the role that different species may play in ecosystem nutrient budgets, and one of the most important comparisons is by analyzing N:P ratios. Mountain whitefish N:P ratios were slightly lower than values for other salmonids (Hendrixson et al, 2007; McIntyre and Flecker, 2009). On the other hand, N:P was higher for whitefish than has been reported for more bony freshwater fish such as centrarchids, and such differences have typically been attributed to the fact that larger scales and bony body structures impart a higher body P content (Vanni, 2002; McIntyre and Flecker, 2009). Our observations suggest that mountain whitefish not only hold large amounts of necessary elements in their tissue, but they also likely contribute large amounts of excreted nutrients into the Big Creek ecosystem. Nutrients in the form of fish excretion can be even more important to Big Creek's food web because they are in a form that is more readily available for stream microbes and primary producers (Vanni, 2002).

The conservation of mountain whitefish is a topic of concern that could have great impacts upon their native ecosystems. In many systems where fish assemblages have been altered, not only has there been affects to trophic structure, but there can be large affects upon ecosystem nutrient cycling (Elser et al. 1998; Vanni, 2002). This could possibly be occurring in areas of the mountain whitefish's native range where more bony non-native centrarchids like smallmouth bass (*Micropterus dolomieu*) have been introduced. Fish excretion rates of N and P are negatively related to body tissue N and P values (Vanni et al. 2002). In situations where non-native centrachids may have displaced a native salmonid component of fish biomass such as whitefish, it is likely that the amount of P that is recycled into the stream through fish excretion diminishes. In streams that may be P limited this could have a large effect on all trophic levels. Another trophic nutrient cycling interaction that mountain whitefish are likely linked with is that of anadromous salmonids. It is unclear at this time how exactly mountain whitefish fit into this role, but it is likely that they can play a large part in recycling ocean derived nutrients from anadromous fish carcasses. In light of the large declines of many anadromous fish populations, it is possible that the role of mountain whitefish in stream ecosystem nutrient budgets could have been largely affected. Likely these sorts of interactions occur throughout the entire coregoninae subfamily. This subfamily (to which mountain whitefish are a member), is found in watersheds throughout the entire northern hemisphere. We are currently unaware of any other studies of contributions by corigoninae fishes to ecosystem processes. It is likely that many other species of corgoninae have similar life histories to mountain whitefish and, likewise, are key players in their respective ecosystems.

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FIGURE LEGENDS

Figure 1. a. Relative abundance of fish observed during single pass snorkel surveys conducted from the mouth to the headwaters of Big Creek. Error bars indicate a 95% confidence interval of abundance estimates.

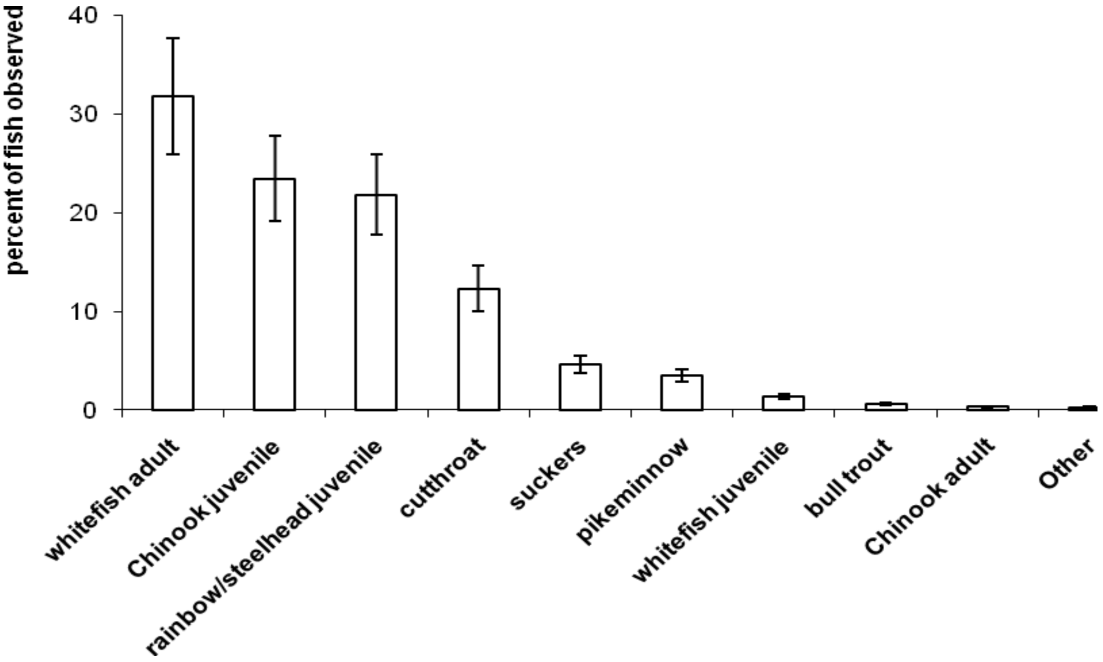
b.Salmonid biomass by percent of the native salmonids observed in Big Creek.

Figure 2. a. Size structure of mountain whitefish populations as determined by multi-pass snorkel surveys. Sub-adults or adults are indicated by the grey bars, and juvenile fish are represented by the white bars.

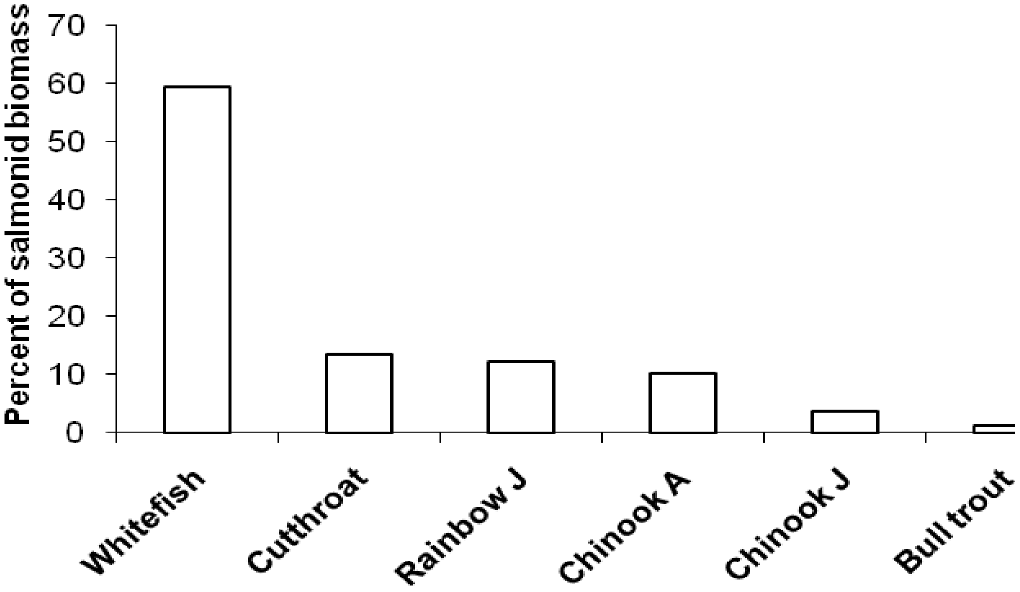
b. Growth rate of mountain whitefish in Big Creek showing the general growth curve ($y = 322.32\ln(x) - 134.01$, $R^2 = 0.9206$).

Lance and Baxter Figure 1

a.

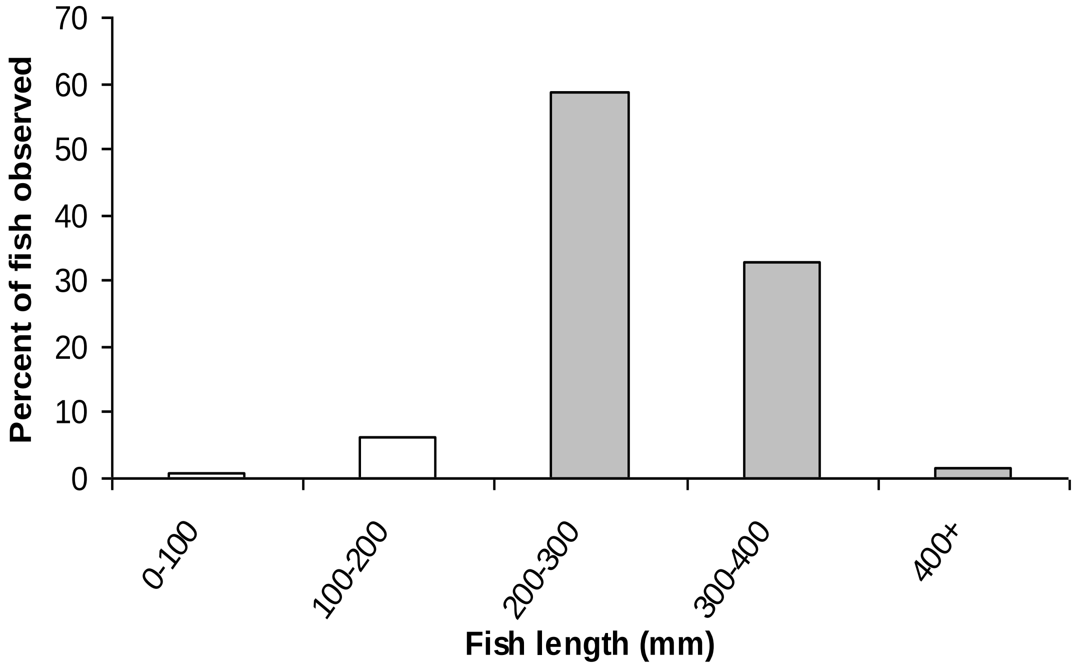


b.



Lance and Baxter Figure 2

a.



b.