

Abundance, Production, and Tissue Composition of Mountain Whitefish (*Prosopium williamsoni*) in a Central Idaho Wilderness Stream

Abstract

Mountain whitefish (*Prosopium williamsoni*) are among the most abundant native fishes in western North America, yet their role in ecosystems is largely unknown. We investigated their ecology in Big Creek, a 7th-order wilderness watershed in central Idaho. Based on underwater visual counts and hook and line surveys conducted during summer months, as well as tissue analysis, we estimated mountain whitefish distribution and abundance, total biomass, production, and energy and nutrient contributions along a 60 km segment of Big Creek. We observed that abundance decreased with distance upstream, and 93% of mountain whitefish surveyed in Big Creek were greater than 200 mm (≥ 3 years); few juveniles were observed, suggesting that rearing occurs in habitats downstream. Mountain whitefish were the dominant fish in Big Creek, in terms of both abundance (33% of fish observed) and biomass (57% of salmonid biomass). We estimated their production averaged across the study segment as $0.51 \text{ g m}^{-2} \text{ yr}^{-1}$, though it ranged up to $6.8 \text{ g m}^{-2} \text{ yr}^{-1}$ in downstream reaches. Mountain whitefish tissue energy content was 5.3 Kcal g^{-1} and its composition was 10.5% N, 3.0% Ca, 2.3% P, 1.2% K, 0.7% S, 0.3% Na, and 0.1% Mg. The ratio of N:P(4.5:1) was slightly lower than those observed in other salmonids and considerably higher than more bony taxa. Our results suggest mountain whitefish constitute an important pool of energy and nutrients in the Big Creek ecosystem, and seem likely to play important roles that have not yet been investigated in this and other rivers throughout their range.

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 large part, to their historical status as a non-game fish. In fact, mountain whitefish have often been viewed by both the public and fisheries managers as undesirable, perceived as competitors with other more desired game species, and in some cases even targeted for extirpation (Erickson 1966, Dufek et al. 1999). Numerous accounts of mountain whitefish relative abundance have been reported (see Northcote and Ennis 1994 for a 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 (but see 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 pools and transport vectors for energy and nutrients in Pacific Northwest watersheds. Efforts to develop ecosystem budgets or food web models are being conducted throughout the Pacific Northwest (e.g., McCarthy et al. 2009, Wipfli and Baxter 2010) and routinely involve gathering information regarding primary producers, invertebrate consumers, and salmonid fishes. However, where mountain whitefish are important contributors, these efforts to study their ecological significance may also require estimates of mountain whitefish production and trophic ecology, as well as information on the energy and elemental composition of their tissues. Describing body stoichiometry is increasingly recognized as a critical first step toward understanding elemental constraints on consumers like fish, their relationship to prey resources and their role in broader ecosystem element dynamics (Schindler and Eby 1997, Elser and Urabe 1999, McIntyre and Flecker 2010). Some ecotoxicological studies have reported characteristics of mountain whitefish tissues (e.g., Campbell et

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al. 2000), but these have typically focused on bioaccumulation of pollutants and indices such as muscle lipid content rather than the analysis of whole organisms needed for assessing their possible role in ecosystems. Although there has been some work on the abundance and tissue energy content of related coregonid fishes in Europe where they are considered an important food fish (Dabrowski 1985), we are aware of no study that has combined estimates of mountain whitefish population characteristics with analysis of their tissue composition.

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 in order to begin to place this species in its broader ecological context. 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 (Figure 1). This watershed is the site of ongoing ecosystem studies, and its wilderness character and unregulated connectivity to larger

streams provides an excellent context within which to investigate the role of mountain whitefish in western stream ecosystems.

Methods

We estimated the abundance of mountain whitefish in Big Creek using underwater survey methods similar to those utilized in other recent fish assemblage studies in Pacific Northwest rivers (Baxter 2002, Torgersen et al. 2006). Snorkeling has been shown to be an accurate method for surveying fish populations (Northcote and Wilkie 1963, Thurow 1994) and is especially useful in several contexts: 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. Faced with all three of these circumstances, snorkeling was the best and most feasible method for this study.

We used single-pass snorkel surveys to estimate the abundance of mountain whitefish, as well as the other fishes dwelling in the water column of Big Creek, which included westslope cutthroat

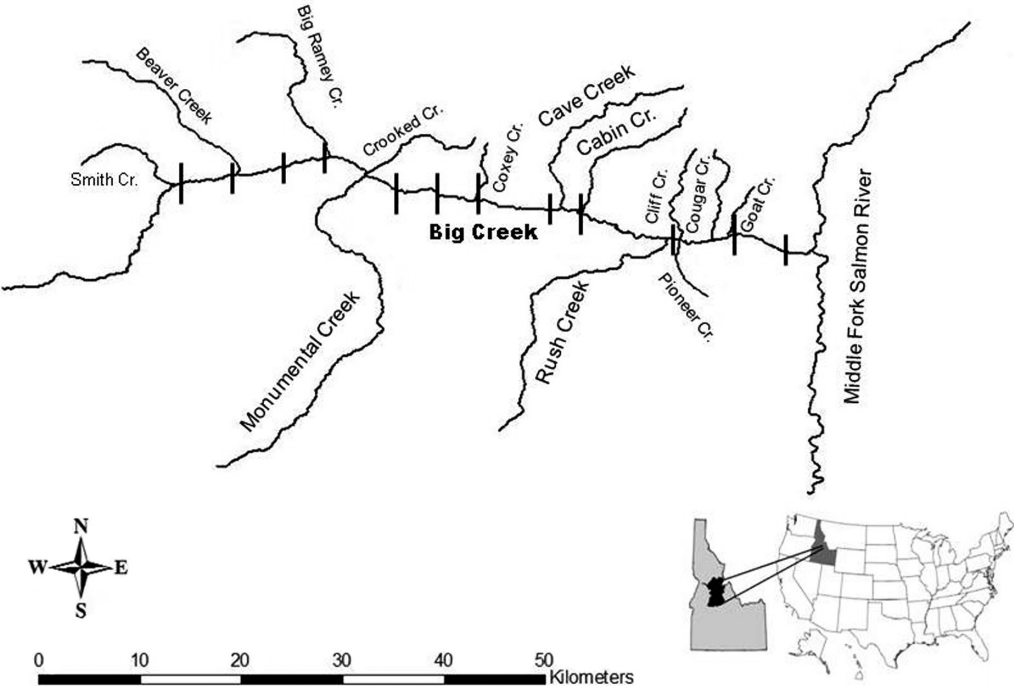


Figure 1. Big Creek, its tributaries, and the Middle Fork of the Salmon River. Hash Marks perpendicular to Big Creek represent the location of the three-pass snorkel sites.

trout (*Oncorhynchus clarkii 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 underwater identification of the two species present in this stream, largescale (*Catostomus macrocheilus*) and bridgelip (*Catostomus columbianus*) suckers. We also counted sculpin (*Cottus* spp.), longnose dace (*Rhinichthys cataractae*), and speckled dace (*Rhinichthys osculus*). However, due to the cryptic, benthic nature of these fish, underwater surveys of these species are not as reliable. Thus, we did not use the counts of these fish as abundance estimates and did not include them in our comparisons to mountain whitefish.

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. These snorkel surveys were conducted by two-person crews consisting of a diver and a data recorder walking along the shore. In each channel unit, the diver counted fish while floating downstream along a single transect of the thalweg, and then worked their way back upstream in a zig-zag fashion that allowed more complex or covered habitats (e.g., undercut, log jams) to be surveyed for fish that may have been missed from the thalweg. Along the surveyed stream segment, the dimensions of every habitat unit were measured, and single-pass 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 (this ensured gaps in our survey of > 500 m did not occur). This approach, which resulted in surveys of 100 pools and 127 riffles, also ensured that our sampling effort was more evenly assigned to pools and riffles than would have occurred if all riffle habitats (which were far more abundant) were surveyed. On average, riffle habitats had maximum depth of 0.85 m (SD = 0.37 m), width of 16 m (SD = 6.7 m), and length of 210 m (SD = 178 m), whereas pools had an average maximum depth of 1.4 m (SD = 0.5 m), width of 14 m (SD = 5.6 m), and length of 36 m (SD = 22 m). Snorkel surveys were conducted in the downstream reaches (1-2 km) of all of the major (4th order or greater) tributaries of Big Creek, but only a few individual mountain

whitefish were observed in the lower sections of Monumental Creek, Cabin Creek, and Rush Creek; therefore we focused our estimates and analyses of the mountain whitefish population in the mainstem of Big Creek rather than its tributaries. All surveys were conducted under conditions of high water clarity that allowed visibility across the entire stream channel. Total abundance of each species was estimated by summing the number of fish observed in surveyed habitats with abundance estimates for the un-surveyed riffles (which were extrapolated based on their habitat surface area).

In order to characterize mountain whitefish size structure in Big Creek and estimate the precision of our underwater surveys, we conducted three-pass snorkel surveys at twelve sites. These sites were positioned every 4-8 km along the 60 km segment of Big Creek that was surveyed using the single-pass technique. Each unit was located in habitat representative of the surrounding stream segment and included a pool and an adjacent riffle. Counting only mountain whitefish, three passes were made through both the pool and riffle units, and mountain whitefish were classified into five different size classes: 0-100 mm, 100-200 mm, 200-300 mm, 300-400 mm, and >400 mm. We observed very few juvenile mountain whitefish (defined by the occurrence of detectable parr marks). Though visual surveys can be less efficient for the smallest size classes of fish, snorkeling has been effective for surveying distribution of juvenile mountain whitefish in similar streams of this region (Torgersen et al. 2006). Moreover, based on previous day-night snorkel surveys of Big Creek (P. Della Croce and C.V. Baxter, unpublished data) juvenile mountain whitefish do not appear to exhibit especially cryptic behavior, suggesting our daytime surveys were likely representative. Similar to methods described by Thurow (1994), a 95% confidence interval on our visual counts was derived from the standard deviation of fish observed in the three passes. This was possible for pool habitats, but there were not enough fish observed in riffles to statistically develop a separate confidence interval; we therefore assumed that because the same methods and efforts were applied, the precision of the estimates was similar in both habitats.

To estimate relationships between length, weight, and age, we collected mountain whitefish from throughout Big Creek using angling techniques. Angling is most effective for adult sized

fishes, but because we observed very few juvenile mountain whitefish in our population surveys (see below) we did not collect juvenile fish for aging. Angling allowed us to selectively target mountain whitefish, and very few of the federally protected fish species found in Big Creek (Chinook salmon, steelhead trout, and bull trout) were encountered during the hook and line survey. Those that were incidentally captured were immediately released unharmed. We captured 64 mountain whitefish that varied in total length from 249 mm to 430 mm, and the majority of fish captured (89%) were between 300 mm and 400 mm. Captured fish 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. Age was determined by counting scale annuli with a microscope, and ages were verified using length frequency models. A growth curve was developed by plotting mountain whitefish weight at age and fitting the von Bertalanffy growth function.

We calculated mountain whitefish weight at length and biomass by combining data from the angling and snorkel surveys. We plotted length and weight for the fish captured by angling and derived the following length-weight regression: $\text{Log}_{10}(y) = -5.11 + 3.04\text{Log}_{10}(x)$, $r^2 = 0.9467$ ($y = \text{mass [g]}$, $x = \text{length [mm]}$). Whitefish used to develop the length-weight regression had a mass between 106 and 654 g and lengths between 249 and 430 mm. For each segment of stream between the three-pass sites, biomass was calculated by multiplying an estimate of mean mass per fish by the abundance of mountain whitefish in that segment. For juvenile fish we used the length-weight relationship to generate an estimate of mean mass per fish, which was then multiplied by their abundance from the single pass snorkel survey. We judged this relatively coarse approach adequate for the smallest size classes because they were rare and represented < 2% of the whitefish biomass. For adult fish, we multiplied the size class proportional abundance derived from three-pass surveys by the average mass for each size class (derived from our angling surveys). The resulting values for each size class were summed in order to generate a mean mass estimate for adult fish.

We estimated mountain whitefish production using the increment summation method (Hayes et al. 2007). For each age-class of fish, we multiplied the average proportional growth between ages by the proportional abundance of fish in that age

class (3-7 yrs). We then summed all the values for all ages in order to estimate the production to biomass ratio. This value was multiplied by our estimate of total mountain whitefish biomass to obtain an estimate of annual production in Big Creek. Because we did not capture any juvenile mountain whitefish that were 0-2 yrs of age, our production estimate does not include these ages. However, because of the rarity of juvenile mountain whitefish in Big Creek we do not expect this was a major source of uncertainty in our estimate. In addition, though the production estimate was based on a relatively coarse, snap-shot survey of abundance, biomass and size structure, this seems unlikely to be the major source of error either. Rather, the principal source of uncertainty was likely associated with the abundance and biomass estimates themselves (see Discussion).

To compare biomass among fish species, abundance of each fish species (as determined from the single-pass snorkel 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 et al. 2009). Estimates of weight for adult Chinook salmon were obtained from local fish biologists (Idaho Department of Fish and Game, personal communication). Weight values for bull trout and westslope cutthroat trout were calculated from the average size of fish we observed during our snorkel surveys using the same length-weight regression equation developed for mountain whitefish. Because bull trout, cutthroat trout, and mountain whitefish all have a relatively similar body form, we assumed that their length-weight regressions would be similar enough to allow us to make coarse 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 from prolonged time required to handle fish to obtain measurements of fish weight.

For analysis of tissue composition, a random sample of 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 total length. Tissue samples were processed as

described by Green et al. (2002). Tissues of each entire fish were ground, dried, and homogenized. Once the tissue powder was dry, 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 Goldfish Extractor and energetic values were measured using a bomb calorimeter. Tissue nutrient, lipid, energy, and mineral content values were multiplied by both the total biomass and production 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 in Big Creek, with a total of 3678 (95% confidence interval = ± 683) observed. Numerically, they comprised 33% of fish observed during summer, single-pass snorkel surveys of Big Creek (Table 1a). Biomass of mountain whitefish in Big Creek during the time frame of our study was 1.48 g m^{-2}

(1250 kg over the entire stream length). Mountain whitefish made up 57% of the salmonid biomass which we estimated was 2.60 g m^{-2} (2107 kg; Table 1b). During the single-pass snorkel survey, 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, and exhibited a general trend of decreasing abundance and biomass with distance upstream.

Of the mountain whitefish observed during the three-pass 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 (Figure 2a). Few juveniles were observed, though searches were rigorously conducted in shallow areas, near woody debris, near habitat structure, and in many side channels. Based on counts of scale annuli, mountain whitefish captured by angling ranged from 3-7 years, and the majority of fish we captured were 4 or 5 years old (median age = 4 yrs). Based on the fish captured by angling, the von Bertalanffy growth curve for mountain whitefish in Big Creek was characterized by the equation $y = 38512(1 - e^{-0.00175x})$ (where y = weight in grams, x = age in years; Figure 2b). Using the growth rates and observed age structure, we estimated mountain whitefish in Big Creek

TABLE 1. (a) Relative abundance of fish observed during single pass snorkel surveys conducted from the mouth to the headwaters of Big Creek. (b) Salmonid biomass observed in Big Creek.

(a)			
Species	Abundance	% of Abundance	95% CI by percent
mountain whitefish adult	3532	32	6
Chinook juvenile	2609	23	4
rainbow/steelhead juvenile	2429	22	4
cutthroat	1368	12	2
suckers	520	5	1
pikeminnow	384	3	0.6
mountain whitefish juvenile	146	1	0.2
bull trout	72	0.6	0.1
Chinook adult	36	0.3	0.1
Other	30	0.3	0.1

(b)				
Species	Total Biomass (kg)	Biomass Per area (g m ⁻²)	% of Total	95% CI(+/-)
mountain whitefish	1253	1.5	57	7
cutthroat	364	0.43	17	2
rainbow/steelhead juvenile	255	0.30	12	1
Chinook adult	216	0.26	10	1
Chinook juvenile	77	0.09	3	0.4
bull trout	31	0.04	1	0.2

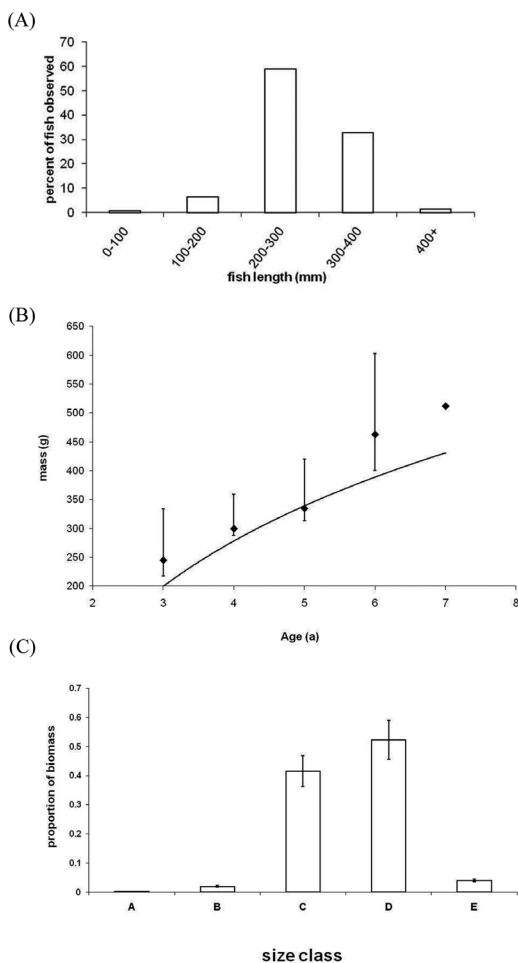


Figure 2. (a) Size structure of mountain whitefish populations as determined by multi-pass snorkel surveys. (b) Growth rate of mountain whitefish in Big Creek showing the Von Bertalanffy growth curve [$y = 38512(1 - e^{-0.00175x})$]. (c) Percent of whitefish biomass by size class.

exhibited a production to biomass ratio of 0.38, and a production rate of 0.56 g m^{-2} per year.

The tissue of the mountain whitefish had, on average (standard deviation in parentheses), a moisture content of 72.1% (1.94); dry weight tissue composition was 65.3% (4.80) proteins, 19.5% (5.48) lipids, and 15.2% (2.85) ash weight. Energy content of dry tissue was 5.3 Kcal g^{-1} and the elemental content of the dry tissue 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 composition was associated with a molar N:P ratio of 10.0:1 (N:P by weight = 4.5:1).

Based on tissue composition and energy content, standing stock biomass of mountain whitefish in Big Creek included (values in parentheses are estimates scaled by the entire stream): 269 mg m^{-2} (227.3 kg) of protein, 82 mg m^{-2} (68.9 kg) of lipids, and $9.2 \times 10^3 \text{ KJ m}^{-2}$ ($7.7 \times 10^9 \text{ KJ}$) 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 our estimates of annual production rates, whitefish produced $94 \text{ mg m}^{-2} \text{ yr}^{-1}$ (78.6 kg) of protein, $29 \text{ mg m}^{-2} \text{ yr}^{-1}$ (23.8 kg) of lipids, and $3.2 \times 10^3 \text{ Kcal m}^{-2}$ ($2.7 \times 10^9 \text{ Kcal}$) of energy. Likewise, we estimated that mountain whitefish annual tissue elaboration was associated with $15 \text{ mg m}^{-2} \text{ yr}^{-1}$ (12.6 kg) of N, $5 \text{ mg m}^{-2} \text{ yr}^{-1}$ (3.7 kg) of Ca, $3.3 \text{ mg m}^{-2} \text{ yr}^{-1}$ (2.8 kg) of P, and $1.8 \text{ mg m}^{-2} \text{ yr}^{-1}$ (1.5 kg) of K.

Discussion

Mountain whitefish likely comprise a large portion of the fish biomass and production in watersheds throughout their range. These results are similar to those reported by Goodnight and Bjornn (1971) whose study in the Lemhi River, another tributary to the Salmon River, generated one of the only other estimates of mountain whitefish biomass and production of which we are aware. In the Lemhi River, mountain whitefish made up 60-80% of the biomass, and 52% of the total fish production. Their estimate of mountain whitefish production (7.1 g m^{-2}) was similar to what we observed in pools in the lower portion of Big Creek (6.8 g m^{-2}), however it was much greater than our estimate for mountain whitefish production as averaged along the entire length of Big Creek (0.51 g m^{-2}). This could be due to differences in habitat or stream productivity between the basins, but may also be because we estimated production based upon all habitats along the length of stream occupied by whitefish, whereas Goodnight and Bjornn's (1971) estimates were based upon electrofishing of selected 30-60 m reaches in the lower half of the Lemhi River. As we observed in lower Big Creek, such larger river reaches may correspond to the most productive habitats for mountain whitefish. It is also possible that our estimates may be smaller than Goodnight and Bjornn's (1971) because underwater counts often underestimate fish population size. This is true in small streams (Mullner et al. 1998) and in larger systems like

Big Creek where more rigorous population estimates rely upon mark-recapture studies. In the meantime, it is important to consider that the abundance, biomass, and production estimates we report here are conservative.

Mountain whitefish population structure and their ecological roles in Big Creek are probably dynamic throughout the year. Multiple studies have shown that mountain whitefish undertake extensive seasonal migrations (Pettit and Wallace 1975, Davies and Thompson 1976, Baxter 2002). Because we only sampled from June to August, our estimates represent a snapshot based on the distribution and tissue composition of fish at that time. Though mountain whitefish are present in Big Creek year-round and some spawning likely occurs there (C.V. Baxter, unpublished data), their abundance probably varies with seasonal migration of some component of the population, and the rarity of juvenile mountain whitefish in Big Creek suggests that rearing occurs in larger river habitats downstream. We speculate that mountain whitefish movements represent an important form of ecological connectivity between Big Creek, the Middle Fork of the Salmon River, the mainstem Salmon River, and the lower Snake River, which together represent one of the largest intact networks in the contiguous United States. Fish migrations transport energy and nutrients against the current, and may help maintain the chemical and metabolic states of ecosystems (Hall 1972). Mountain whitefish movements may play such a role in Big Creek, and their importance in this respect may have increased during the decades of diminished returns of anadromous salmon and steelhead, whose migrations are thought to have effects on stream-riparian ecosystems in this region (Naiman et al. 2002). We suspect that if measurements of mountain whitefish abundance, biomass, production, tissue composition, and energy contributions were conducted in the larger segments of the Salmon and Snake River network, the potential ecological importance of mountain whitefish might appear even greater.

The body protein and lipid content of mountain whitefish tissue may be important with respect to their role in food webs. Such 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. Selong et al. (2001)

reported that bull trout tissue composition was 15.8% protein and 6.0% lipids, and Beckman et al. (2000) reported juvenile Chinook tissue composition was 6.0% lipids. 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 may constitute a very large, nutritious prey population for predators like bull trout, otters, bears, and piscivorous birds.

Mountain whitefish may play an important role in the cycling of nutrients in Big Creek, as has been demonstrated for fish in other contexts (McIntyre and Flecker 2010). Fish 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 utilize (mainly phosphate [PO_4^{3-}], ammonium [NH_4^+], and urea [$(\text{NH}_2)_2\text{CO}$]) (Schindler and Eby 1997, McIntyre et al. 2007). The relative amount of nutrients incorporated into tissue and excreted by fish can be affected by multiple factors including taxonomy, size and diet (Schindler and Eby 1997, Hendrixson et al. 2007, McIntyre and Flecker 2010). In light of this, ecological stoichiometry can be used as an indicator of the role that different species may play in ecosystem nutrient budgets, and an important comparison involves analyses of N:P ratios (Elser and Urabe 1999). Mountain whitefish tissue N:P ratios were slightly lower than values for other salmonids (4.5:1 for mountain whitefish compared to approximately 5:1 for other salmonids; Hendrixson et al 2007, McIntyre and Flecker 2010), likely because coregonids are bonier and have larger scales than members of the genera *Oncorhynchus*, *Salmo*, or *Salvelinus*. On the other hand, N:P was higher for whitefish than has been reported for even more bony freshwater fish such as centrarchids (centrarchid N:P was approximately 2.5:1; McIntyre and Flecker 2010).

In addition to retaining critical nutrients in their tissue, mountain whitefish may also recycle large amounts of nutrients through excretion. Nutrients excreted by fish can exceed amounts stored in biomass, and can be important to stream food webs because their form is readily available for uptake by microbes and primary producers (Vanni 2002). Such mediation of nutrient availability by

fish may be important in oligotrophic streams like those of central Idaho, where primary producers are usually limited by N or a combination of N and P (Sanderson et al. 2009), as are microbial heterotrophs (Marcarelli et al. 2009). Though we did not measure excretion by mountain whitefish directly, we can arrive at a coarse estimate by combining production with literature derived efficiencies (e.g., Schindler et al. 1993) for growth (~10% of consumption) and waste excretion (~35% of consumption) for similar invertivorous fish. Such calculations suggest that fluxes of N and P associated with excretion may be 3-4 times greater than those of whitefish production. Nutrient budgets have not yet been constructed for the Big Creek watershed, so we cannot compare the stocks or flows associated with mountain whitefish to other components of such budgets. Coarse comparisons with much smaller watersheds elsewhere in the Pacific Northwest (e.g., Triska et al. 1984), suggest that flows of N and P associated with mountain whitefish are likely small relative to total inputs or exports. However, the magnitude of their production and excretion, combined with the relatively high quality (in terms of utility to primary producers and consumers) of the associated forms of N and P, may mean they play a role in nutrient dynamics and flow in food webs disproportionate to quantity alone (e.g., Marcarelli et al. In Press). We therefore reason that future investigation into the role of mountain whitefish in stream nutrient dynamics is warranted.

In oligotrophic streams like those in central Idaho, there are potentially strong imbalances between mountain whitefish and their resources in terms of N and P, which could amplify their roles, either as reservoirs or recyclers, in ecosystem nutrient dynamics. For instance, our estimates suggest whitefish tissue is considerably more enriched in P than is likely for their invertebrate prey or primary producers in streams of this region. In another stream of the Salmon Basin, Rothlisberger et al. (2008) reported a N:P (molar) value of ~22 for a heptageniid mayfly that is also common in Big Creek. This is less than half the proportion of P we estimated for whitefish, and though investigations along these lines are just beginning, we expect such imbalances are common in watersheds of this region.

Our results suggest that conservation of mountain whitefish may have important consequences for their native ecosystems and may extend to implications for flows of energy and cycling of nutrients. Because fish excretion rates of N and P are negatively related to body tissue N and P values (Elser and Urabe 1999, Schindler et al. 1997), in many systems where fish assemblages have been altered, not only have there been effects on trophic structure, but large effects have been documented on ecosystem nutrient cycling as well (Elser et al. 1998, Vanni 2002, Taylor et al. 2006, McIntyre et al. 2007). Although studies regarding the impact of excreted nutrients have been conducted mostly in lakes and tropical streams, we expect that similar interactions occur in temperate streams like those found in the Pacific Northwest. The loss and/or replacement of mountain whitefish and other often overlooked, non-game fishes (e.g., native catostomids, cyprinids) in rivers of the Pacific Northwest may therefore have ecosystem consequences that have not yet been appreciated. Such hypotheses deserve future study. Moreover, similar hypotheses may be applicable to other members of the Coregoninae subfamily. These are found in watersheds throughout the northern hemisphere, and there have been very few studies regarding the contributions of these fishes to ecosystem processes.

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