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COMPARATIVE FOOD HABITS AND HABITAT SELECTION
OF MOUNTAIN WHITEFISH AND RAINBOW TROUT
IN THE KOOTENAI RIVER, MONTANA

by

Joseph Michael DosSantos

A thesis submitted in partial fulfillment
of the requirements for the degree

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APPROVAL

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VITA

Joseph Michael DosSantos was born on June 29, 1954 in Chicopee, Massachusetts to Alfredo and Carmina DosSantos. He attended Chicopee High School and was graduated in June 1972. In September 1972 he enrolled at Ricker College in Houlton, Maine and later received a Bachelor of Science degree in Wildlife Biology from the University of Montana in June 1978. In January 1980 he began work toward a Master of Science degree in Fish and Wildlife Management at the University of Idaho and in January 1981 transferred to Montana State University.

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ABSTRACT

Food habits and habitat selection of mountain whitefish and rainbow trout within the Kootenai River, Montana, and two of its major tributaries were studied to assess possible competitive interactions between the species. Analysis of stomach contents revealed that chironomids were the major food item of mountain whitefish, ranging from 42.7% to 62.4% total stomach volume. Smaller whitefish showed the most consistent and heaviest use of chironomids, whereas larger whitefish showed the largest deviation from chironomid utilization, exhibiting high seasonal use of Trichoptera and Gastropoda. Rainbow trout utilized more Ephemeroptera and Trichoptera, ranging as high as a combined 95.8% total stomach volume, and were more diverse in food preference, feeding on all major invertebrates found in the Kootenai. Small trout derived up to 85.7% of their winter food bulk from chironomids. Percent overlap in diet between mountain whitefish and rainbow trout ranged from 11.0% to 90.6%. Overlap in the diets of smaller fish, less than 20.0 cm TL, was the greatest. Whitefish appear to be more selective feeders than rainbow trout, keying in on chironomids from both the benthos and drift. Rainbow trout appear to be an opportunistic water column and surface feeder, selecting insects in relation to their seasonal abundance. Only slight differences exist between microhabitat selection of sympatric mountain whitefish and rainbow trout. Average water column velocities occupied by both species were virtually the same. Whitefish chose deeper areas and substrates with a higher percent of gravel and cobble. Rainbow trout occupied areas with a high percent of boulder. Allopatric trout were found in areas with lower average water column velocities than sympatric trout. The combination of substrate characteristics and water depths was most important in influencing mountain whitefish habitat selection. The interplay of water depths and velocities was dominant in influencing rainbow trout habitat selection. Total water depth contributed the most in formulating the best descriptive habitat functions for both species.

INTRODUCTION

The Kootenai River, with an average flow at Libby of 12,000 cubic feet per second (cfs), is Montana's second largest river. Since the completion of Libby Dam in 1975, the remaining 80.5 free-flowing kilometers (km) of the Kootenai in Montana have undergone considerable environmental alterations. Not only physical parameters, such as flow regimes, temperature patterns, and water quality have been altered, but also dramatic changes in the aquatic invertebrate and vertebrate communities have occurred (May and Huston 1979).

Mountain whitefish (Prosopium williamsoni) and rainbow trout (Salmo gairdneri) are indigenous to the Montana portion of the Kootenai River (Allendorf 1980, Brow 1971) and are also the predominate game fish species. Numbers of both species have increased four and five fold, respectively, since regulation of the river, with a resultant decrease in both average size and growth rates (May et al. 1981).

Numbers of mountain whitefish in the Pipe Creek section of the Kootenai River have increased from 171 fish per 300

meters (m) in 1974 to 770 in 1981. Year class strength and growth rates for mountain whitefish have oscillated more than those of rainbow trout, but have decreased overall since reaching their peak in 1977. Three-year-old fish in 1977 averaged 35.8 centimeters (cm) total length (TL), as compared to 29.7 cm in 1980. The growth of fish up to age II did not change as markedly as the growth of older fish.

Numbers of rainbow trout in the Pipe Creek section of the Kootenai River have increased from 24 per 300 m in 1973 to 126 in 1980. Although the total number of rainbow trout has increased markedly, the abundance and percent of fish larger than 35.5 cm peaked in 1977 at 32.8 percent, dropped markedly in 1978 to 10.3 percent, and fell to 2.5 percent in 1981 (May et al., 1981). The marked reduction in the percent of the population over 35.5 cm TL appears to have resulted from a decline in growth rates, with increasing angler harvest also being a contributing factor (Graham 1979). Three-year-old fish in 1977 averaged 45.5 cm, whereas three-year-old fish in 1981 only averaged 34.3 cm. Growth of fish is often inversely related to fish densities (Chapman 1966). The reduced growth rates appear to be primarily a result of increased fish densities.

The Montana Department of Fish, Wildlife and Parks

management program emphasizes maintaining a viable wild rainbow trout fishery in the Kootenai River. More liberal fishing regulations on mountain whitefish have been initiated in response to their growing population and possible competition with the still increasing rainbow trout population. This study addressed possible competitive interactions between mountain whitefish and rainbow trout.

Competition can occur between species when a necessary resource is in limited supply or if the quality of that resource varies and demand is quality dependent (McNaughton and Wolf 1973). With the Kootenai's biotic and abiotic environment in a constant state of flux due to power peaking, it is hypothesized that the opportunities for competitive interactions between mountain whitefish and rainbow trout are increased. This study was concerned with possible competition for food and space, among the most fundamental environmental components necessary for any organism to survive (Chapman 1966, McNaughton and Wolf 1973). The two objectives of this study were; (1) to determine the seasonal food habits of select size groups in mountain whitefish and rainbow trout as related to availability of aquatic insects in the Kootenai River; and (2) to study the macro- and micro-habitat selection of

select size groups in sympatric mountain whitefish and rainbow trout within the Kootenai River drainage.

DESCRIPTION OF STUDY AREA

Kootenai River

The Kootenai River, the second largest tributary of the Columbia, drains approximately 50,000 square kilometers (km²). The river originates in Kootenay National Park, British Columbia, flows south into Montana, then northwest through Montana and Idaho and into Kootenay Lake in Canada; it then flows southwest from Kootenay Lake and joins the Columbia River at Castlegar, British Columbia (Figure 1). The Kootenai River is approximately 780 kilometers (km) in length of which 266 km are in the states of Montana and Idaho. Elevation of the Kootenai in the United States ranges from about 533 m to 704 m above mean sea level with a gradient of 0.6 m/km (Bonde and Bush 1975).

The Kootenai River was impounded by Libby Dam in March, 1972, leaving only 80.5 km free-flowing in Montana. Libby Dam discharges have reversed the natural river hydrograph. Historically, the highest flows occurred from April through July, with the median peak flow of about 43,000 cfs occurring during May and June. Low discharge of about 2,000 cfs occurs during winter and early spring.

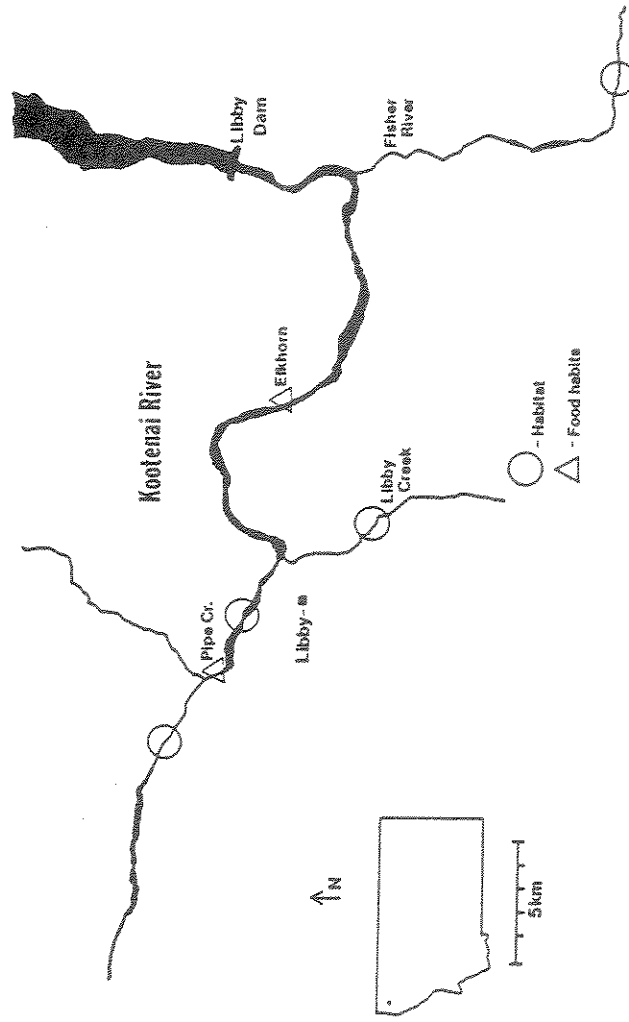


Figure 1. Map of Kootenai River, Fisher River and Libby Creek food habits and habitat selection study areas.

The average annual discharge is about 12,000 cfs. Since impoundment, lowest mean flows of 4,000 cfs occur from April through June, with highest mean flows of 20,000 cfs occurring from November through January (Figure 2a). Maximum discharge prior to impoundment was 121,000 cfs as compared to 40,000 cfs following impoundment (Shields et al. 1982).

The daily flow regime, which was stable under natural conditions, now fluctuates from 4,000 to 23,000 cfs due to power peaking capacity of Libby Dam. These daily flows can fluctuate an allowable maximum of 1.2 vertical meters per day from April through September and 1.8 m per day from October through March. Actual fluctuations have been less than the maximum allowed on most days (May et al. 1981).

Kootenai River water temperature has also been altered by regulation. Although Libby Dam is equipped with a selective withdrawal system, operational constraints result in water temperatures which are warmer than the natural regime from October to March, and cooler from April to September (Figure 2b).

Two sections of the Kootenai River were selected to determine seasonal food availability and food habits of

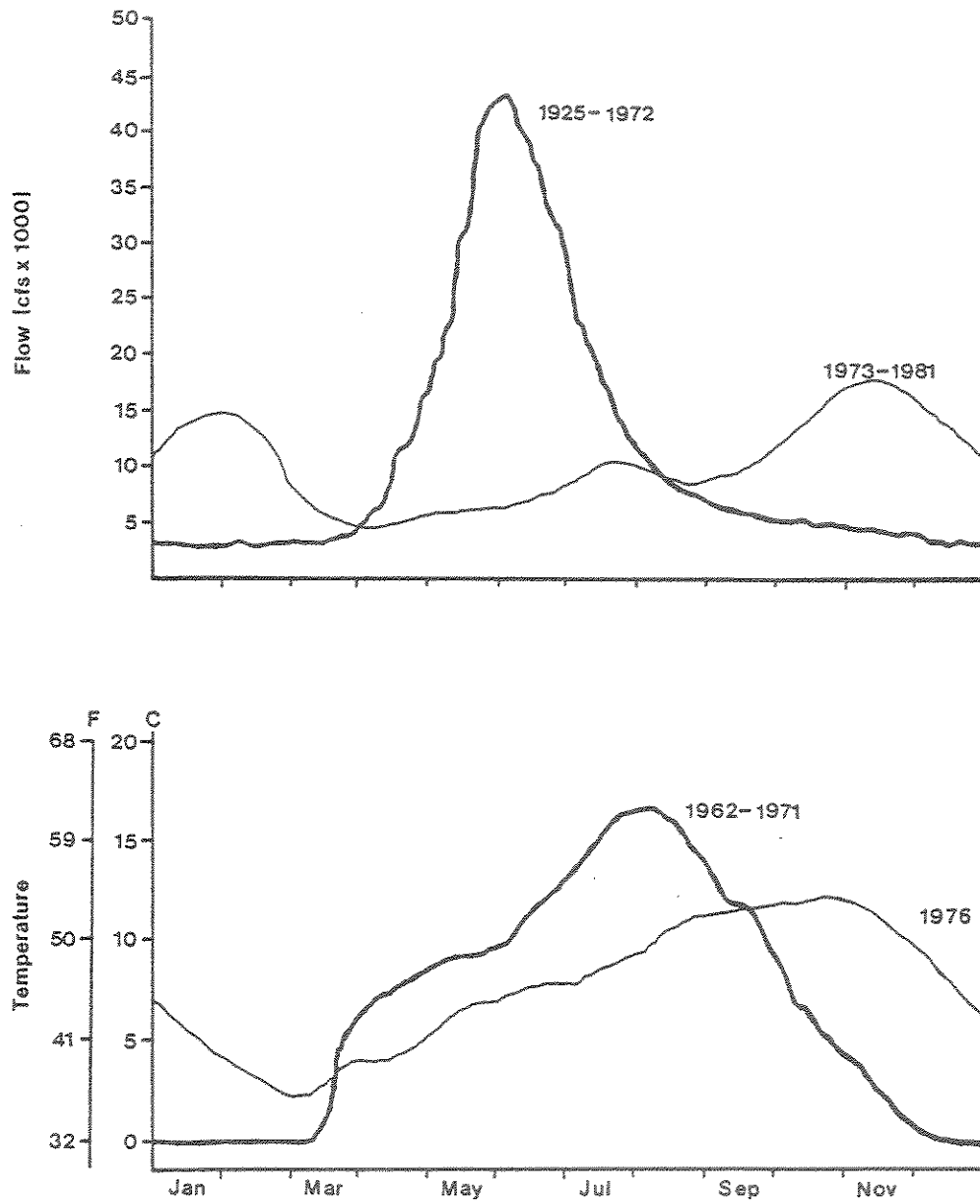


Figure 2. The median flows and mean daily water temperatures recorded in the Kootenai River before and after construction of Libby Dam.

mountain whitefish and rainbow trout. The Elkhorn study section is approximately 16 km downstream from Libby Dam, near the construction site of a proposed reregulation dam; the Pipe Creek study section is 32 km downstream from the dam (Figure 1). These areas differ in gradient, velocity, substrate size, and width of channel.

Fourteen fish species inhabit the Kootenai River and its tributaries above Kootenai Falls, approximately 56.3 km below the dam site. Mountain whitefish and rainbow trout are the predominate fish species in this area (Graham 1979).

Fisher River

The Fisher River is the largest tributary to the free flowing Kootenai in Montana. It drains approximately 4,748 km² of northwest Montana. The river originates in Pleasant Valley approximately 80.5 km west of Kalispell, Montana, and flows west for 86 km before joining the Kootenai 2.6 km below Libby Dam. Average annual discharge for the study period was 212.6 cfs, with a low flow of 118 cfs occurring in September 1981 (Shields et al. 1982).

To avoid extensive railroad and road construction rip-rapping, study sections were established approximately

38.6 to 47.6 km above the mouth of the river (Figure 1).

The Fisher River exhibits the same general fish species composition as does the Kootenai River itself. Mountain whitefish and rainbow trout are year-long residents of the river.

Libby Creek

Libby Creek is the second largest tributary to the Kootenai above Kootenai Falls, entering the river at the town of Libby. Originating in the northern slopes of the Cabinet Mountain Wilderness, Libby Creek and its many feeder streams drain approximately 665 km² and flows 36.7 km before entering the Kootenai. During 1981, flows ranged from 370 cfs in May to only 8.4 cfs in September.

Study sections were established 8 to 9.5 km above the mouth of Libby Creek (Figure 1). Mountain whitefish use Libby Creek extensively for spawning and rearing, but adult fish were rarely present during the summer months. Rainbow trout are year-long residents of Libby Creek.

METHODS

Food Habits

Fish were collected from the Kootenai River in the Elkhorn and Pipe Creek study sections (Figure 1) during early night hours using boat mounted electrofishing gear (Loeb 1957) from June to October 1980 and January, March and May 1981. Each month 20 mountain whitefish and 20 rainbow trout were collected from each of the two study sections. When possible, samples of each species were made up of ten small (10.0 - 19.9 cm TL), five medium (20.0 - 27.8 cm TL), and five large (27.8 - 43 cm TL) fish. Sample size, however, was less during certain months due to fish availability. These size grouping, in general, represent age I+, II+, and III+ and older mountain whitefish and rainbow trout (May 1982).

Rainbow trout less than 20 cm TL and all whitefish were sacrificed, stomachs removed and contents preserved in 10% formalin for later analysis during June, July and August 1980. Stomach contents of rainbow trout longer than 20 cm TL were obtained with stomach pumps (Seaburg 1957, Meehan and Miller 1978) and the fish were released.

During the remainder of this study this size group of rainbow trout was handled in the same manner as all other fish. Total length and weight were recorded and scale samples taken from each fish collected.

Stomach contents of mountain whitefish and rainbow trout were hand picked, sorted to order and placed in vials containing 75% alcohol. Samples collected in July and October 1980 and January and May 1981 were evaluated for seasonal food habits and food organisms identified to the lowest taxonomic level possible. All macroinvertebrates were identified with the aid of a variable power dissecting microscope and numerous invertebrate keys (Jensen 1966, Merritt and Cummins 1978, Pennack 1978, Wiggins 1977) and enumerated using a laboratory counter.

Food biomass was measured by volume displacement, with any volume less than 0.05 milliliters (ml) assigned a trace volume (T) of 0.0125 ml. Volumetric measurements were made using a 10 ml graduated centrifuge tube or a 50 ml graduated cylinder.

Benthic invertebrates were sampled at both study sections within the 24 hours (hrs) prior to stomach sampling. Three samples were taken with each of three different samplers, to reduce biases associated with any

one sampling device. At the Elkhorn study section a modified Knapp-Waters sampler (Waters and Knapp 1961) was used to collect invertebrates. This sampler could not be effectively used at the Pipe Creek section due to very large substrate. The other two samplers used, a modified kick net and a circular depletion sampler (Carle 1976), were designed for use in large substrate. Both samplers are 0.33 square meters (m^2) and have a mesh size of 150 microns, compared with a sample area of $0.093_2 m^2$ and a mesh size of 471 microns for the Knapp-Waters sampler. The circular sampler was used at the Pipe Creek section in place of the Knapp-Waters sampler and the kick net was used at both study sections. Drifting invertebrates were sampled in conjunction with fish sampling periods. Drift samples in both study sections were taken 1 hour (hr) before and 1 to 2 hrs into the fish sampling period. Two drift nets were run concurrently. These nets were set parallel to each other and to the shore line in water from 15 to 30 cm deep for 1 hr intervals. Net openings measured $0.145 m^2$ and nets were 1.5 m long. Mesh size was 355 microns. Velocity readings were taken at the net openings and volumes of water filtered were calculated. For further

details on invertebrate sampling and analysis procedures see Appert-Perry and Huston (1982).

Habitat Selection

Snorkeling was used to evaluate habitat selection, feeding, and interactions of mountain whitefish and rainbow trout during daylight hours from June to September, 1980 and 1981, in sections of the Kootenai River, Libby Creek and the Fisher River (Figure 1). One 9.6 km section of the Kootenai River, encompassing the Pipe Creek study section, was snorkelled on two separate occasions in August of 1980 (Figure 1). Qualitative notes on general macrohabitat selection, intra- and interspecific distributional patterns and general behavioral interactions among and between mountain whitefish and rainbow trout were recorded. Approximately 14 hrs of underwater observation time was logged in this section of the Kootenai River.

All quantitative habitat work was conducted in Libby Creek in September 1980 and July to September 1981, and in the Fisher River from July to October 1981. Stream sections were first snorkelled to determine areas with

adequate fish densities. Fish locations and physical stream characteristics at selected sampling sites were later documented using the planimetric method and spot observations (Bovee and Cochnauer 1977).

The planimeter method involved making detailed contour maps of selected stream sections. Two differing stream sections were established in both Libby Creek and the Fisher River, totalling 58 and 68 stream meters, respectively. First, a base line was established parallel to the stream edge. Then, perpendicular lines from the base line were strung at 1 m intervals across the stream channel (Figure 3a). Measurements of water depth and average water velocity (0.6 depth) were taken at 1 m intervals along these transects from the base line toward the opposite water's edge. Small painted rocks were placed on the stream bottom every 3 m to aid in future fish location work (Figure 3b). Major physical cover components (boulder, wood debris, etc.) were also added to this depth - velocity map (Figure 3c).

After mapping was completed, 2 days were allowed for fish to redistribute themselves within the study section before habitat utilization data were collected. Habitat utilization was evaluated by snorkeling, usually during

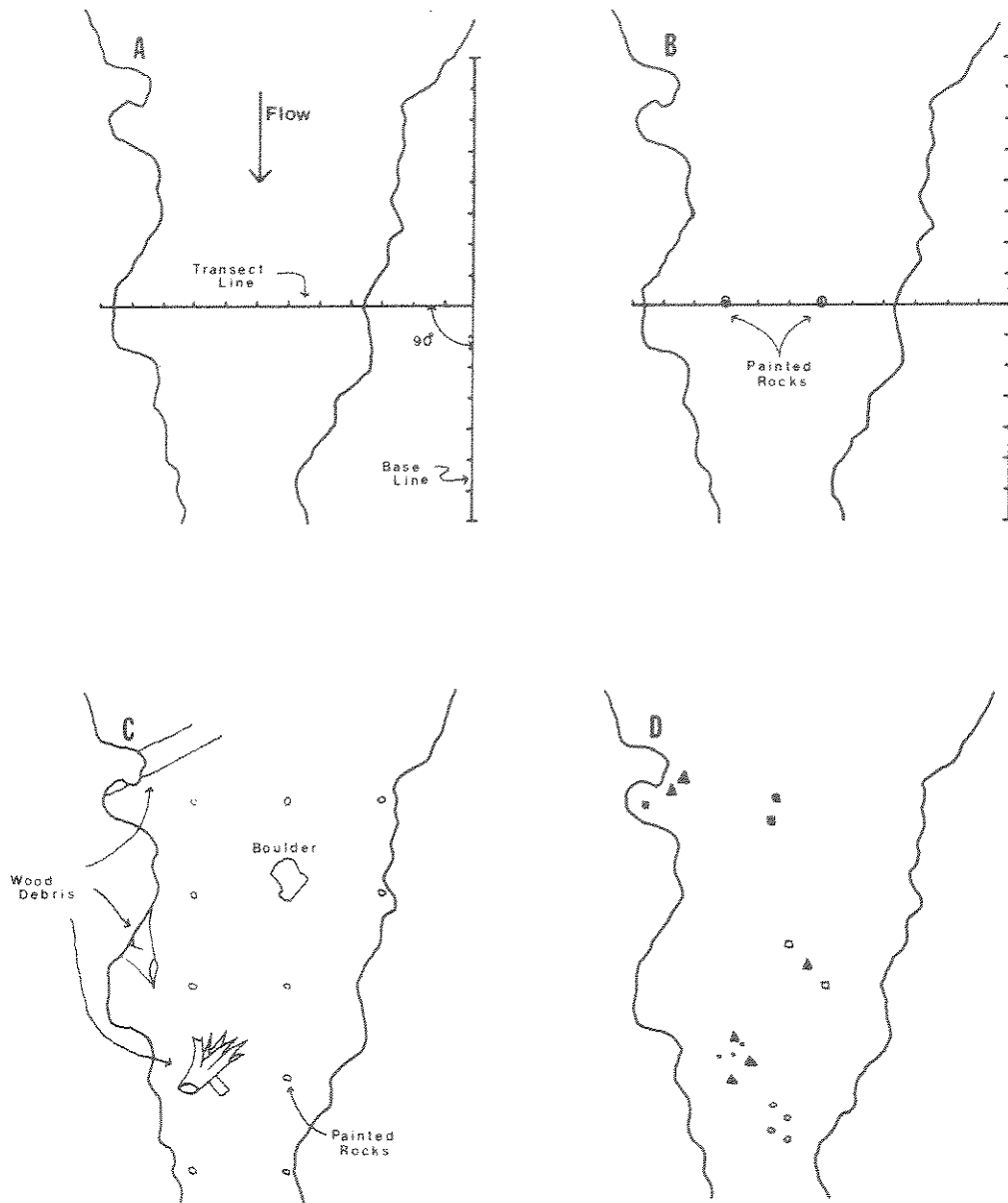


Figure 3. Procedures in establishing a planimetric study area. A) establishment of base and transect lines; B) total depth and average velocity (0.6 depth) taken at one meter intervals; C) major cover components and snorkeling reference rocks; D) fish locations coded for size and species.

mid-day hours, facing upstream and observing fish in relation to the 3 m² grids previously established. Working in this upstream zig-zag pattern allowed me to cover the entire stream section with minimum chance of disturbing the fish. Fish were observed for as long as 20 minutes to determine if habitat utilization was influenced by my presence. An individual fish location was then marked on a "poly-paper" stream section depth-velocity map I carried with me. Symbols were used to denote size and species of fish. Individual fish were periodically collected, using an underwater percussion gun (Everest 1979), to verify my accuracy in estimating fish sizes underwater. Stomachs and scale samples were also taken from these fish.

By transferring observed fish locations onto the original depth-velocity map, additional parameters of habitat utilization and species associations could be quantified. These parameters included; average velocity (0.6 depth) and total stream depth at individual fish focal points; distance to other species and number of other fish within the stream study section; distance to major cover components and closest waters' edge (Figure 3d).

Snorkeling sections, situated to encompass the

planimetric study areas, were also established on the Fisher River and Libby Creek. Equipped with a measuring rod, pencil, "poly-paper", clip board, and several weighted floats, I snorkelled downstream making spot observations. When fish were observed, I would float past them and then return to their location by moving back upstream. I observed fish for some time to assure that they had not been temporarily displaced by my presence and then place a weighted marker at the focal point of the fish under observation. I would then leave the water to record the size and species of that fish, the distance above the substrate which that fish maintained, and the estimated distances, species, and number of other fish within my field of vision. I would re-enter the water and continue downstream, making these observations until I had run out of markers. I would then return to the most upstream marker and, with the aid of a field worker, make additional measurements at each observation point. These measurements included: total depth; facing, average (0.6 depth), and surface velocities at the focal point (marker); average (0.6 depth) velocities within a 0.5 m radius of the focal point; and distance to cover. Pre-dominate substrate composition (%) within a 0.5 m radius

of the focal point was also estimated. Substrate categories were; sand, particle diameter less than 0.1 cm; gravel, from 0.1 to 10 cm; cobble, from 10 to 30 cm; boulder, greater than 30 cm. These categories represent a condensed Wentworth's (Cummins 1964) particle size classification. Approximately 60 and 84 hrs, respectively, were logged in making spot observations in Libby Creek and the Fisher River.

Detailed notes on intra- and interspecific behavior, feeding behavior, and distribution patterns of mountain whitefish and rainbow trout were recorded during all snorkel activities. General data on time of day, weather conditions, air and water temperatures were also recorded. Many underwater photographs were taken to record general distribution patterns of the species and their association with differing cover components.

Simple summary statistics and Student's t-tests were hand calculated following procedures by Huntsberger and Billingsley (1977). Percent overlap in the dietary composition of mountain whitefish and rainbow trout was estimated using a formula developed by Schoener (1970). All percentage data were transformed using an angular transformation in order to assure normality (Snedecor and Cochran

1980). Pearson correlations and discriminant analysis were made using the SPSS (Nie et al. 1975) statistical package at the Montana State University Computer Center.

RESULTS AND DISCUSSION

Food Habits

Stomach contents of 340 mountain whitefish and 298 rainbow trout collected during the 8 months of sampling were utilized in evaluating food habits. The sample consisted of 174 small, 83 medium and 83 large mountain whitefish. Size group distribution of rainbow trout was 129, 85 and 81, respectively (Tables 1 and 2).

The efficiency of stomach pumping for obtaining stomach contents of rainbow trout greater than 20 cm total length was considered to be too low for this quantitative study (Table 3), and thus was discontinued after the first 3 months of sampling. Of the 68 rainbow trout greater than 20 cm total length collected during June, July and August, 1980, 19 were randomly sacrificed after stomach pumping. Volume of contents pumped was then compared to the volume remaining within the stomach. These relatively low efficiencies obtained by using the stomach pumping methods were most likely due to my own inexperience in using them. However, regardless of the method I employed, the fuller or more compact a stomach was, the less

Table 1. Percent of total stomach volume (ml) of select size groups of mountain whitefish collected from the Elkhorn (EH) and Pipe Creek (PC) study sections of the Kootenai River. June to October 1980 and January, March and May 1981.

Month	Sample Group	Size	Diptera		Chironomidae		Ephemeroptera		Trichoptera		Plecoptera		Terrestrial		Other*		Total Stomach	
			EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	EH	PC
June 1980	S	21	9.2	8.6	61.3	59.9	22.3	20.5	6.6	1.8	T**	0.0	0.0	0.1	0.6	2.2	16.8	28.2
	M	5	3.4	3.5	74.2	61.4	2.7	15.8	19.7	3.9	0.0	0.0	0.0	0.0	0.6	0.8	14.7	13.7
	L	8	3.1	1.6	41.5	4.7	5.4	17.6	30.0	60.0	0.0	0.0	T	0.0	6.5	1.7	21.3	26.4
	Total	34	6.9	6.0	58.5	50.8	15.5	19.1	14.0	14.2	T	0.0	T	T	1.9	2.3	52.8	68.3
July 1980	S	10	2.3	0.4	71.1	68.8	24.0	27.0	2.1	3.7	0.0	0.0	0.0	T	0.5	0.1	3.6	6.4
	M	5	0.2	0.2	67.9	52.5	18.6	10.2	13.2	37.0	0.0	0.0	T	0.0	0.0	0.1	2.5	2.4
	L	5	0.6	3.7	8.3	9.4	8.6	5.2	82.5	81.6	0.0	0.0	0.0	0.0	0.2	0.1	3.6	4.6
	Total	20	1.4	1.2	54.6	49.9	18.8	17.4	24.9	31.5	0.0	0.0	T	0.0	0.3	0.1	9.7	13.4
August 1980	S	1	0.0	0.0	60.4	57.4	9.4	20.7	30.2	21.7	0.0	0.0	0.0	0.0	0.0	0.0	0.2	4.1
	M	5	2.3	0.6	69.8	64.5	12.8	18.2	12.3	15.4	0.0	0.0	0.4	0.0	1.9	0.0	2.6	3.3
	L	5	0.3	2.8	17.3	70.0	9.4	4.4	40.2	20.5	0.0	0.0	0.3	0.0	27.6	1.1	4.9	2.1
	Total	11	1.2	0.8	45.1	62.4	10.9	16.1	26.6	19.6	0.0	0.0	0.3	0.0	13.4	0.3	7.7	9.5
September 1980	S	10	2.3	2.3	58.1	50.9	39.2	45.7	0.5	2.2	0.0	0.0	0.0	0.0	0.0	0.0	1.6	2.7
	M	5	2.3	9.2	6.9	23.3	47.9	51.8	22.9	15.7	0.0	0.0	0.0	0.0	0.0	0.0	2.4	3.6
	L	5	2.4	0.0	64.0	45.7	8.0	5.8	5.6	8.4	0.0	0.0	0.0	0.0	20.0	20.1	4.0	2.7
	Total	20	2.3	3.3	44.6	42.7	32.1	37.3	7.0	7.1	0.0	0.0	0.0	0.0	9.3	5.0	8.0	9.0
October 1980	S	10	12.3	1.6	44.3	76.1	31.3	12.2	11.7	9.7	T	0.0	0.0	0.0	0.1	0.4	4.2	2.4
	M	5	2.2	7.7	58.5	69.2	23.5	2.3	7.4	20.4	T	0.0	0.0	0.0	0.1	0.4	5.0	4.2
	L	5	2.2	0.0	66.5	24.0	5.2	4.9	25.4	12.6	0.0	0.0	0.0	0.0	0.8	58.6	1.3	5.3
	Total	20	9.3	2.7	53.4	61.4	24.0	7.9	14.1	13.1	0.2	0.0	0.0	0.0	0.3	14.9	10.5	11.9
January 1981	S	10	6.7	1.5	44.2	59.4	37.3	27.9	10.8	10.8	1.0	0.5	0.0	0.0	0.0	T	2.1	4.1
	M	5	18.8	5.0	56.1	38.8	8.1	11.7	16.9	44.3	0.1	0.1	0.0	0.0	T	0.1	6.0	3.8
	L	5	36.8	5.7	40.9	35.7	10.4	26.2	11.4	31.9	T	0.2	0.0	0.0	T	0.3	14.0	5.7
	Total	20	17.3	3.4	46.3	48.3	23.4	23.4	12.5	24.4	0.5	0.3	0.0	0.0	T	0.1	22.1	13.6
March 1981	S	10	10.9	0.2	76.2	50.1	3.5	36.0	9.4	6.2	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.9
	M	5	17.6	2.3	52.6	75.6	1.6	2.1	28.2	19.5	0.0	0.0	0.0	0.0	0.0	0.0	4.6	1.4
	L	5	9.6	0.0	54.6	89.5	13.7	6.9	22.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	5.6	3.2
	Total	20	12.2	0.7	64.9	62.2	5.6	24.3	17.3	8.1	0.0	0.0	0.0	0.0	0.0	0.0	11.4	6.5
May 1981	S	10	1.1	1.8	60.5	64.0	23.8	28.0	14.5	5.8	0.0	T	0.1	0.3	0.0	T	2.4	2.9
	M	5	0.5	4.6	59.1	54.6	7.0	16.0	33.4	24.5	0.0	0.2	0.0	0.1	0.0	0.1	2.5	3.2
	L	5	0.1	0.2	52.4	45.6	9.1	8.2	38.5	6.1	0.0	0.0	0.0	0.0	0.1	39.8	1.6	4.6
	Total	20	0.7	2.1	58.1	57.1	15.9	20.1	25.2	10.6	0.0	T	T	0.2	T	10.0	6.5	10.7
Entire sampling period:																		
	S	82	5.5	2.1	59.5	60.8	23.8	27.2	10.7	7.7	0.1	T	T	T	0.2	0.3	32.1	52.7
	M	40	5.9	4.1	55.6	55.0	15.3	16.1	19.2	22.6	0.0	T	T	T	0.3	0.2	40.3	35.6
	L	43	6.8	1.8	52.5	40.6	8.7	9.9	32.0	27.7	0.0	T	T	0.0	6.9	15.2	56.3	54.6
	Total	165	6.4	2.5	53.2	54.3	18.3	20.7	17.7	16.1	T	T	T	T	3.2	4.1	128.7	142.9

* Other includes: Nematoda, Coleoptera, Gastropoda, Annelida, Hemiptera and Hirudinea.
 ** Trace (T) is any amount less than 0.1%.

Table 2. Percent of total stomach volume (ml) of select size groups of rainbow trout collected from the Elkhorn (EH) and Pipe Creek (PC) study sections of the Kootenai River. June to October 1980 and January, March and May 1981.

Date	Size Group	Sample Size	Total Stomach Volume (ml)																
			Diptera		Chironomidae		Ephemeroptera		Trichoptera		Plecoptera		Terrestrial		Other*		Total		
			EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	EH	PC	
June 1980	S	7	20	12.6	17.6	10.7	7.5	48.0	31.6	7.2	10.1	0.0	0.1	4.2	2.3	17.3	7.2	3.6	29.9
	M	3	9	1.7	8.7	1.1	5.8	69.5	39.0	5.2	6.0	0.0	0.0	21.4	14.5	1.1	26.0	3.6	8.0
	L	8	7	10.6	15.0	3.4	16.3	17.4	32.6	16.4	7.0	0.1	0.0	5.5	0.3	13.6	35.4	12.1	4.9
	Total	18	36	9.9	14.9	5.8	8.8	38.0	33.6	11.0	8.5	Trace	Trace	7.6	5.0	12.8	12.8	19.3	42.8
July 1980	S	11	10	0.1	0.2	7.4	2.1	62.8	10.7	39.6	86.6	Trace	Trace	Trace	Trace	Trace	Trace	11.1	9.3
	M	5	5	0.1	0.1	1.1	1.0	49.3	0.5	49.4	88.6	Trace	Trace	Trace	Trace	Trace	Trace	9.3	7.1
	L	5	5	0.1	Trace	1.1	0.4	36.9	1.4	61.7	84.6	Trace	Trace	Trace	Trace	Trace	Trace	10.3	12.2
	Total	21	20	0.1	0.1	4.2	1.4	50.6	5.8	45.2	89.1	Trace	Trace	Trace	Trace	Trace	Trace	30.7	28.6
August 1980	S	10	10	3.1	2.2	9.3	6.9	14.3	15.6	63.1	51.4	0.0	0.0	6.0	0.4	3.9	7.3	6.9	4.4
	M	5	5	5.4	2.0	3.0	1.4	5.7	27.9	52.1	68.7	0.0	0.0	2.4	0.0	16.9	0.0	5.5	3.5
	L	6	5	1.1	0.3	7.3	6.9	31.6	53.4	58.3	39.4	0.0	0.0	0.6	0.0	0.0	0.0	4.9	2.2
	Total	21	20	3.1	1.7	7.2	5.5	17.2	28.1	59.1	52.7	0.0	0.0	3.6	0.2	6.0	3.7	17.3	10.1
September 1980	S	4	10	8.4	6.6	30.1	18.0	53.9	16.2	7.7	18.6	0.0	0.0	0.0	0.0	0.0	4.4	3.3	2.6
	M	5	5	0.3	0.0	10.3	20.8	38.6	0.0	0.1	12.5	0.0	0.0	0.1	26.7	0.7	8.0	5.5	1.6
	L	3	5	0.4	20.1	11.1	6.0	41.7	0.1	14.6	14.9	0.0	0.0	0.0	0.0	32.3	39.0	2.3	4.2
	Total	12	20	3.0	8.3	17.1	17.2	44.4	8.1	6.3	16.2	0.0	0.0	0.1	6.7	20.9	12.0	11.1	8.4
October 1980	S	3	10	2.7	3.2	42.6	57.1	15.3	12.9	37.4	22.3	1.9	0.3	0.0	0.0	0.5	4.6	0.2	1.0
	M	5	5	0.7	2.2	54.7	62.7	24.4	15.7	11.8	9.9	0.0	0.2	Trace	Trace	8.1	9.5	3.5	0.8
	L	5	5	0.9	0.7	25.6	61.9	12.1	4.9	19.3	5.4	0.0	0.0	0.0	0.0	42.2	27.1	10.5	2.4
	Total	13	20	1.2	2.3	40.7	59.7	17.6	11.6	20.6	15.0	0.4	0.2	Trace	Trace	19.5	11.4	14.2	4.2
January 1981	S	1	10	4.8	3.9	85.7	3.0	0.0	87.3	8.9	0.7	0.0	5.0	0.0	Trace	Trace	0.1	15.2	
	M	5	5	13.5	0.7	45.0	1.4	34.0	89.1	7.4	1.1	0.0	7.5	0.0	0.0	0.4	0.3	0.6	6.5
	L	6	5	3.6	0.6	10.0	0.6	52.3	84.6	14.6	9.8	0.1	3.4	0.0	0.0	19.3	1.3	6.4	7.3
	Total	12	20	8.2	2.3	32.9	2.0	39.2	87.1	10.0	3.0	0.1	5.2	0.0	0.0	9.0	0.4	7.1	29.0
March 1981	S	0	11	Trace	0.8	Trace	29.9	Trace	51.2	Trace	0.0	Trace	Trace	Trace	Trace	Trace	Trace	Trace	Trace
	M	7	6	35.1	4.7	11.3	51.5	34.1	13.4	6.2	14.0	0.0	0.0	0.0	0.0	0.0	2.6	3.9	9.9
	L	3	4	5.7	0.9	3.0	14.8	28.0	25.4	1.3	14.0	0.4	1.3	0.0	0.0	0.0	43.7	8.3	22.7
	Total	10	21	26.3	2.5	8.9	33.2	32.3	35.5	4.7	6.7	0.1	0.3	0.0	0.0	0.0	13.8	12.2	34.3
May 1981	S	3	10	2.0	2.2	34.4	41.1	29.7	30.6	0.0	7.3	0.0	4.5	0.6	0.6	33.3	13.3	6.8	1.0
	M	5	6	6.2	1.4	36.7	27.8	18.9	26.7	15.7	11.4	Trace	Trace	Trace	Trace	22.2	32.7	6.2	5.1
	L	5	5	1.4	13.6	69.3	13.2	6.1	3.5	3.6	7.1	0.1	15.2	19.0	11.1	0.6	36.4	12.7	8.3
	Total	13	21	4.8	4.7	48.7	36.8	16.5	23.0	7.4	8.2	0.1	6.1	7.6	3.1	16.4	23.9	25.7	14.8
Entire sampling period:			S	39	91	4.8	4.6	27.2	20.7	32.0	32.0	0.3	1.2	1.5	0.4	7.9	5.8	32.0	65.1
	M	40	46	7.9	2.5	20.4	21.6	34.3	26.5	25.5	27.7	0.0	1.0	3.1	5.2	6.2	8.9	38.1	42.5
	L	41	41	3.0	6.4	16.4	15.0	28.3	25.7	23.7	22.8	0.1	2.5	3.2	1.4	13.5	24.6	67.5	64.2
	Total	120	178	7.1	4.6	20.7	19.8	32.0	29.1	20.5	24.9	0.1	1.5	2.4	1.9	10.6	10.2	137.6	171.8

* Other includes: Nematoda, Coleoptera, Gastropoda, Annelida, Hemiptera and Hirudinea

** Trace (T) is any amount less than 0.1%.

Table 3. Stomach pumping efficiency on rainbow trout greater than 20 cm TL. Mean efficiency expressed in percent of total stomach volume removed.

Total length (centimeters)	Number of fish	Mean Efficiency%	Standard Deviation
20.0 - 27.7	7	51.75	36.30
27.8 - 43.0	12	31.14	17.13
	19	38.73	27.13

efficient was the removal of the contents.

During the entire sampling period, Chironomidae larvae and adults were the major food item of mountain whitefish, ranging from 42.7% to 62.4% total combined stomach volume (Table 1 and Figures 4 and 5). The smaller whitefish (10.0 to 19.9 cm) showed the most consistent and heaviest use of the Chironomidae, with an overall mean utilization in the two study sites of 60.1% (Standard deviation = 9.78) (Tables 1). Larger whitefish (27.7 to 43+ cm TL) showed the largest deviate from chironomid utilization, exhibiting relatively high seasonal use of Trichoptera larvae and adults and Gastropoda (Other* category, Table 1). Mountain whitefish in general also utilized Ephemeroptera

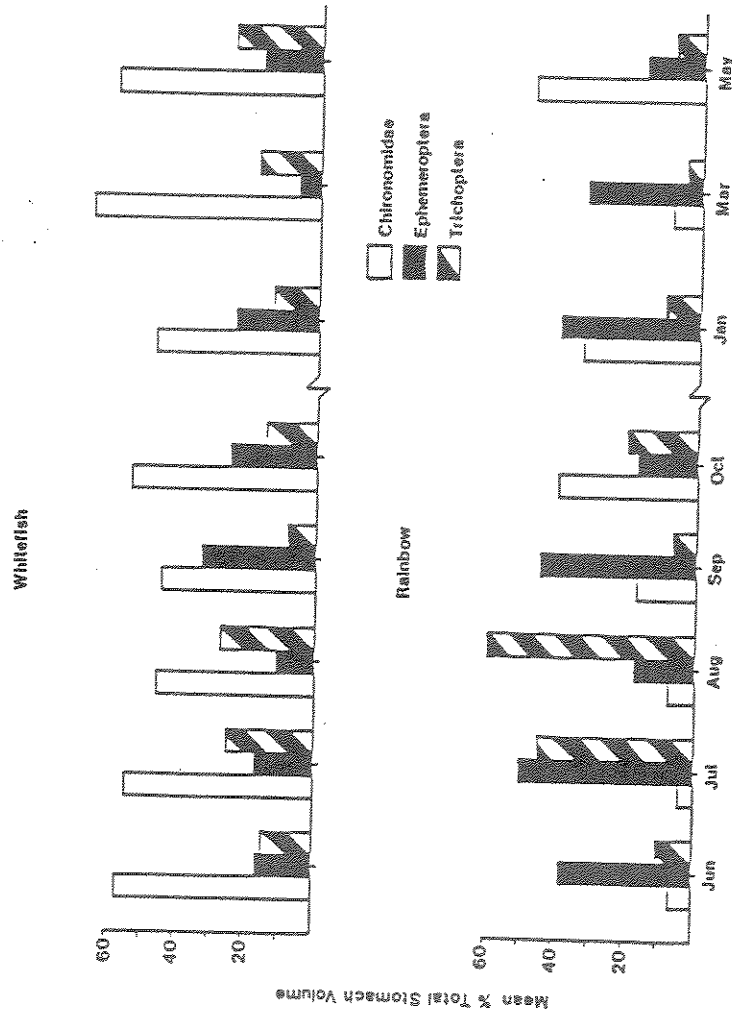


Figure 4. Monthly variation in diet, by percent total stomach volume (ml), for mountain whitefish and rainbow trout collected from the Elkhorn study section of the Kootenai River. June to October 1980 and January, March and May 1981. Only the three major invertebrate groups are shown.

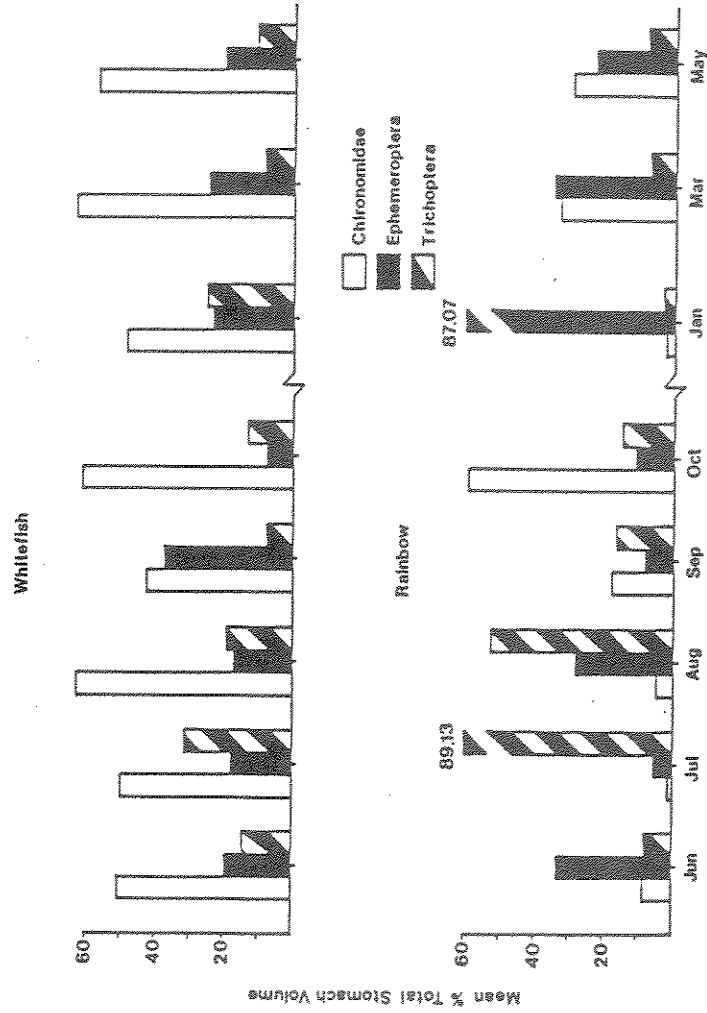


Figure 5. Monthly variation in diet, by percent total stomach volume (ml), for mountain whitefish and rainbow trout collected from the Pipe Creek study section of the Kootenai River. June to October 1980 and January, March and May 1981. Only the three major invertebrate groups are shown.

and Trichoptera to a significant extent, showing overall yearly means in the two study sections of 20.7 and 17.7%, respectively.

Many authors have previously reported a high utilization of Chironomidae by mountain whitefish (McHugh 1940, Sigler 1951, Daily 1971, Pontius and Parker 1973 and White and Wade 1980). Laakso (1951), Brown (1970), and Stalnaker and Gresswell (1974) also reported a general broadening in food selection as mountain whitefish size increased.

Seasonal food habits of mountain whitefish were generally consistent between the two study sections. Utilization of the three major food groups, Chironomidae, Ephemeroptera and Trichoptera, was also quite consistent throughout the year (Table 1 and Figures 4 and 5).

Individual size groups of whitefish from the Elkhorn study section derived as much as 36.8% of their food bulk from several Diptera genera (Antocha sp., Hexatoma sp., Simulium sp.) during the months of January and March 1981: the overall relative utilization of these genera combined was 17.3 and 12.2%, respectively. This resulted in the relative importance of the three major food groups. Larger whitefish (27.8 to 43+ cm TL) derived 27.6 and

20.0% of their food bulk from Gastropods (Other* category) during the months of August and September, 1980, respectively. This shift resulted in a marked decrease in relative importance of Chironomidae during August 1980 and of Ephemeroptera and Trichoptera during September 1980 (Table 1 and Figure 4). Whitefish from the Elkhorn study section derived 89.2% of their annual food bulk from the three major food groups: Chironomidae, Ephemeroptera, and Trichoptera.

Whitefish from the Pipe Creek study section derived 91.1% of their total annual food bulk from the three major food groups. In contrast to findings in the Elkhorn section, there was no increased use of Dipterans, other than Chironomidae during January and March 1981. Larger whitefish (27.8 to 43+ cm TL) acquired 20.1, 58.6, and 39.8% of their total monthly food bulk primarily from Gastropods (Other* category) during the months of September, October 1980, and March 1981, respectively. This resulted in a marked decrease in the relative importance of Ephemeroptera and Trichoptera for this size group of mountain whitefish during these 3 months. Utilization of Chironomidae decreased only slightly for these months (Table 1 and Figure 5).

Rainbow trout utilized more Ephemeroptera and Trichoptera than whitefish with totals ranging as high as 95.8% of total stomach volume (Elkhorn section, July 1980, Table 2 and Figures 4 and 5). Rainbow trout also showed a more diverse food preference and fed on Other* invertebrates such as Nematoda, Coleoptera, Gastropoda, Annelida, Hemiptera, and Hirudinea. Utilization of these invertebrates ranged as high as 43.7% in an individual size group (overall mean = 10.4%). The overall mean of utilization of this group by whitefish was only 3.8% (Table 1).

Seasonal food habits of rainbow trout were generally consistent between the two study sections, however, fish size class and monthly variations in diet were much more variable than those exhibited by mountain whitefish (Table 2). From June to August 1980, and during March 1981, utilization of Chironomidae by rainbow trout in the Elkhorn study section never exceeded 11% total stomach volume for any one size group. During the other 4 months of sampling, utilization of Chironomidae was never lower than 10% total stomach volume. In January 1981, small rainbow (10.0 to 19.0 cm TL) derived 85.7% of that month's food bulk from Chironomidae alone (Table 2). Bisson (1975) and Johnson (1981) also reported a high utilization of

Chironomidae by small rainbow trout. White and Wade (1980) also found that the relative importance of Chironomidae was highest during the winter months.

White and Wade (1980), in their study of the South Fork Boise River in Idaho, also found that rainbow trout diets became increasingly diverse in spring and summer, with the highest number of terrestrial organisms being consumed in the summer. This general scenario of rainbow trout food habits can also be applied to the Kootenai River. During the late spring, and early summer months (June 1980 and May 1981) medium (20.0 to 27.7 cm TL) and large (27.8 to 43+ cm TL) rainbow trout obtained 21.3 and 19.0%, respectively, of their monthly food bulk from terrestrial invertebrates. Utilization of Other* invertebrates was evident during all months except July 1980 and March 1981. The three major food groups; Chironomidae, Ephemeroptera and Trichoptera made up 73.2% of the total annual diet of rainbow trout in the Elkhorn Section (Table 2 and Figure 4).

From June to August 1980, and during January 1981, utilization of Chironomidae by rainbow trout in the Pipe Creek study section rarely exceeded 7.5% total stomach volume by any one size group. During the other 4 months

of sampling, utilization of Chironomidae dropped as low as 6% total stomach volume but averaged 33.7% for that same time period. All sizes of rainbow trout fed heavily on Chironomidae during the month of October 1980 (Table 2). Utilization of Ephemeroptera and Trichoptera fluctuated throughout the sampling period, varying from 0.0% to as high as 89.1% total stomach volume for any one size group during any one month. When utilization of Ephemeroptera and Trichoptera was relatively high, size group variations were low (Table 2). Again, as in the Elkhorn study section, the shifting between utilization of Chironomidae and Ephemeroptera-Trichoptera was evident. Other* invertebrates were utilized during all months except January 1981. Rainbow trout from the Pipe Creek study section derived 73.8% of their total annual food bulk from the three major food groups; Chironomidae, Ephemeroptera and Trichoptera (Table 2 and Figure 5).

Percent Overlap

Differences or similarities in food habits alone do not adequately reflect the relationship of diet overlap and potential competition between mountain whitefish and rainbow trout. There are three basic methods of food habit

analysis; frequency of occurrence, percent of total numbers and percent of total volume (Bagenal 1978). Some investigators have used an index of relative importance (IRI) to evaluate diet overlap (George and Hadley 1979, McMullin 1979). This IRI is essentially a mean of the three dietary measures. Frequency of occurrence and percent of total numbers are heavily influenced by the smaller food items which may contribute little to the total volume of an individual stomach. For this reason, the average of the volume percentages appears to be the least objectionable measure of the diet when calculating overlap (Wallace 1981).

The percent overlap in diet between mountain whitefish and rainbow trout in any one size group, month or section ranged from 11% in June, 1980 to 90.6% in October, 1980 (Table 4). Total overlap (for all size groups) for any one month ranged from 31% January, 1981 at Pipe Creek section to 94.3% in October, 1980 also at Pipe Creek. Total percent overlaps in the Elkhorn section were more consistent than those for the Pipe Creek study section.

Percent overlap in the diets of small fish, less than 20.0 cm TL, was higher than those of fish greater than 20.0 cm TL (Table 4). Small fish are more restricted to

Table 4. Percent overlap in the dietary composition of mountain whitefish and rainbow trout stomachs collected from the Elkhorn (EH) and Pipe Creek (PC) study sections of the Kootenai River.

Size group: Study section: Month	S		M		L		Total	
	EH	PC	EH	PC	EH	PC	EH	PC
June 1980	49.34	55.90	11.03	33.52	16.17	36.58	50.14	56.67
July 1980	28.61	16.80	32.98	38.56	71.47	83.46	48.00	38.93
August 1980	49.13	52.40	33.18	36.23	60.51	32.70	55.43	46.67
September 1980	71.98	56.28	65.82	53.30	45.07	54.50	73.52	58.83
October 1980	72.27	80.80	90.67	77.42	51.71	61.31	73.40	94.32
January 1981	57.88	33.58	73.88	15.06	35.85	37.47	74.85	31.11
March 1981	No fish	74.38	43.35	77.28	54.58	23.73	45.25	71.24
May 1981	59.42	77.03	59.92	56.69	62.16	59.29	72.04	71.54
Overall Mean	55.52	55.90	51.35	48.51	49.69	48.63	61.58	58.66
Standard Deviation	15.14	22.19	25.89	21.87	17.37	19.51	13.03	20.33

smaller food organisms than larger fish (Laakso 1951, Bisson 1978) and, therefore, would be expected to have more diet overlap. Small whitefish fed heavily on Chironomidae and small rainbow trout utilized more Chironomidae than larger rainbow trout (Tables 1 and 2). Therefore, if competition for food is occurring, it is most likely taking place among fish less than 20.0 cm TL.

Selection vs Availability

The measured or apparent availability of benthic insects may have little relationship to the actual ingestion of the items by a fish. Prey which appear abundant may be relatively inaccessible, less desirable, protectively camouflaged, or hard to catch (Wallace 1981). Fish develop and maintain definitive feeding images (Ivlev 1961). Therefore, food utilization by fish can be less than, equal to, or greater than measured availability. The behavior and size of both predator and prey must be considered before decisions about selectivity can be made. Without these biological considerations, the interpretation of either raw data or any form of mathematical computation could be deceptive (Williams 1983).

When selection of a food organism is significantly

lower ($p \leq 0.05$) than its measured availability, one could postulate that some environmental or behavioral characteristic of either predator or prey actually decreases the preys' availability below that which was measured. This point is best demonstrated by using Chironomidae as an example. Chironomidae are one of the most abundant insect families found in the Kootenai River (Appert 1983) and are also known to demonstrate a high propensity to drift. However, they usually comprise only a small percentage of the overall diet in rainbow trout over 20 cm TL (Tables 2, 5 and 6). Rainbow trout are known to be primarily drift feeders (Bryan 1973, White 1973, Irvine and Northcote 1982), however, utilization of drifting Chironomidae by rainbow trout was usually well below their presence in drift samples at both study sections (Tables 5 and 6).

When utilization is relatively equal to availability, the food organism's measured availability is realistic and the fish is feeding opportunistically. This type of feeding relationship with any one of the seven food groups can be seen in both mountain whitefish and rainbow trout at both study sections throughout the sampling period.

In the Elkhorn study section, mountain whitefish fed upon Trichoptera larvae approximately in proportion to

Table 5. Pearson correlation coefficients for the percent of total stomach volume (ml) of mountain whitefish (WF) and rainbow trout (RB) as related to both benthic (Ben) and drift (Dri) insect samples (ml) from the Elkhorn study section of the Kootenai River. June to October 1980 and January, March and May 1981.

	Jun - 1980					Jul - 1980					Aug - 1980					Sep - 1980				
	WF	RB	Ben	Dri		WF	RB	Ben	Dri		WF	RB	Ben	Dri		WF	RB	Ben	Dri	
Diptera	6.92	9.94	10.39	6.28		1.35	0.08	13.49	5.38		1.17	3.1	11.45	2.01		2.31	2.98	10.57	7.02	
Chironomidae	58.53	5.84	15.9	39.82		54.63	4.24	13.4	41.06		45.06	7.24	12.2	37.36		44.63	17.08	17.0	57.25	
Ephemeroptera	15.46	37.99	38.2	27.4		18.79	50.58	28.0	38.15		10.91	17.19	30.3	27.76		32.05	44.44	18.4	15.13	
Trichoptera	14.02	10.97	11.8	11.89		24.92	45.18	29.3	4.71		26.62	59.1	22.4	7.59		7.63	6.26	28.4	9.2	
Plecoptera	0.03	0.03	0.0	0.96		0.0	0.01	0.7	0.04		0.0	0.0	3.9	0.11		0.0	0.0	4.1	0.78	
Terrestrial	0.02	7.63	0.0	11.79		0.01	0.06	0.0	7.12		0.31	3.58	0.0	11.49		0.0	0.05	0.0	8.42	
Other*	1.92	12.78	23.71	1.86		0.3	0.06	15.11	3.55		13.39	6.02	19.85	13.58		9.33	20.85	21.73	2.18	
WF Corr			.2337	.8903				.3884	.7713				.3244	.7241				.3781	.8639	
P value			.307	.004				.195	.021				.239	.033				.201	.006	
RB Corr			.8839	.3428				.8569	.3667				.5255	.0434				.4641	.2326	
P value			.004	.226				.007	.209				.113	.463				.147	.368	
Diptera	9.28	1.24	17.22	11.57		17.26	8.2	52.09	10.48		12.22	26.25	41.17	14.95		0.67	4.84	19.42	12.62	
Chironomidae	53.4	40.68	19.24	15.0		46.34	32.88	3.76	25.81		64.93	8.85	11.86	26.13		58.12	48.68	16.99	26.36	
Ephemeroptera	24.04	17.56	20.39	38.58		23.37	39.23	26.17	37.5		5.86	32.25	28.48	33.34		15.94	16.46	43.31	11.15	
Trichoptera	14.07	20.55	22.41	26.37		12.48	10.0	6.22	13.31		17.29	4.71	12.08	6.19		25.19	7.42	13.72	0.86	
Plecoptera	0.15	0.44	4.22	1.75		0.54	0.05	6.17	0.0		0.0	0.11	2.27	0.17		0.0	0.06	0.35	0.07	
Terrestrial	0.0	0.01	0.0	2.16		0.0	0.0	0.0	2.02		0.0	0.0	0.0	3.23		0.06	7.59	0.0	48.75	
Other*	0.27	19.45	16.52	4.58		0.01	8.96	5.59	10.89		0.0	27.84	4.14	15.98		0.02	16.44	6.21	0.19	
WF Corr			.5390	.4524				.1617	.7252				.0808	.4329				.2921	.1314	
P value			.106	.154				.365	.033				.432	.166				.263	.389	
RB Corr			.6636	.3969				.1426	.9821				.6815	.7242				.2541	.2515	
P value			.062	.189				.380	.000				.053	.033				.291	.293	

*Other includes: Nematoda, Coleoptera, Gastropoda, Annelida, Nemiptera and Hirudinea

Table 6. Pearson correlation coefficients for the percent of total stomach volume (mL) of mountain whitefish (WF) and rainbow trout (RB) as related to both benthic (Ben) and drift (Dri) insect samples (mL) from the Pipe Creek study section of the Kootenai River. June to October 1980 and January, March and May 1981.

	Jun - 1980					Jul - 1980					Aug - 1980					Sep - 1980				
	WF	RB	Ben	Dri	WF	RB	Ben	Dri	WF	RB	Ben	Dri	WF	RB	Ben	Dri	WF	RB	Ben	Dri
Diptera	5.92	16.89	11.22	2.05	1.18	0.1	6.61	12.8	0.82	1.65	10.23	8.41	3.26	12.31	10.58	9.27				
Chironomidae	50.77	40.77	26.0	65.79	49.88	1.4	8.8	12.99	62.44	5.53	14.1	50.43	42.69	19.2	15.7	38.25				
Ephemeroptera	19.07	35.64	27.8	14.26	17.35	5.84	27.1	33.02	16.12	28.09	28.6	24.93	37.29	11.13	19.6	22.19				
Trichoptera	14.21	10.49	8.3	3.44	31.51	89.13	40.7	13.73	19.55	52.73	15.8	8.41	7.13	19.15	31.0	11.59				
Plecoptera	0.0	0.03	0.0	0.05	0.0	0.0	0.0	0.0	0.0	0.0	3.0	2.03	0.0	0.0	1.3	0.66				
Terrestrial	0.04	6.96	0.0	8.46	0.0	0.09	0.0	13.73	0.0	0.21	0.0	4.64	0.0	9.67	0.0	9.6				
Other*	2.3	14.78	26.68	5.95	0.07	3.44	16.79	13.73	0.26	3.65	28.27	1.16	5.02	17.96	21.82	8.44				
WF Corr			.5703	.9451			.4158	.1982			.1470	.9474			.3196	.9282				
P value			.091	.001			.177	.335			.377	.001			.242	.001				
RB Corr			.6914	.8296			.8110	.0160			.3745	.0432			.7724	.5556				
P value			.043	.475			.013	.486			.204	.463			.021	.098				
Diptera	2.72	2.3	12.93	9.94	3.43	2.25	36.11	16.0	0.7	2.52	10.17	19.67	2.12	4.71	8.26	2.24				
Chironomidae	61.34	59.72	14.48	10.39	48.33	2.02	5.52	12.25	62.16	33.17	22.98	33.53	57.06	30.8	34.37	55.77				
Ephemeroptera	7.9	11.63	13.42	21.23	23.41	87.07	40.76	53.76	24.29	35.47	38.43	34.28	20.06	22.98	34.64	28.55				
Trichoptera	13.1	14.96	36.29	33.73	24.82	3.02	6.46	10.34	8.11	6.66	14.73	4.17	10.56	8.23	10.83	0.37				
Plecoptera	0.0	0.23	2.61	1.36	0.32	5.21	3.75	2.21	0.0	0.25	2.33	2.24	0.06	6.06	0.84	0.0				
Terrestrial	0.0	0.0	0.0	4.07	0.0	0.0	0.0	0.4	0.0	0.0	0.0	3.43	0.15	3.07	0.0	6.1				
Other*	14.93	11.43	20.27	19.28	0.09	0.43	7.3	5.04	0.0	13.83	11.36	2.68	9.99	23.9	11.06	6.97				
WF Corr			.2224	.0715			.0342	.3407			.5952	.7759			.8274	.9599				
P value			.316	.439			.471	.227			.079	.020			.011	.000				
RB Corr			.2401	.1086			.7026	.9576			.9117	.8446			.8427	.8158				
P value			.302	.408			.039	.000			.002	.008			.009	.013				

*Other includes: Hematoda, Coleoptera, Gastropoda, Annelida, Hemiptera and Hirudinea

their composition in the benthic insect community during June, July and August 1980 (Table 5). In the Pipe Creek study section, rainbow trout utilized Ephemeroptera larvae and adults approximately in proportion to percent composition in the drifting insect community during August 1980 and February and May 1981 (Table 6).

When utilization is higher than availability, either our habitat sampling techniques are biased or the fish are selecting that particular food item. Mountain whitefish and rainbow trout differ the most in their apparent selectivity of preferred food.

Mountain whitefish in the Kootenai River fed on Chironomidae from both the water column and by actively foraging through river substrates. Underwater observations revealed that foraging was a common feeding behavior. By using their snouts, whitefish turn over rocks and literally "plow" through smaller substrates during bottom feeding. Utilization of Chironomidae by whitefish averaged 53.8% (Standard deviation = 7.17) and ranged as high as 64.9%. With few exceptions, utilization of Chironomidae was well above their measured availability in both the benthos or drift (Tables 5 and 6). Conversely, utilization of Chironomidae by rainbow trout was usually

below measured availability.

Although only occasionally comprising a substantial part of the benthic biomass, Chironomidae accounted for a considerable percentage of the total drift sampled. Whitefish food habits were positively correlated ($p \leq 0.05$) to the total drifting community 62% of the time. No positive correlations were found with the benthic insect community (Tables 11 and 12). However, without direct observation of the feeding behavior of mountain whitefish or the awareness of inherent mathematical biases, the implications of these results could not be fully realized.

I believe that a considerable amount of Chironomidae utilization occurs during substrate foraging and not from drift feeding alone. Small, slow moving, high density insects such as Chironomidae would be highly susceptible to a foraging predator such as whitefish. Also, mountain whitefish were observed capturing only larger bodied insects such as Ephemeroptera and Trichoptera during drift feeding. Kiefting (1978) reported that the lack of terrestrial insects in the stomachs of whitefish from the Snake River also suggests that surface feeding is not an important source of food to whitefish. Terrestrial insects never comprised more than 1% of the total stomach volume

for mountain whitefish from the Kootenai River (Table 1). Inorganic material such as sand and gravel, which was almost always present in whitefish stomachs from the Kootenai River, also supports their adaption to bottom feeding. Pontius (1972) also found this to be true.

Rainbow trout food habits positively correlated with drift samples only 25% of the time, and 50% of the time with benthic samples (Tables 11 and 12). However, underwater observations indicated that rainbow trout fed primarily on drifting insects and were only occasionally observed picking insects from the surface of the substrate. Never were they observed actively foraging through the substrate or in and around submerged objects as did whitefish. Rainbow food habits, however, showed little correlation with the drifting insect community. Possibly, the timing of insect sampling did not adequately represent the fish's time of feeding.

Rainbow trout food habits in the Kootenai River are quite variable, but after studying both empirical and behavioral data, certain trends in utilization of available food become apparent. Rainbow trout appeared to preferably feed on three families of both Ephemeroptera and Trichoptera. Utilization of these insects was usually

at or above their measured benthic availability and showed no consistent correlation with drifting insect availability. During those months when utilization of these two food groups was well above measured availability, emergent and/or adult forms were being heavily preyed upon. Rainbow trout switched to any other food organisms (ie: Nematoda, Coleoptera, Annelida) as they became seasonally abundant (Table 6). My observations indicated that Kootenai River rainbow are opportunistic, energy efficient, water column and surface feeders that select insects in relation to their seasonal availability. Although Chironomidae may sometimes comprise the majority of the drift biomass, they apparently were not selectively taken as long as other, larger bodied insects were abundant. During winter months, when most other aquatic insect activity and production are slowed, utilization of drifting Chironomidae was high (Table 6).

Habitat Selection

High discharge of 6,000 cfs and larger from Libby Dam from June through September, 1981, made habitat analysis in the Kootenai River operationally impossible. All habitat work was conducted in the Fisher River and Libby

Creek, the two largest tributaries to the Kootenai River above Kootenai Falls (Figure 1).

In Libby Creek, mountain whitefish are abundant only during spawning; therefore the rainbow trout population is existing in generally an allopatric situation. Both species occur in the Fisher River in about equal numbers throughout the year; these populations exhibit sympatry similar to the situation in the Kootenai River.

Only slight differences existed between the micro-habitat selection of these sympatric salmonids within the Fisher River. Whitefish chose deeper areas than rainbow trout; 0.957 m total depth as compared to 0.762 m total depth, respectively. Average (0.6 depth) velocities occupied by both species were virtually the same; 13.38 cm/sec for whitefish and 13.11 cm/sec for rainbow trout (Table 7). Rainbow trout chose substrate areas with a higher percentage of sand (19.32%) than did mountain whitefish (9.64%). Sandy areas can only be maintained in areas with relatively low velocities (Chorley 1969), and sympatric rainbow trout were found to occupy areas with a slightly smaller facing velocity than whitefish, 1.49 and 2.22 cm/sec, respectively (Table 7). Bovee (1978), in the formation of probability-of-use criteria for the habitat

Size Group (total length)		p = .05	RB (Libby Cr.)		RB (Fisher R.)		WF (Fisher R.)		p = .05
			Mean (No.)	SD	Mean (No.)	SD	Mean (No.)	SD	
Small (10.0 - 19.9 cm)	Velocity(cm/sec)								
	facing	no	0.91 (53)	2.13	0.91 (56)		3.44 (20)	4.88	yes
	average	yes	7.25 (60)	5.79	12.25 (56)		16.06 (20)	5.18	yes
	Depth(m)								
Medium (20.0 - 27.8 cm)	total	no	0.841 (60)	0.35	0.744 (56)		0.695 (20)	0.20	no
	Velocity(cm/sec)								
	facing	no	2.41 (21)	3.05	2.32 (18)		1.86 (35)	4.27	no
	average	yes	2.41 (29)	6.10	14.69 (18)		13.47 (35)	7.32	no
Large (27.8 - 43 + cm)	Depth(m)								
	total	no	0.719 (29)	0.26	0.789 (18)		0.988 (35)	0.30	yes
	Velocity(cm/sec)								
	facing	no	4.63 (3)	7.32	4.18 (5)		1.13 (14)	2.44	no
Total (10.0 - 43 + cm)	average	no	14.30 (10)	7.32	16.34 (5)		9.48 (14)	7.92	yes
	Depth(m)								
	total	yes	0.613 (10)	0.27	0.878 (5)		1.250 (14)	0.13	yes
	Velocity(cm/sec)								
Total (10.0 - 43 + cm)	facing	no	1.49 (77)	2.74	1.49 (79)		2.22 (69)	4.27	no
	average	yes	8.26 (99)	6.40	13.12 (79)		13.38 (69)	7.32	no
	surface	-	12.44 (21)	14.94	-----		16.43 (14)	10.36	no
	Depth(m)								
	fish	-	0.143 (21)	0.08	-----		0.061 (14)	0.03	yes
	total	no	0.783 (99)	0.33	0.762 (79)		0.957 (69)	0.31	yes
	% Substrate								
	Composition								
	sand	-	19.32 (22)	16.71	-----		9.64 (14)	15.38	yes
	gravel	-	35.91 (22)	20.74	-----		44.64 (14)	26.20	no
	cobble	-	30.91 (22)	19.19	-----		38.21 (14)	21.63	no
	boulder	-	13.86 (22)	16.83	-----		7.50 (14)	14.24	no

parameters of total depth, average velocity and substrate composition, found few dissimilarities between the probability curves developed for mountain whitefish and rainbow trout.

Rainbow trout larger than 27.8 cm TL occupied areas with both higher facing and average velocities than mountain whitefish of the same size (Table 7). This appears to be due to the fact that this size group of rainbow trout occupied significantly shallower areas than similar sized mountain whitefish, (0.878 and 1.25 m, respectively) and velocities were greater. Higher velocity areas would be transporting more drifting insects than slower areas, thus benefiting rainbow trout feeding on drift.

Although there were not always statistically significant differences between microhabitat parameters, the aspect of morphological differences may play a significant role. The general body shape of a rainbow trout could be described as a laterally depressed fusiform, whereas a mountain whitefish can be described as a ventrally depressed fusiform. By angling the leading edge of their pectoral fins downward, whitefish "sit" on the substrate. Water passing over their fusiform dorsal

area and angled pectoral fins compresses their bodies onto the substrate. As a consequence mountain whitefish chose substrate areas with higher percent gravel (44.64%) and cobble (38.21%) composition than did rainbow trout (35.91 and 30.91%, respectively, Table 7). Because of their planing ability, whitefish can maintain position in these higher velocity areas, whereas rainbow trout would be forced to swim constantly. This type of substrate also facilitates their benthic feeding habits (May et al. 1981, DosSantos and Huston 1983).

Rainbow trout occupied areas with a higher percent composition of boulders (13.86%), almost double the boulder composition associated with mountain whitefish (7.50%). Rainbow trout are not a planing fish, and use reduced velocity areas associated with boulder substrate. In this manner, they can occupy low velocity resting positions and still be near high velocity waters where drifting insects are available to them. Direct underwater observations in the Kootenai River and the two study tributaries showed this to be true. Dettman (1973) also observed this type of feeding behavior in sympatric rainbow trout from a tributary to the Sacramento River.

Discriminant analysis results were somewhat inconclusive, however they did reveal the importance of certain habitat parameters which influence the habitat selection of rainbow trout and mountain whitefish. When using three physical habitat variables [facing velocity, average (velocity at 0.6 depth) velocity and total depth] the best generated size-species function accounted for only 63% (canonical correlation = 0.4389) of the observed data variation (Table 8(a)). Classification of individual fish into correct size and species groups averaged only 33.6%. When the substrate variable, percent sand composition, was added percent classification into correct size and species groups increased to an average of 91.7%. The best function generated with this combination of variables now accounted for 71.1% (canonical correlation = 0.9276) of the observed variation (Table 8(b)). When evaluating the best canonical discriminant function at the size-species group centroids (Figure 6), most habitat similarities between mountain whitefish and rainbow trout are found in size group I (10.0 - 19.9 cm TL). The largest food habit overlap was also found in this size group.

The importance of different habitat parameters on habitat selection can also be interpreted from the

Table 8. Results of stepwise discriminant analysis. a) three variable analysis for 178 rainbow trout and 69 mountain whitefish. b) nine variable analysis for 22 rainbow trout and 14 mountain whitefish. Only those variables passing the F-to-enter test are given. Fish from both Libby Creek and the Fisher river were lumped for this analysis.

Variable	Increase in Rao's V	p =	Variable	Canonical Coefficients	Size-Species Group	% Correct Classification
a)						
Total depth	53.87	0.00	Total depth	1.037	RB-1	38.8
Average velocity	29.92	0.00	Average velocity	0.350	RB-2	19.1
Facing velocity	7.36	0.20	Facing velocity	0.035	RB-3	33.3
Best function described 63.1% of total variation. Canonical correlation = 0.4389					WF-1	30.0
					WF-2	17.1
					WF-3	85.7
					mean	33.6
b)						
Total depth	41.38	0.00	Facing velocity	0.420	RB-1	83.3
Fish depth	28.52	0.00	Total depth	0.390	RB-2	100.0
Facing velocity	21.47	0.00	Fish depth	0.242	RB-3	100.0
% Sand	15.92	0.01	% Sand	0.085	WF-1	85.7
Best function described 71.1% of total variation. Canonical correlation = 0.9276					WF-2	100.0
					WF-3	100.0
					mean	91.7

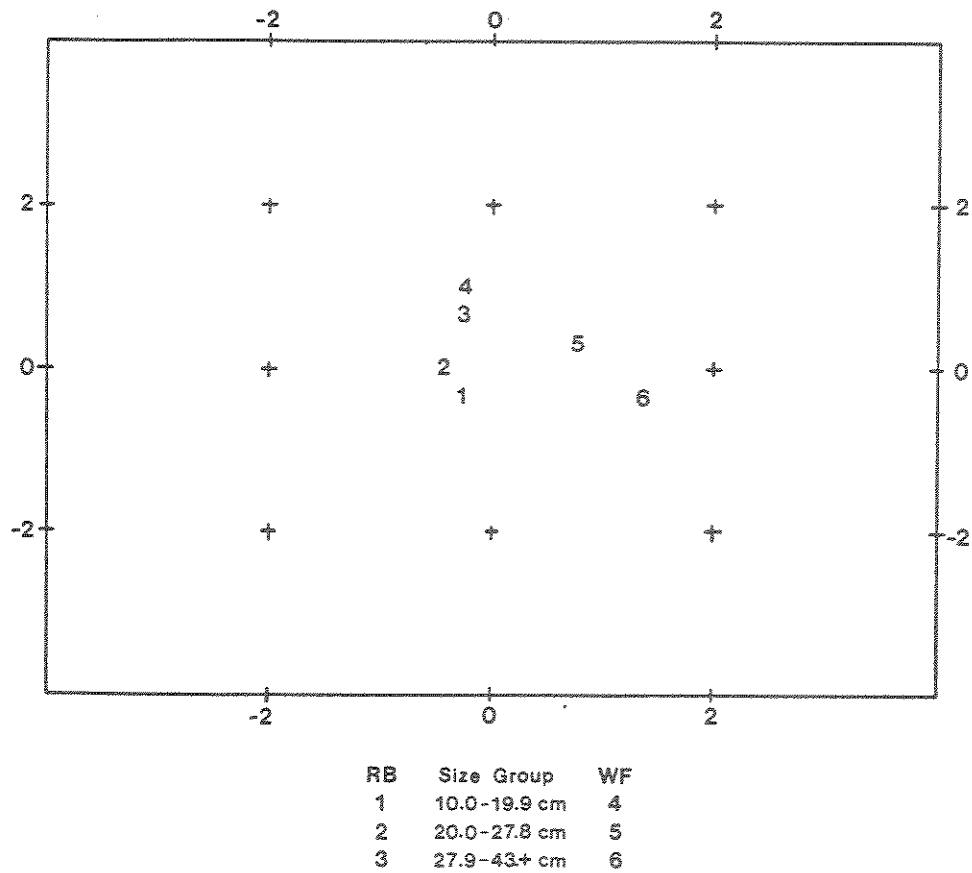


Figure 6. Territorial map of size-species group centroids generated by the two best canonical discriminant functions.

discriminant analysis results. When subjecting all 9 measured habitat parameters to a stepwise discriminant technique, different combinations of variables, passing the F-to-enter test, were more significant in determining the best functions for the two species. The interplay of substrate characteristics and water depths was most important in influencing mountain whitefish microhabitat selection. Only three variables (percent boulder and sand composition and fish depth) were needed to describe whitefish habitat selection and described 95.7% of the total data variation (canonical correlation = 0.9763). Although sample size was small ($n = 14$), this function correctly classified each fish into its proper size group (Table 9).

The interplay of water depths and velocities was dominant in influencing rainbow trout habitat selection. Facing velocity was the most important, whereas percent sand composition was the least important of the five variables describing rainbow trout habitat selection. This function described 82.7% of the total data variation (canonical correlation = 0.9280). Although sample size was small ($n = 22$), this function correctly classified each fish into its proper size group (Table 9). Hanson

Table 9. Results of stepwise discriminant analysis on nine habitat variables for 22 rainbow trout and 14 mountain whitefish. Only those variables passing the F-to-enter test are given. Fish from both Libby Creek and the Fisher River were lumped for this analysis.

Variable	Increase in Rao's V	p =	Variable	Canonical Coefficients	Size Group	% Correct Classification
Rainbow trout						
Facing velocity	18.29	0.00	Total depth	0.699	S	100.0
Average velocity	16.79	0.00	Facing velocity	0.531	M	100.0
Fish depth	11.56	0.00	Average velocity	0.417	L	100.0
Total depth	10.62	0.01	Fish depth	0.240	mean	100.0
% Sand	9.29	0.01	% Sand	0.069		
Best function described 82.7% of total variation.						
Canonical correlation = 0.9280						
Mountain whitefish						
% Boulder	79.20	0.00	Fish depth	1.396	S	100.0
% Sand	53.67	0.00	% Sand	0.983	M	100.0
Fish depth	32.30	0.00	% Boulder	0.752	L	100.0
					mean	100.0
Best function described 95.7% of total variation.						
Canonical correlation = 0.9763						

(1977), in his work with sympatric steelhead trout (Salmo gairdneri), also found that facing velocity was the most descriptive habitat variable.

No one variable was found to have a truly dominant influence on habitat selection for these sympatric species. Total depth, however, consistently contributed the most in discriminating the best functions. Also, this variable usually produced the largest canonical discriminant coefficients within that function (Table 8).

Some differences emerge in habitat selection when comparing allopatric and sympatric rainbow trout populations. Position relative to water velocity provides a possible indication of habitat displacement caused by the presence of mountain whitefish. Although there were never any significant differences in the facing velocities exhibited by any size group of rainbow trout, average (0.6 depth) velocities at the fish location were always greater when rainbow trout were sympatric (Fisher River) with mountain whitefish (Table 7). The ranges of available water depths and velocities were similar between habitat study sections in both Libby Creek and the Fisher River; therefore it could be postulated that the presence of mountain whitefish displaces rainbow trout into higher

average velocity areas requiring a greater expenditure of energy to move about.

Discriminant analysis showed that facing and average velocities and total depth contributed nearly equally to the generation of the best possible sympatric rainbow trout function, with facing velocity being slightly more important. In the allopatric situation, facing velocity was the most important variable in generating the best function, followed by average (0.6 depth) velocity. Total depth only contributed slightly to this function (Table 10).

The preceding analysis and repeated underwater observations suggest that rainbow trout were able to find adequate focal point velocities both when allopatric or sympatric with whitefish, even though they occupied higher average velocity areas when sympatric. In the presence of mountain whitefish, water depth becomes more important to rainbow trout. With mountain whitefish generally occupying the lower strata of water, a greater water depth becomes important in insuring that adequate velocity areas are available to rainbow trout. This increased water depth allows for easier vertical stratification among the two species.

Griffith (1972) and Dettman (1973) have both previously

Table 10. Results of direct discriminant analysis on three habitat variables for 79 sympatric rainbow trout, 69 sympatric mountain whitefish and 99 allopatric rainbow trout.

	Variable	Canonical Coefficients	Size Group	% Correct Classification
Rainbow trout - Sympatric:	Facing velocity	0.705	S	57.1
	Total depth	0.683	M	33.3
Best function described 99.2% of total variation.	Average velocity	0.607	L	60.0
Canonical correlation = 0.3997			mean	51.9
Mountain whitefish - Sympatric:	Total depth	1.005	S	75.0
	Facing velocity	0.159	M	25.7
Best function described 98.2% of total variation.	Average velocity	0.089	L	85.7
Canonical correlation = 0.6312			mean	52.2
Rainbow trout - Allopatric:	Facing velocity	0.859	S	73.6
	Average velocity	0.437	M	28.6
Best function described 74.0% of total variation.	Total depth	0.099	L	33.3
Canonical correlation = 0.3618			mean	59.7

recognized the importance of water depth to sympatric salmonids as a means of minimizing the chances of direct interspecific interactions. Based upon my work, I certainly support this theory.

CONCLUSIONS

A basic fisheries management question prompted this research: Can the biomass of a salmonid more desirable to anglers, such as rainbow trout, be increased by reducing mountain whitefish biomass? This yet unresolved ecological question has troubled many western anglers and fisheries managers for nearly half a century. Early studies (McHugh 1940, Sigler 1951 and Laakso 1951) concluded that mountain whitefish were serious competitors for food and space with rainbow trout. Recent investigations (Pontius and Parker 1973, Thompson 1974 and Kiefling 1978), however, have questioned this theory of competition between these two salmonids. Most recently, investigators (Schoener 1982, MacNally 1983 and Williams 1983) have cautioned about the interpretation of mathematical results in assessing the level of interspecific interactions.

Through evolutionary time, mountain whitefish and rainbow trout may have competed for food and/or space within the Kootenai drainage. However, as natural selection favored individuals that utilized widely different habitats, the progeny of these fish flourished

to produce the subtle pattern of habitat segregation observed today. "Habitats may thus be the arenas rather than the objects of competition" (Schoener 1974). Both mountain whitefish and rainbow trout flourish in the Kootenai today, demonstrating a prime example of ecological compatibility between species.

The potential for competition for a specific food item (Chironomidae) does exist between small rainbow trout and small whitefish, but only if this prey item is limited. Habitats occupied by these smaller fish are also quite similar. Odum (1971) defines interspecific competition as "any interaction between two or more species populations which adversely affects their growth and survival". This definition does not apply to present-day salmonid populations within the Kootenai River. Kiefling (1978) concluded that mountain whitefish and cutthroat trout (Salmo clarki) did not compete for resources within the Snake River, Wyoming. Quantitative results and underwater observations conducted in this study, indicate that mountain whitefish and rainbow trout do not actively compete for resources within the Kootenai River drainage.

Mountain whitefish are the most common salmonids inhabiting our larger Montana rivers. Population levels

of trout species more desirable to anglers never approach those of whitefish. Disproportionate populations levels of coexisting salmonids reflect not only habitat adaptability but also may be the result of angler selectivity. Mountain whitefish are basically a schooling fish, tolerant of the close proximity of other similar-sized whitefish. Intraspecific aggression and territoriality within trout species is well documented and was a commonly observed behavior of rainbow trout in this study. Therefore, rainbow trout intraspecific behavior may limit their population density more than the presence of mountain whitefish.

The whitefish controversy, however, still continues. The Montana Department of Fish, Wildlife and Parks has long recognized this relatively unexploited whitefish resource and today has taken a somewhat passive approach to whitefish management in large rivers. As trout fishing regulations have become more restrictive over the years, whitefish bag limits have steadily increased. At this level of population experimentation, the whitefish controversy is sure to continue.

Fortunately, Montana has the perfect large scale study area: The 56 kilometer section of the Kootenai River

isolated between Libby Dam and Kootenai Falls is an ideal area for studying the effects of whitefish removal on a big river trout fishery. Mountain whitefish are highly susceptible to river electrofishing operations and fall tributary trapping within the Kootenai drainage. With a minor expenditure of man power and available funds, large numbers of whitefish could be removed from the Kootenai in a relatively short period of time. If this whitefish removal continued for several years, and were coupled with a follow-up monitoring program to assess salmonid population levels, the whitefish controversy could finally be resolved.

LITERATURE CITED

LITERATURE CITED

- Allendorf, F.W., D.M. Espeland, D.T. Seow and S. Phelps. 1980. Coexistence of native and introduced rainbow trout in the Kootenai River Drainage. Proceedings of the Montana Academy of Sciences 39:28-36.
- Appert-Perry, S. and J. Huston. 1983. Section A; Aquatic insect study. October 1979 - June 1982 in Kootenai River investigations final report, 1972 - 1982. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- Begenal, T., editor. 1978. Methods of assessment of fish production in fresh water. IBP Handbook No. 3. Blackwell Scientific Publications, London, England. 365 pp.
- Bisson, P.A. 1978. Diel food selection by two sizes of rainbow trout (Salmo gairdneri) in experimental stream. Journal of the Fisheries Research Board of Canada 35:971-975.
- Bonde, T.J.H. and R.M. Bush. 1975. Kootenai River water quality investigations, Libby Dam Preimpoundment Study. 1967 - 1972. U.S. Army Corps of Engineers, Seattle, Washington, USA. 124 pp.
- Bovee, K.D. and T. Chochnauer. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fisheries. Instream Flow Information Paper No. 3, FWS/OBS-77/63, U.S. Fish and Wildlife Service, Fort Collins, Colorado, USA.
- Bovee, K.D. 1978. Probability-of-Use criteria for the family salmonidae. Instream flow information paper No. 4, FWS/OBS-78-07. U.S. Fish and Wildlife Service, Fort Collins, Colorado, USA.
- Brown, C.J.D. 1971. Fishes of Montana. Big Sky Books, Bozeman, Montana, USA. 207 pp.

- Brown, L.G. 1972. Early life history of the mountain whitefish (Prosopium williamsoni) (Girard) in the Logan River, Utah. M.S. Thesis, Utah State University, Logan, Utah, USA. 40 pp.
- Bryan, J.E. 1973. Feeding history, parental stock and food selection in rainbow trout (Salmo gairdneri). Behavior XLV I:123-153.
- Carle, F.L. 1976. An evaluation of the removal and method for estimating benthic populations and diversity. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA. 108 pp.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist. 100:345-357.
- Chorley, R.J., editor. 1969. Introduction to fluvial processes. Methuen University Paperbacks (U.S. distributor Harper & Row). 218 pp.
- Cummins, K.W. 1964. Factor limiting the microdistribution of larvae of caddisflies Pycnopsyche lepida (Hagen) and Pycnopsyche guttifer (Walker) in a Michigan stream (Trichoptera: Limnephilidae). Ecological Monographs 34:271-295.
- Daily, M.K. 1971. The Mountain Whitefish: a Literature Review. University of Idaho, College of Forestry Wildlife and Range Sciences. Experiment Station Paper #8, Moscow, Idaho, USA.
- Dettman, D.H. 1978. Distribution, abundance and microhabitat segregation of rainbow trout and Sacramental squawfish in Deer Creek, California. M.S. Thesis, University of California, Davis, California, USA.
- DosSantos, J.M. and J. Huston. 1983. Section B; Food habits of rainbow trout and mountain whitefish in Kootenai River investigations final report, 1972-1982. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

- Everest, F.H. 1978. Diver operated device for immobilizing fish with a small explosive charge. *The Progressive Fish Culturist* 40:121-122.
- George, E.L. and W.F. Hadley. 1979. Food and habitat partitioning between rock bass (Ambloplites rupestris) and smallmouth bass (Micropterus dolomieu) young-of-the-year. *Transactions of the American Fisheries Society*. 108:253-261.
- Graham, P.J. 1979. Kootenai Falls aquatic environment study. Final Report. Northern Lights, Inc. and Montana Department of Natural Resources and Conservation, Helena, Montana, USA. 84 pp.
- Griffith, J.S. 1972. Comparative behavior and habitat utilization of brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo clarki) in small streams in northern Idaho. *Journal of the Fisheries Research Board of Canada* 29:365-273.
- Hanson, D.E. 1977. Habitat selection and special interactions in allopatric and sympatric populations of cutthroat and steelhead trout. PhD Dissertation. University of Idaho, Moscow, Idaho, USA. 66 pp.
- Huntsberger, D.V. and P. Billingsley. 1977. Elements of Statistical Influence. Allyn and Bacon, Inc., Boston, Massachusetts, USA. 385 pp.
- Irvine, J.R. and T.G. Northcote. 1982. Significance of sequential feeding patterns of juvenile rainbow trout in a large lake-fed river. *Transactions of the American Fisheries Society* 111:446-452.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA. 302 pp.
- Jenson, S.L. and G.F. Edmonds. 1976. The Mayflies of North and Central America. University of Minnesota Press. Minneapolis, Minnesota, USA. 303 pp.
- Johnson, J.H. 1981. Comparative food selection by coexisting subyearling coho salmon, chinook salmon and rainbow trout in a tributary of Lake Ontario. *New York Fish and Game Journal* 28:150-161.

- Kiefling, J.W. 1978. Studies on the ecology of the Snake River cutthroat trout. Fisheries Technical Bulletin No. 3. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA. 198 pp.
- Laakso, M. 1951. Food habits of the Yellowstone Whitefish, Prosopium williamsoni cismontanous (Jordo. Transactions of the American Fisheries Society 80:99-109.
- Leob, H.A. 1957. Night collection of fish with electricity. New York Fish and Game Journal 4:109-118.
- MacNally, R.C. 1983. On assessing the significance of interspecific competition to guild structure. Ecology 64:1646-1652.
- May, B. and J.E. Huston. 1979. Kootenai River Fisheries Investigations. Completion Report. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA. 57 pp.
- May, B., S. Appert, J. Huston and J.M. DosSantos. 1981. Kootenai River Investigations. Annual progress report, July 16, 1980 - July 15, 1981. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- May, B. and J. Huston. 1983. Section C. Fisheries Investigations. July 1972 - September 1982, in Kootenai River investigations final report, 1972 - 1982. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- McHugh, J.L. 1940. Food of the Rocky Mountain Whitefish, Prosopium williamsoni (Girard). Journal of the Fisheries Research Board of Canada 5:131-137.
- McMullin, S.L. 1979. The food habits and distribution of rainbow and cutthroat trout in Lake Koocanusa, Montana. M.S. Thesis, University of Idaho, Moscow, Idaho, USA.
- McNaughton, S.J. and L.L. Wolf. 1973. General ecology. Holt, Rinehart and Winston. New York, New York, USA. 710 pp.

- Meehan, W.R. and R.A. Miller. 1978. Stomach flushing: Effectiveness and influence of survival and condition of juvenile salmonids. *Journal of the Fisheries Research Board of Canada* 35:1359-1363.
- Merritt, R.W. and K.W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa, USA. 441 pp.
- Nie, N.H., C.H. Hull, J.C. Jenkins, K. Steinbrenner and D.H. Bent. 1975. Statistical package for the social sciences. McGraw-Hill Book Company. New York, New York, USA. 675 pp.
- Odum, E.P. 1971. Fundamentals of Ecology. W.B. Saunders Company, Philadelphia, Pennsylvania, USA. 574 pp.
- Pennack, R.W. 1978. Freshwater invertebrates of the United States. John Wiley and Sons, New York, USA. 803 pp.
- Pontius, R.W. and M. Parker. 1973. Food habits of the mountain whitefish (Prosopium williamsoni) (Girard). *Transactions of the American Fisheries Society* 102:764-773.
- Schoener, T.W. 1970. Nonsynchronous spacial overlap of lizards in patchy habitats. *Ecology* 51:408-418.
- Schoener, T.W. 1974. Competition and the form of habitat shift. *Theoretical Population Biology* 6:265-307.
- Schoener, T.W. 1982. The controversy over interspecific competition. *American Scientist* 70:586-595.
- Seaburg, K.G. 1957. A stomach sampler for live fish. *Progressive Fish Culturist* 19:137-139.
- Shields, R.R., J.R. Knapton, M.A. Jacobson and M.L. Kasman. 1982. Water resource data, Montana water year 1982, Volume 2, Columbia River Basin. United States Geological Survey Water data Report MT-82-2, Helena, Montana, USA.

- Sigler, W.F. 1951. The life history and management of the mountain whitefish (Prosopium williamsoni) (Girard) in the Logan River, Utah. Agricultural Experiment Station, Bulletin #347, Utah State Agricultural College, Logan, Utah, USA. 20 pp.
- Snedecor, G.W. and W.G. Cochran. 1980. Statistical methods. The Iowa State University Press. Ames, Iowa, USA. 507 pp.
- Stalnaker, C.B. and R.E. Gresswell. 1974. Early life history and feeding of young mountain whitefish. Environmental Protection Agency, Ecological Research Series, EPA-660/3-73-019. Washington, D.C., USA.
- Thompson, G.E. 1974. The ecology and life history of the mountain whitefish (Prosopium williamsoni) (Girard) in the Sheep River, Alberta. Fisheries Research Report Number 12. Alberta Lands and Forests, Fish and Wildlife Division, Alberta, Canada. 122 pp.
- Wallace, Jr., R.K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110:72-76.
- Waters, T.F. and R.J. Knapp. 1961. An improved stream bottom fauna sampler. Transactions of the American Fisheries Society 90:225-226.
- Wiggins, G.B. 1977. Larvae of the North American Caddisfly genera (Trichoptera). University of Toronto Press, Toronto, Canada. 401 pp.
- Williams, B.K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283-1291.
- White, R.J. 1973. Proceedings of the 28th Annual Meeting of the Soil Conservation Society of America, pp. 61-79. Hot Springs, Arkansas, USA.
- White, R.G. and D.T. Wade. 1980. A study of fish and aquatic macroinvertebrate fauna in the South Fork Boise River below Anderson Ranch Dam with emphasis on the effects of fluctuating flows. Idaho Cooperative Fisheries Research Unit, University of Idaho, Moscow, Idaho, USA.

APPENDIX

Table 11. Pearson correlation coefficients for the percent of total stomach volume (ml) of select size groups of mountain whitefish and rainbow trout as related to both benthic (Ben), and drift (Dri) in insect samples (ml) from the Elkhorn study section of the Kootenai River. June to October 1980 and January, March and May 1981.

	Jun - 1980		Jul - 1980		Aug - 1980		Sep - 1980		Oct - 1980		Jan - 1981		Mar - 1981		May - 1981	
	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI
Whitefish																
10.0-19.9 cm	.3059 p=.252	.9218 p=.002	.1404 p=.382	.8629 p=.006	.1645 p=.435	.7056 p=.038	.2114 p=.325	.8940 p=.003	.5950 p=.079	.6170 p=.072	.0514 p=.456	.8913 p=.004	.0341 p=.471	.4398 p=.162	.3988 p=.188	.1865 p=.344
20.0-27.8 cm	.0510 p=.457	.7955 p=.016	.2023 p=.332	.6126 p=.013	.0772 p=.435	.8121 p=.013	.4187 p=.175	.0646 p=.445	.4350 p=.185	.3638 p=.211	.0821 p=.461	.4570 p=.151	.1514 p=.373	.2982 p=.256	.1534 p=.371	.0960 p=.419
27.8-43+ cm	.1167 p=.402	.6788 p=.047	.6335 p=.063	.1368 p=.388	.5805 p=.086	.1716 p=.356	.2895 p=.264	.9277 p=.001	.4367 p=.164	.2059 p=.329	.5078 p=.122	.3988 p=.188	.1328 p=.388	.5068 p=.183	.1810 p=.385	.0336 p=.472
10.0-43+ cm	.2337 p=.307	.8903 p=.004	.3884 p=.195	.7713 p=.021	.3244 p=.239	.7241 p=.033	.3781 p=.201	.8639 p=.006	.5390 p=.106	.8524 p=.154	.1617 p=.365	.7252 p=.033	.0808 p=.432	.4329 p=.166	.2921 p=.263	.1314 p=.369
Rainbow																
10.0-19.9 cm	.9325 p=.001	.4073 p=.185	.8111 p=.013	.4781 p=.140	.4501 p=.155	.0558 p=.453	.3001 p=.257	.4908 p=.132	.6278 p=.066	.5248 p=.113	.2268 p=.312	.3755 p=.203	99.0000 p=none	99.0000 p=none	.4472 p=.157	.0796 p=.433
20.0-27.8 cm	.6771 p=.047	.3814 p=.199	.8542 p=.007	.2882 p=.265	.4611 p=.149	.1937 p=.339	.4532 p=.154	.2313 p=.309	.5089 p=.122	.3999 p=.167	.1683 p=.359	.8579 p=.007	.9283 p=.001	.7175 p=.035	.3977 p=.188	.1025 p=.413
27.8-43+ cm	.6399 p=.081	.0459 p=.478	.8219 p=.012	.1033 p=.413	.6508 p=.057	.0845 p=.429	.6305 p=.054	.0133 p=.489	.5418 p=.105	.0878 p=.426	.1675 p=.360	.8513 p=.008	.0603 p=.449	.3710 p=.206	.0381 p=.468	.4823 p=.131
10.0-43+ cm	.6829 p=.004	.3428 p=.276	.8589 p=.007	.3657 p=.208	.5255 p=.113	.0434 p=.463	.4641 p=.147	.2326 p=.308	.6636 p=.052	.3969 p=.169	.1426 p=.380	.9821 p=.000	.6615 p=.053	.7243 p=.033	.2441 p=.291	.2515 p=.293

Table 12. Pearson correlation coefficients for the percent of total stomach volume (ml) of select size groups of mountain whitefish and rainbow trout as related to both benthic (Ben) and drift (Dri) in insect samples (ml) from the Pipe Creek study section of the Kootenai River. June to October 1980 and January, March and May 1981.

	Jun - 1980		Jul - 1980		Aug - 1980		Sep - 1980		Oct - 1980		Jan - 1981		Mar - 1981		May - 1981	
	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI	BEN	DRI
Whitefish																
10.0-19.9 cm	.5864 p=.083	.9731 p=.000	.0070 p=.494	.2482 p=.296	.2059 p=.329	.9479 p=.001	.2142 p=.322	.9120 p=.002	.0929 p=.421	-.0339 p=.471	.0589 p=.450	.3543 p=.218	.7855 p=.018	.8793 p=.005	.9567 p=.007	.9828 p=.000
20.0-27.8 cm	.5267 p=.112	.9698 p=.000	.4069 p=.182	.0725 p=.439	.1953 p=.371	.9660 p=.000	.4124 p=.179	.6147 p=.071	.2245 p=.314	.0454 p=.462	-.1484 p=.378	.0871 p=.426	.3110 p=.249	.5408 p=.105	.7431 p=.028	.9484 p=.008
27.8-43+ cm	-.0443 p=.462	-.1504 p=.374	.7869 p=.016	.0100 p=.492	-.0401 p=.466	.8942 p=.003	.3512 p=.220	.8508 p=.008	.2912 p=.193	.3189 p=.243	.1512 p=.373	.4597 p=.150	.3399 p=.228	.4195 p=.063	.5397 p=.106	.6689 p=.050
10.0-43+ cm	.5703 p=.091	.9451 p=.001	.4358 p=.177	.1862 p=.335	.1470 p=.377	.9474 p=.001	.3196 p=.242	.9282 p=.001	.2224 p=.316	.0715 p=.439	.0343 p=.471	.3407 p=.227	.5952 p=.079	.7758 p=.020	.8274 p=.011	.9589 p=.000
Rainbow																
10.0-19.9 cm	.5964 p=.079	.0122 p=.490	.0268 p=.011	.0694 p=.450	.3119 p=.240	-.0002 p=.492	.7939 p=.017	.7412 p=.028	.3251 p=.238	.1999 p=.338	.7147 p=.036	.9604 p=.000	.9323 p=.001	.8447 p=.008	.9561 p=.000	.9477 p=.001
20.0-27.8 cm	.6352 p=.062	-.1078 p=.409	.7808 p=.019	-.0258 p=.478	.2638 p=.284	-.0419 p=.464	.0015 p=.499	.6129 p=.072	.1505 p=.374	.0424 p=.464	.6907 p=.043	.9455 p=.001	.5063 p=.123	.6891 p=.044	.7495 p=.026	.6134 p=.071
27.8-43+ cm	.8344 p=.004	.0651 p=.445	.8067 p=.014	-.0208 p=.482	.5476 p=.102	.2287 p=.311	.4775 p=.139	.1742 p=.353	.1568 p=.369	.0042 p=.496	.8867 p=.044	.9559 p=.000	.4616 p=.149	.0854 p=.428	-.2708 p=.278	-.1763 p=.353
10.0-43+ cm	.6914 p=.043	.0296 p=.475	.8110 p=.013	.0160 p=.486	.3745 p=.204	.0432 p=.463	.7724 p=.021	.5556 p=.058	.2401 p=.302	.1086 p=.408	.7026 p=.039	.9576 p=.000	.9117 p=.002	.8446 p=.008	.8427 p=.009	.8158 p=.013