

Seasonal Food Habits of Bull Trout from a Small Alpine Lake in the Canadian Rocky Mountains

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Abstract.—We investigated the seasonal diet of a native, undisturbed population of bull trout *Salvelinus confluentus* in an alpine lake to examine predation patterns between fish size-classes and in relation to available invertebrate prey. The diets of small (≤ 250 mm in fork length, FL) and large (> 250 mm FL) bull trout were similar. Bull trout fed on seasonally abundant prey species. After ice-out in July, the diet was dominated by chironomid pupae. *Daphnia pulex* var. and the amphipod *Gammarus lacustris* dominated the diet in August and September. Both *Daphnia* and *Gammarus* reproduced before bull trout switched to preying on them in early August. Bull trout fed size-selectively on large individuals of both *Daphnia* and *Gammarus*. Large bull trout preyed on larger *Daphnia* than did small bull trout. Fish of both size-classes consumed large *Gammarus*. Bull trout were spatially segregated; small fish occupied shallow water (< 1 m deep), while large fish occupied the profundal offshore zone. Spatial segregation prevented small bull trout from cropping small immature *Daphnia* in offshore areas. Average total food volume in stomachs of small fish increased between July and September whereas it decreased in large fish. The latter were frequently emaciated, indicating that large individuals may be food limited for much of the open-water period. Our data and observations suggest that prey switching, timing of prey reproduction, and spatial segregation of the fish population by size are tightly coupled and contribute to the survival of the key prey species. The survival of a variety of invertebrate species, including large *Gammarus*, in the presence of bull trout suggests that stocks of this fish species could be increased by stocking small mountain lakes without severely affecting the native invertebrate fauna.

Past surveys of mountain lakes in western Canada have shown that plankton communities in lakes with populations of native cutthroat trout *Oncorhynchus clarki* and bull trout *Salvelinus confluentus* were more similar to those of fishless lakes than were lakes stocked with nonnative salmonids (Anderson 1980). Plankton communities in mountain lakes stocked with nonnative salmonids such as brook trout *S. fontinalis* were severely impoverished in terms of abundance and species diversity (Reimers 1958; Amann 1980; Anderson 1980; Parker and Schindler 1995; McNaught et al. 1999). Anderson (1980) suggested that the lack of feeding by cutthroat trout during their spring reproduction coincided with the critical reproductive period of many invertebrates, allowing their populations to coexist. However, no explanation was offered for

the coexistence of plankton and fall-spawning bull trout. These findings suggest that (1) stocking programs should focus on native species to preserve and maintain plankton diversity; and (2) it may be possible to increase the number of bull trout populations in mountain lakes without severely affecting native plankton communities.

The decline and local extirpation of bull trout populations in northwestern North America as a result of overharvest, habitat destruction, and the introduction of other *Salvelinus* species (Roberts 1987; Buktenica 1997; Colpitts 1997; Fitch 1997; Rhude and Stelfox 1997) has led to concern among fisheries managers and prompted the implementation of recovery plans (Berry 1994). For such plans to be effective, the ecology of the species must be understood. However, the past unfavorable status of bull trout among fishermen and managers (Colpitts 1997) and the difficulty of access to remote mountain lakes have meant that few detailed studies of the ecology of bull trout in high-elevation lakes were conducted. A few of these lakes were spared introductions of other fish species during

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Received March 12, 1998; accepted February 3, 1999

the past stocking era and today contain bull trout populations in a pristine state. It is estimated that only six or seven lakes with native adfluvial bull trout populations remain in the Canadian Rocky Mountains (Donald and Alger 1993; Donald and Stelfox 1997). These populations are valued as important gene pools and have been considered as possible donor stocks for introduction to other lakes (Carl et al. 1989). They also represent a valuable resource from which to collect baseline data and examine the mechanism by which bull trout coexist with a diverse invertebrate prey fauna.

To our knowledge, no thorough investigation of the seasonal diet of adfluvial bull trout populations in high-elevation lakes has been undertaken. Information on diet and feeding strategy is necessary to assess the suitability of potential lakes for stocking or restoration. Knowledge of the feeding habits is also important to evaluate potential impacts of bull trout on food webs in lakes identified for potential stocking and could indicate possible mechanisms whereby bull trout coexist with invertebrate populations. Here we describe the seasonal food habits of an unmanipulated adfluvial bull trout population from a small alpine lake in relation to the availability of prey species in the lake.

Methods

Study area.—Harrison Lake (Figure 1) is a small oligotrophic alpine (2,243 m above sea level) lake in Banff National Park, Alberta, Canada (51°32'W, 115°48'N). It has a surface area of 8.4 ha and a maximum depth of 10.7 m. The ice-free season lasts approximately 100 d from early July until late September to mid-October. Generally, maximum surface water temperatures reach approximately 12°C in August (Anderson and Donald 1978; D. W. Schindler, unpublished data). The lake weakly stratifies; temperature differences between the surface and bottom are usually less than 3°C.

Three small streams—one on the west side and two on the southwest side—direct snowmelt runoff into the lake. Inflow volume decreases as the catchment snowpack diminishes throughout the summer. A single shallow outflow is on the north shore of the lake. A small waterfall approximately 20 m downstream of the outlet prevents immigration of fish from the stream. Bull trout is the only fish species present in Harrison Lake as determined from fishing records earlier this century, gill-net surveys in 1977, and continued monitoring in 1996, 1997, and 1998.

Harrison Lake is approximately bowl shaped with a shallow shelf scoured by ice to a depth of

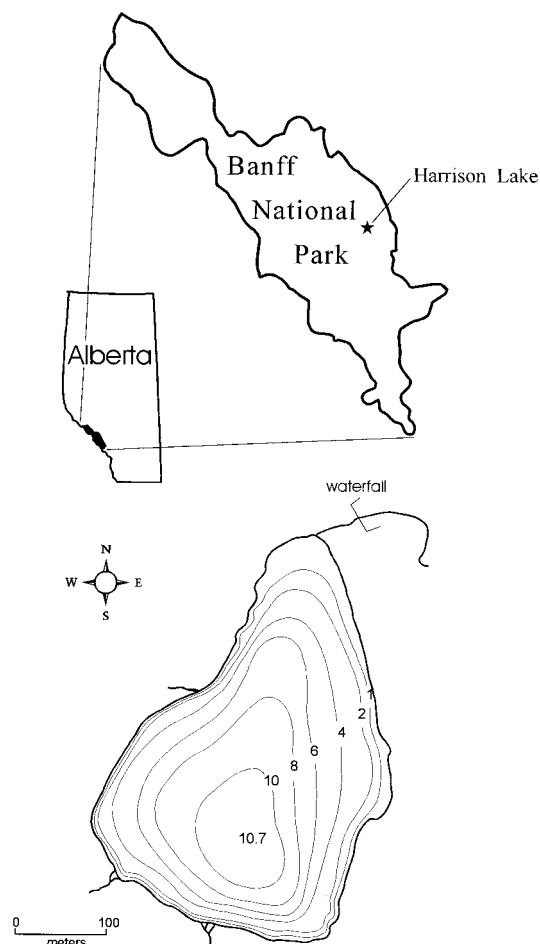


FIGURE 1.—Location of Harrison Lake and bathymetric map showing inflows and outflow.

approximately 1 m that extends 1–5 m from shore (Figure 1). Macrophytes are absent, and chironomids, cyclopoid copepods (mostly *Diacyclops bicuspidatus thomasi*), *Daphnia pulex* var., and the amphipod *Gammarus lacustris* are the most abundant invertebrates. The bull trout population is considered unexploited because of the lake's remote location; it is approximately 36 km from the nearest motor vehicle access.

Bull trout sampling.—On August 17, 1977, bull trout were collected with monofilament gill nets of mixed mesh sizes (9 m each of 25-, 38-, 51-, 76-, and 102-mm-stretch mesh). Of the 18 fish ranging in size from 350 to 440 mm in fork length (FL), all contained food and were examined. Although no effort was made to capture young fish, they were observed in shallow (<15 cm deep) wa-

ter close to shore along the east and north side of the lake.

In 1996, bull trout were caught by angling on August 2, 7, and 9, using artificial lures with barbless hooks. Captured bull trout ranged from 170 to 450 mm FL, but only fish longer than 250 mm FL were examined for stomach contents. Of the 31 fish examined, 6 had empty stomachs.

In 1997 sampling occurred on July 1, 13, 14, and 24; August 10, 22, and 24; and September 23 and 24. Adult bull trout were angled as in 1996, and juveniles were obtained with coarse-mesh (approximate aperture = 1 mm) dip nets. The 323 captured fish ranged in size from 29 to 540 mm FL with most individuals in the 120–280-mm-FL range, reflecting our increased effort to capture juvenile fish. Of the 126 individuals examined for stomach contents, 32 had empty stomachs. Of the 94 with gut contents, 45 were small (≤ 250 mm FL) and 49 were large (> 250 mm FL).

Fork lengths were recorded to the nearest millimeter in 1996. In 1997, both weight and fork length were recorded. For data analysis, bull trout were grouped into small (≤ 250 mm FL) and large (> 250 mm FL) size-classes corresponding to their spatial segregation in the lake. Small fish were caught from beneath two cut banks close to the lake outflow and were observed mainly near shore in shallow (< 1 m deep) water, whereas large fish were caught from deep (> 1 m) water and were rarely seen in shallow water. Sampling times were combined by month.

Diet analysis.—To analyze diet, entire stomachs were removed and preserved in dilute formaldehyde in 1977. In 1996 and 1997, we anesthetized fish with MS-222 (tricaine methanesulfonate) and used a flushing technique similar to that employed by Meehan and Miller (1978) to retrieve the stomach contents. Fish were held in a recovery tank until fully recovered from anesthesia and then released back into the lake. Stomach contents were transferred to labeled plastic bags and fixed with 4% sugared formalin for transport back to the laboratory where samples were transferred to glass jars and 70% ethanol for storage until analysis. We used a dissecting microscope to sort and count prey items. The majority of sampled stomachs yielded intact prey items that were easily identified and counted. For broken up or partially digested food items, we used head capsules of chironomids and *Gammarus* or carapaces of *Daphnia* to identify and count prey items.

We used measures of frequency of occurrence, mean contribution (volume %) to the stomach con-

tents, and prey-specific volume to describe diet. Frequency of occurrence indicates the percentage of fish that had eaten the prey. The mean contribution to the stomach contents expresses the average degree of fullness of each prey taxon as a percentage of the average degree of total fullness (based on points estimates, see below) in the sample (Wallace 1981). Prey-specific volume is the volumetric percentage a prey taxon comprises of all taxa in only those predators in which the prey occurs (Amundsen et al. 1996). Limitations of these methods have been discussed by Hyslop (1980), Wallace (1981), and Amundsen et al. (1996).

Volume was subjectively estimated by a “points” method (Donald and Alger 1993). The stomach contents of each fish were assigned a total of 10 points. Then, each of the major food groups in a stomach was assigned from 1 to 10 points, depending on its contribution to the total volume of food, regardless of stomach size or total content volume. Empty stomachs were not included in the calculations. The points for each food category in a sample of N fish were then summed and expressed as a percentage of the total points ($N \times 10$) for the sample. In 1996, we measured the volume of intact invertebrates by water displacement in a graduated cylinder to compare displacement mean volume with estimates of the points method. We placed as many individuals as possible in the cylinder and calculated the volume displaced per individual. Mean prey volumes estimated with the points method compared well with volumes from displacement measurements (Table 1), indicating that prey volumes estimated via the points method yielded reliable volume estimates. Further, because data were analyzed only with the points method in 1977, we could compare it with our current data.

Prey-specific volume (defined above; Amundsen et al. 1996) was calculated from points volumes as follows:

$$P_i = \frac{\sum S_i}{\sum S_{ii}} \times 100; \quad (1)$$

P_i = prey-specific volume of prey i ;

S_i = stomach content (volume %) comprised of prey i in individual fish; and

S_{ii} = total stomach content in only those predators with prey i in their stomach.

Prey-specific volume was plotted versus frequency of occurrence to compare the among-year

TABLE 1.—Comparison of bull trout diet mean volume (%) obtained from displacement volume calculations and the points method. Blank cells indicate not enough items occurred in stomachs to obtain accurate volume measurements; a plus sign (+) in the points column indicates prey were present, but were an insignificant contribution to total stomach volume.

Prey species	Mean volume (%) by	
	Displacement	Points
<i>Daphnia pulex</i> var.	45.1	49.6
<i>Gammarus lacustris</i> (adult and immature)	33.4	25.2
Chironomidae (pupae)	19.7	20.8
<i>Pisidium</i> spp.		0.8
Conifer needles	1.8	2.0
Trichoptera		+
Plecoptera		+
Corixidae		0.8
Adult diptera		0.8

and seasonal among-size-class feeding strategy of the bull trout population.

We used the graphical method of Amundsen et al. (1996) to present our diet data because it offers advantages over traditional tabular methods. This method allows prey importance, feeding strategy, and the inter- and intra-individual components of diet niche width to be easily interpreted (see Amundsen et al. 1996 for a detailed description of the method). Briefly, prey importance and predator feeding strategy information are given by the distribution of points along the diagonals and axes of the plot (Figure 2). A measure of prey importance is provided by the percent abundance, increasing along the diagonal from the lower left to the upper right corner. Dominant prey will be clustered in the upper right, whereas rare and unimportant prey are represented in the lower left corner. The feeding strategy in terms of specialization or generalization is represented on the vertical axis (Figure 2). Prey points in the upper part of the graph indicate predators with specialized feeding. If prey points are positioned in the lower part, generalized feeding is inferred. Prey points in the upper left corner indicate specialization of individual predators, whereas points in the upper right represent specialization of the predator population as a whole and indicate a narrow niche width. A broad niche width for the population is indicated by the location of prey points along or below the diagonal from the upper left to the lower right and a lack of points in the upper right of the plot.

Prey items clustered in the upper left or the low-

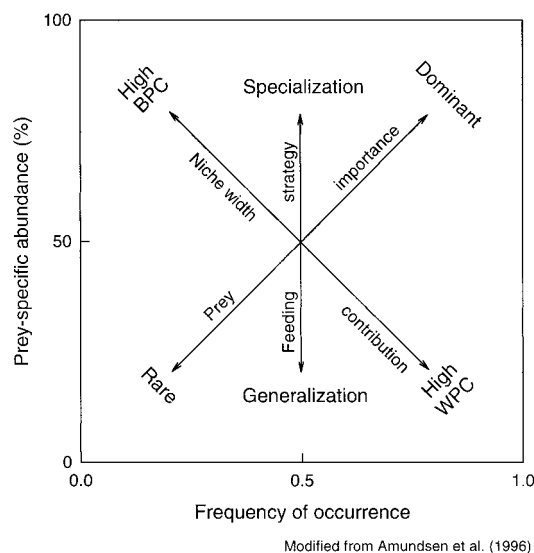


FIGURE 2.—A feeding strategy plot (modified from Amundsen et al. 1996; see text for details); BPC = between-phenotype components, WPC = within-phenotype components.

er right corner represent prey types that make the same overall contributions to the population diet, but are indicative of different feeding strategies of individual predators. Prey with high specific abundance and low occurrence will have been consumed by few individuals (specialization), whereas prey with a low specific abundance and a high occurrence will have been eaten occasionally by most individuals. Thus the distribution of prey points along this diagonal are indicative of the contributions of between-phenotype components (BPC) and within-phenotype components (WPC) to the diet niche width (Figure 2). This graphical method allows the rapid interpretation of predator feeding strategies in terms of specialization and generalization, both at the individual and population level. As well, the contributions of between- and within-phenotype components to niche width can be inferred.

Zooplankton and benthos sampling.—Zooplankton were sampled with a 30-cm-diameter, 64- μ m-mesh, Wisconsin-style plankton net. Five replicate hauls from 9 m were taken on August 9, 1996, and on July 1, 13, and 24, August 10 and 22, and September 23, 1997, and preserved with 4% sugared formalin. *Daphnia* density was estimated in 1997 for the July 13, August 10, and September 23 samples by bringing the preserved volume to 500 mL, thoroughly mixing the sample and withdrawing three 10-mL subsamples. All *Daphnia*

were counted under a Wild M5 dissecting microscope, and density was calculated as individuals per liter.

Gammarus and other benthic invertebrates were sampled from the benthos on August 9, 1996, and on July 13, August 11, and September 23, 1997, by scraping the substrate with a dip net (mesh aperture = 500 μm) along the ice-scoured shelf at a water depth of approximately 1 m. This area was chosen because bull trout were repeatedly observed feeding there (Wilhelm 1998). The dip net was scraped across 1 m² of shelf bottom to disturb the top layer of sediment and organisms. Organisms were then collected from the water column with the dip net. Contents of the dip net were emptied into a sieve, and *Gammarus* were separated from the sediment and debris by trapping them in the surface tension of water (Wilhelm and Hiebert 1996). Other invertebrates were counted and released or preserved. We calculated relative densities of *Gammarus* and "other" (all remaining invertebrates) for the 1997 sampling dates.

Dietary overlap.—Dietary overlap among fish size-classes was calculated using Schoener's (1970) similarity index (a):

$$a = 1 - 0.5(\sum |P_{xi} - P_{yi}|), \quad (2)$$

where P_{xi} and P_{yi} are the proportions, by points, of food category i in the diets of size-classes x and y . Values for a range from 0, representing no overlap, to 1, for complete overlap. Overlap values greater than 0.60 are generally considered to indicate significant overlap in the diets (prey items) of size-classes x and y (Wallace 1981; Brodeur and Pearcy 1990).

Prey size selection.—Lengths of *Daphnia* and *Gammarus* in the stomach contents from 1996 and 1997 samples were measured and compared with size distributions present in the lake to test for size-selective predation by bull trout. *Daphnia* size was measured from the top of the head to the inflection of the tailspine (see Dodson 1981) with the aid of an ocular micrometer. *Daphnia* were measured from all fish stomachs in which they occurred. All *Daphnia* or a minimum of 50 were counted from stomachs containing 1,000 or fewer individuals, whereas a minimum of 100 *Daphnia* were measured when more than 1,000 individuals were present. To estimate the *Daphnia* size distribution in the lake, lengths of the first 200–240 *Daphnia* encountered from zooplankton samples (depending on *Daphnia* density in the sample) were measured.

We also measured 30 of the largest *Diacyclops bicuspidatus thomasi* copepods from the August 22, 1997, sample to examine maximum sizes of copepods in relation to *Daphnia* ingested by the bull trout. We were interested to determine if copepods reached a size vulnerable to bull trout predation because we only found one copepod in one bull trout stomach.

Gammarus from benthic samples were transported live to our field camp for measurement under a dissecting microscope. Body length of all individuals was measured from the tip of the rostrum to the tip of the telson after straightening the body with fine forceps. The body size of *Gammarus* from fish stomachs was estimated from head capsule lengths (see Wilhelm and Lasenby 1998) based on a regression established from fresh monthly samples collected in the summers of 1995 through 1997. All *Gammarus* occurring in fish stomachs were measured. Young-of-the-year (age-0) *Gammarus* from fish stomachs were not included in the analyses because it was impossible to determine whether young of year were consumed by the fish or had been released from ingested ovigerous females (see Wilhelm 1996). The 1996 stomach samples were taken at the time of peak young-of-year release (F. Wilhelm, unpublished data). Lack of young of year in 1997 stomach samples suggested that their presence in stomachs during 1996 likely resulted from the ingestion of ovigerous females.

We used nonparametric Kolmogorov–Smirnov two-sample tests (Sokal and Rohlf 1981) to successively test the similarity of *Daphnia* and *Gammarus* size-frequency distributions in the lake versus in small and large fish. Comparisons between sampling dates were also conducted. The level of significance was Bonferroni-corrected ($P = 0.003$) to maintain the overall significance level of $\alpha = 0.05$.

Seasonal food volume.—To examine patterns in the seasonal volume of food ingested by each fish size-class, we calculated the average total food volume present in small and large fish for each month. Total volume (mL) in individual fish was determined from the number of prey items present and their displacement volumes (Table 1). Volume for each fish size-class was obtained by averaging the stomach content volumes from individual fish over the sampling days in each month. Large fish with less than 1 mL of food were considered to have empty stomachs for this analysis and were not included. We used a one-way analysis of variance (ANOVA) for each fish size-class to test the

TABLE 2.—Mean percentage points (i.e., relative volume) of the various prey taxa found in nonempty stomachs of small (≤ 250 mm FL) and large (> 250 mm FL) bull trout from Harrison Lake, Alberta, by month. A plus sign (+) indicates the prey item was present in the stomach but contributed insignificantly to the overall stomach content volume compared with other prey items. Blank cells indicate the food item was absent.

Prey taxa and life stage	≤ 250 mm FL			> 250 mm FL				
	Jul 1997	Aug 1997	Sep 1997	Jul 1997	Aug			Sep 1997
					1977	1996	1997	
Chironomidae								
Larvae	1.4	+	0.6	0.3			+	+
Pupae	43.4	+		82.4	0.8	20.8	0.2	
Adults	13.2	1.3		8.3			0.7	
<i>Daphnia</i>	8.3	60.9	65.5	6.0	58.5	49.6	72.3	44.0
<i>Gammarus</i>	21.2	28.4	25.1	1.2	24.0	25.2	12.3	44.8
Fish							4.5	
<i>Pisidium</i>	+	+	+	0.7	11.4	0.8	+	+
Oligochaeta					4.4			
Trichoptera	1.8	1.3	5.6	+	0.3	+	4.5	10.0
Ephemeroptera	0.9	6.8	+	0.3			0.7	
Corixidae		0.8		+		0.8		
Adult Diptera	0.3	+	0.6	+		0.8	0.7	0.4
Plecoptera			1.0	+	0.6	+	+	0.8
Conifer needles	0.3	0.5	+	0.8		2.0	0.5	+
Stones	+		+	+		+	+	+
Simuliidae	9.2			+				
Copepoda				+				
Coleoptera							3.6	
Lepidoptera			1.6					

hypothesis that food volumes were similar between sampling dates. Significant results were further examined with a Tukey posthoc test to determine which means differed. Data were log transformed to meet ANOVA assumptions of homogeneity of variance and normality. We plotted log-back-transformed means and 95% confidence intervals (Sokal and Rohlf 1981).

Results

Bull Trout Diet

Overall, the Harrison Lake bull trout population displayed a narrow feeding niche throughout the open-water season. After ice-out, the population mainly fed on chironomid pupae, switching to *Daphnia pulex* and *Gammarus lacustris* in mid-August and September (Table 2). Only two cases of piscivory were observed, one successful, and one resulting in the death of both the predator and prey fish (Wilhelm 1998). Only one large copepod was found in one bull trout, suggesting copepods (mean length of *Diacyclops bicuspidatus thomasi*, $0.49 \text{ mm} \pm 0.04 \text{ SD}$, $N = 30$) were either too small to be retained by bull trout gill rakers or were not selected. Sixty-four percent and 53% of all fish stomachs in 1996 and 1997, respectively, contained *Gammarus*, conifer needles, *Pisidium* spp.,

or stones, indicating the bull trout were benthivorous when feeding on *Gammarus*.

Between-Year Diet Comparison of Large Bull Trout

The between-year diet of large fish in August was remarkably similar and included *Daphnia* and *Gammarus* as the major prey items (Figures 3, 4d), indicated by their high placement along the prey importance diagonal. In August 1996, chironomid pupae were present in the diet in a large proportion of the population but were less important than either *Daphnia* and *Gammarus* (Figure 3b). The chironomid hatch was delayed in 1996 because a high snowpack slowed the thaw and prevented early warming of the water. In 1997, chironomids hatched during a short time interval during July, explaining their absence from the fish diet in August and September (Figure 4).

Small bull trout.—In July 1997, after ice-out, small bull trout fed on a wide variety of invertebrates, but their diet was dominated by chironomid pupae (Figure 4a). A small proportion also fed on *Gammarus* (Figure 4a). In August 1997, small bull trout switched prey and fed primarily on *Daphnia* and *Gammarus* (Figure 4c). Other prey taxa such as Ephemeroptera, Trichoptera, corixids, and chi-

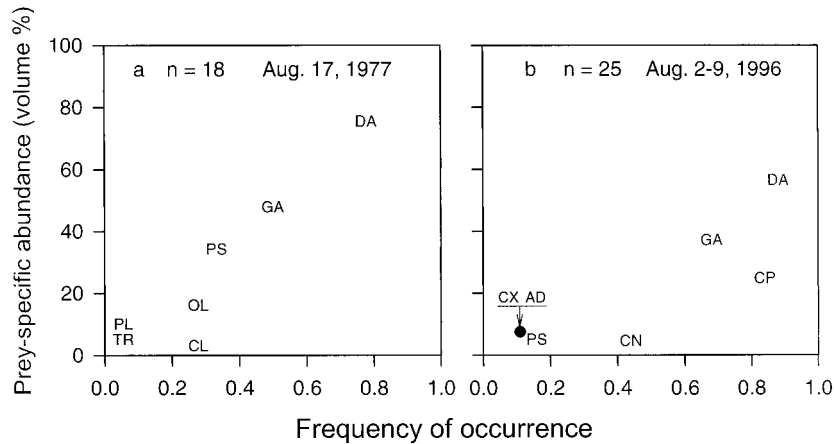


FIGURE 3.—Feeding strategy plots for large (>250 mm) bull trout from Harrison Lake in August for (a) 1977 and (b) 1996; n is the number of fish examined with food in their stomachs. Prey items identified in Figures 3 and 4: CL = chironomid larvae, CP = chironomid pupae, CA = chironomid adults, DA = *Daphnia*, GA = *Gammarus*, SI = Simuliidae larvae, TR = Trichoptera nymphs, EP = Ephemeroptera nymphs, PL = Plecoptera nymphs, PS = *Pisidium* spp., CX = Corixidae, AD = adult diptera, LE = Lepidoptera adults, CO = Coleoptera, FI = fish, OL = oligochaeta, CN = conifer needles.

ronomids were also consumed, but they contributed little to the diet of the small fish. In September 1997, small bull trout continued to specialize on *Daphnia* and *Gammarus* (Figure 4e). As in August, other prey taxa were consumed but they did not contribute significantly to the overall diet (Figure 4e).

Large bull trout.—In July, large bull trout fed almost exclusively on chironomid pupae (Figure 4b). Although chironomid adults were present in some bull trout stomachs, these individuals still had their pupal case attached to their abdomen. Only one large bull trout fed exclusively on *Daphnia* at the end of July (Figure 4b). Large bull trout switched prey species in August, with the majority of the population feeding on *Daphnia*. *Gammarus* were the second most important prey (Figure 4d) but were less important in the diet of the large fish compared with small fish (Figure 4c). Some individual fish specialized on Coleoptera and, in one case, on small (approximately 40 mm FL) bull trout (Figure 4d). In September 1997, large bull trout continued to specialize on *Daphnia* and *Gammarus* (Figure 4f). At this time, *Gammarus* and *Daphnia* codominated the diet of large trout (Figure 4f). Several large bull trout specialized on Trichoptera larvae, which had large (approximately 35–40 mm long \times 6–8 mm in diameter) cases built of dark stones making them highly visible on the silty lake bottom and susceptible to predation. The reliance among large trout on three prey species coupled with the

decline in food volume in the stomachs over the open-water season (see below) suggests a high potential for intra-size-class competition.

Prey Availability

Prey availability changed during the open-water season. Emerging chironomids were abundant after ice-out until the end of July. The large proportion of chironomid pupae in the diet of all bull trout in July followed by their near absence from the diet in August (Figure 4) mirrors our personal observations of the abundance of emerging adults and is probably a reasonable, if coarse, index of their availability in the lake.

Although *Gammarus* abundance increased from July to September, this increase was due to the release of young by mature females in August (Figure 5). These young of year were too small to be susceptible to bull trout predation; therefore, the abundance of *Gammarus* available to bull trout declined from approximately 129 to 50 individuals/m² (Figure 5). Adult *Gammarus* increased in size with age, making them increasingly susceptible to bull trout predation as the season progressed (see below). Other benthic invertebrates, such as Trichoptera and Ephemeroptera nymphs, corixids, Coleoptera, and fingernail clams collected with *Gammarus* in benthic sweeps were not abundant, and together averaged between 18 and 20 individuals/m² between July and September (Figure 5).

Daphnia density peaked in August at 9.9 indi-

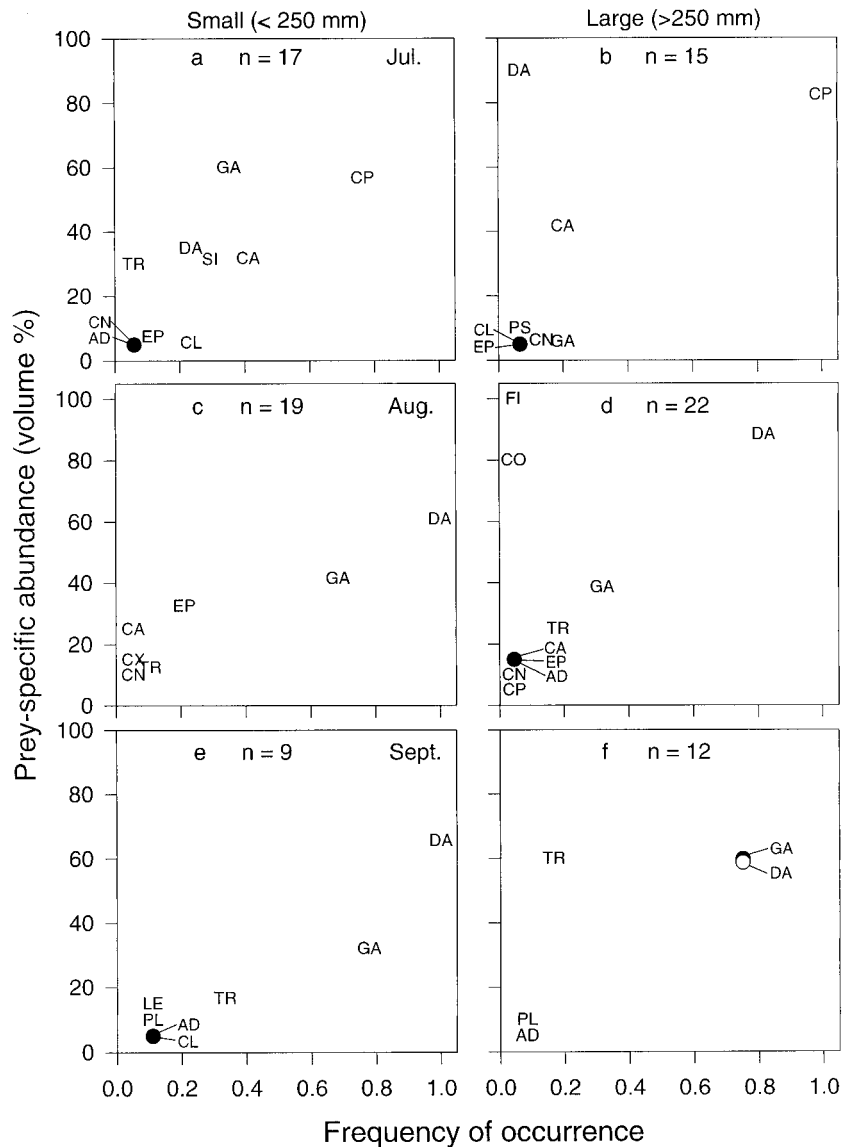


FIGURE 4.—Seasonal feeding strategy plots from (a, b) July, (c, d) August, and (e, f) September 1997 for small (≤ 250 mm FL; a, c, e) and large (>250 mm FL; b, d, f) bull trout from Harrison Lake; n = number of fish with food in their stomachs examined in each size-class for each month. Prey abbreviations are defined in Figure 3.

viduals/L, increasing from 2.7 individuals/L in July and decreasing to 3.5 individuals/L at the end of September (Figure 5). Most gravid females were observed after ephippial egg production in early August. Ephippia were produced by females ranging between 1.5 and 2 mm in size.

Dietary Overlap

Diets of both bull trout size-classes overlapped considerably each month (July $a = 0.60$, August

$a = 0.76$, September $a = 0.76$). Both size-classes fed largely on chironomid pupae in July and on *Daphnia* and *Gammarus* in August and September. However, each bull trout size-class concentrated on a different size of *Daphnia* (see below). The predominance of one or two prey items in the diet of the bull trout population (Figures 3, 4) also indicates a strong overlap among individuals in each fish size-class.

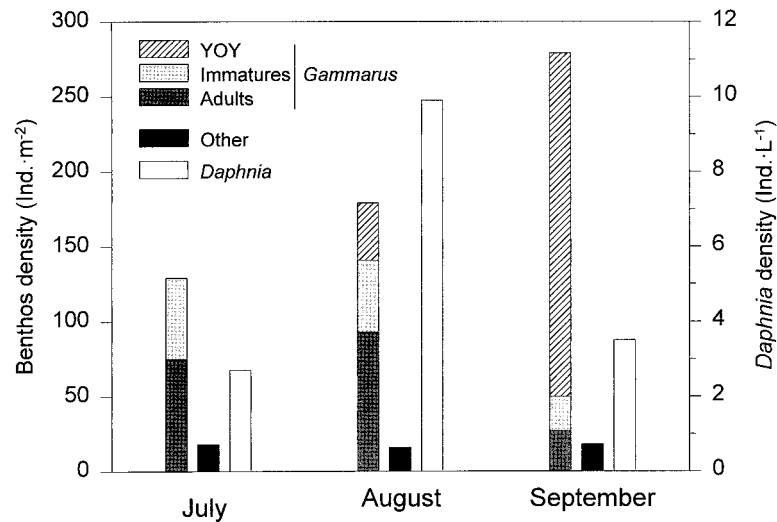


FIGURE 5.—Seasonal abundance of prey organisms in Harrison Lake in 1997. *Gammarus* (YOY = young of year) and other benthic invertebrate densities are approximate individuals per square meter (see methods) and *Daphnia* densities are given as individuals per liter.

Prey Size Selection

Bull trout selectively preyed on large *Daphnia*. The mean sizes of *Daphnia* from bull trout stomachs were significantly ($P < 0.003$) larger than those in the lake for all months (Figures 6a, 7). Although large *Daphnia* were present in the water column in 1997 shortly after ice-out (Figure 7a), few were consumed by bull trout until early August (Figures 4b, 4d, 7a, 7b). Widespread ephippial egg production was noted during the first week of August, before *Daphnia* occurred frequently in many bull trout stomachs. The average size of *Daphnia* collected from the lake increased ($P < 0.001$) between July and September from 1.2 mm to 1.6 mm (Figure 7c, 7d). This increase in mean size could be attributed to the late-season decline in production of young (Figure 5).

Large bull trout preyed on the largest *Daphnia* in 1996 and 1997, consistently focusing on the 2.5-mm size-class (Figures 6a, 7). The size distributions of consumed *Daphnia* in August were similar between years. Between-month comparisons in 1997 showed that large bull trout selected similar-sized *Daphnia* in July and August (mean size = 2.5 mm). However, in September, significantly ($P = 0.001$) smaller (mean size = 2.3 mm) *Daphnia* were selected (Figure 7).

Small bull trout preyed on intermediate-sized *Daphnia* (mean length, 1.9–2.0 mm) during the open-water season in 1997. The mean size of consumed *Daphnia* was larger ($P < 0.001$) than the

mean size in the lake (Figure 7b–d). Between-month comparisons showed that the mean size of *Daphnia* selected by small bull trout decreased significantly ($P < 0.001$) between July and August but remained constant ($P = 1.00$) between August and September.

Bull trout selectively preyed on large *Gammarus* (Figure 6b, 8). In 1996, the mean size of *Gammarus* preyed on by large bull trout was larger ($P < 0.001$) than the mean size in the lake (Figure 6b). In July 1997, small and large bull trout selected similar-sized ($P = 0.42$) *Gammarus* (mean sizes 8.7 and 8.8 mm, respectively) that were larger ($P < 0.001$) than the mean size (7.5 mm) present in the lake (Figure 8a). In August 1997, small and large bull trout selected similar-sized ($P = 0.113$) *Gammarus* (mean sizes 9.7 and 9.1 mm, respectively). Although these were larger than the mean size (7.5 mm) in the lake, we could only conclude that *Gammarus* in the small fish were larger ($P = 0.001$) than in the lake given our Bonferroni-corrected significance level. In September, small and large bull trout preyed on similar-sized ($P = 0.081$) *Gammarus* (mean sizes 9.9 and 9.4 mm respectively) that were significantly smaller ($P < 0.001$) than the mean size (10.6 mm) in the lake (Figure 8c). Bull trout predation probably explains the absence of large *Gammarus* in Harrison Lake compared with nearby fishless Snowflake Lake, where adult *Gammarus* reach sizes of 15–20 mm and densities of 400 individuals/m² (Parker et al. 1996).

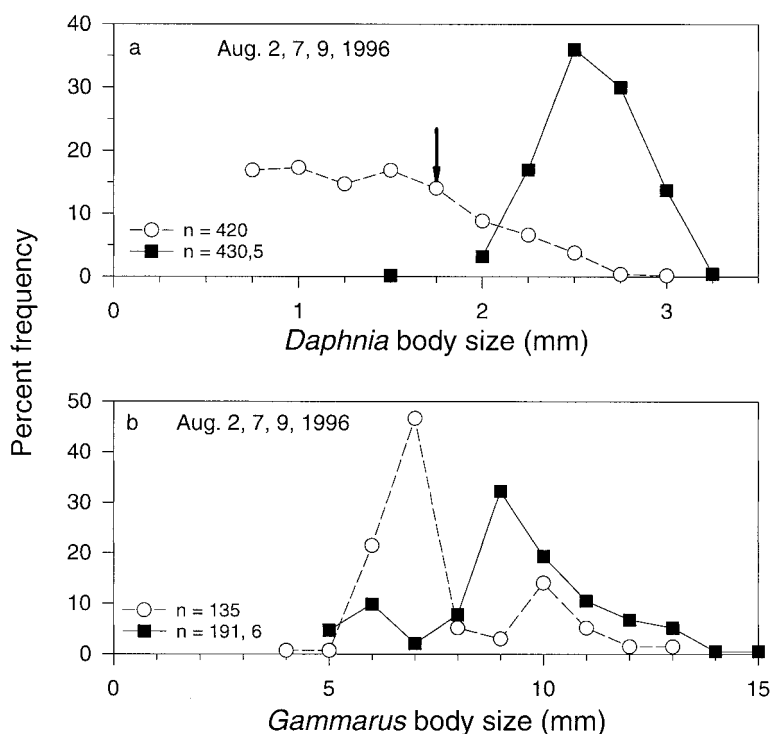


FIGURE 6.—Size distributions for prey in stomachs (■) of large bull trout (>250 mm) and for invertebrates in the lake (○) showing size-selective predation for (a) *Daphnia* and (b) *Gammarus lacustris* in 1996; n = number of prey measured (first number) or number of stomachs containing that prey (second number). Arrow indicates the smallest *Daphnia* size-class with eggs.

Seasonal Food Volume

Average total volume of food in small fish increased during the season (ANOVA, $F = 7.18$, $df = 2, 42$; $P = 0.002$). Food volume was constant ($P = 0.904$) in July and August at 1.1 and 1.3 mL, respectively but increased ($P = 0.006$) to 3.0 mL in September. The higher food volume in small bull trout during September resulted from a larger volume of *Daphnia* (Figure 9). In large fish, food volume declined significantly from July to August and September (ANOVA, $F = 5.75$, $df = 2, 34$; $P = 0.007$) due to the loss of chironomid pupae from the diet (Figure 9). Food volume in July (7.0 mL) was greater ($P = 0.022$) than in August (3.2 mL) and September (2.6 mL), when food volume was constant ($P = 0.748$; Figure 9).

Length–Weight Relationship

The 1997 length–weight relationship for bull trout was best described by the allometric function

$$\text{weight (g)} = 4.8 \cdot 10^{-6} \cdot \text{FL (mm)}^{3.15}, \quad (3)$$

for which $r^2 = 0.995$ and $N = 142$ (Figure 10). The data were normally distributed and residual variance was homogeneous. However, a large proportion of adults greater than 425 mm FL were in poor condition (Figure 10). These emaciated individuals had disproportionately large mouths and heads and slender bodies. These individuals were predicted to be 14–41% underweight based on the above length–weight relationship.

Discussion

Factors Allowing Survival of Bull Trout and Prey Species

Size-selective predation by bull trout in Harrison Lake is similar to that reported for other salmonid and zooplanktivorous species (Brooks and Dodson 1965; Galbraith 1967; Wellborn 1994). However, bull trout did not eliminate *Daphnia* as stocked, nonnative salmonids did in nearby Snowflake and Pipit lakes (Anderson and Donald 1978; McNaught et al. 1999) or in Sporely Lake, Michigan (Galbraith 1967). The size distribution of *Daphnia* in Harrison Lake has remained constant

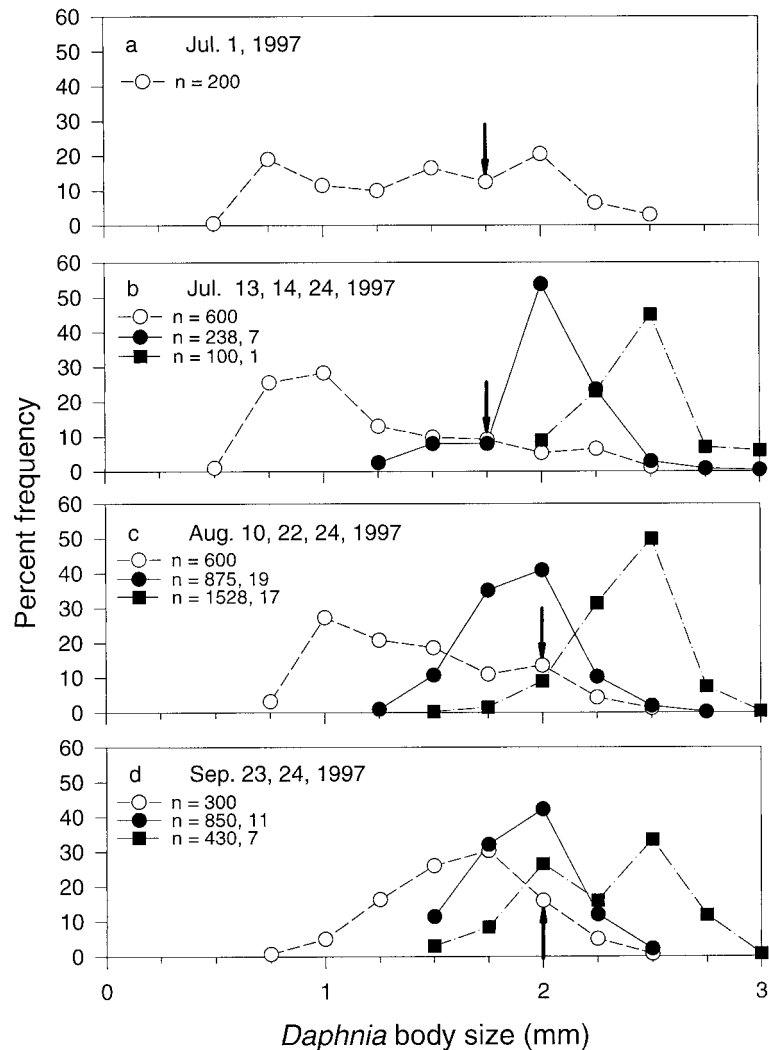


FIGURE 7.—A comparison of seasonal size distributions of *Daphnia* in bull trout stomachs (●, fish ≤ 250 mm, and ■, fish > 250 mm) with those in Harrison Lake (○) in 1997 showing size-selective predation on large *Daphnia* for (a) early July, (b) middle–late July, (c) mid-August, and (d) late September; n = number of *Daphnia* measured (first number), or number of stomachs containing *Daphnia* (second number). Arrows indicate smallest *Daphnia* size-class with eggs. Ephyppia were only observed in the August 10 sample. No predation on *Daphnia* was observed on July 1.

among years. Although individual *Daphnia* attain a large size (3.0–3.25 mm), they are smaller than the 4-mm *Daphnia* present in nearby fishless Pipit Lake (Wilhelm et al. 1998). Bull trout predation might have resulted in a smaller maximum adult size in the *Daphnia* population as predicted from life history theory (Roff 1992; Stearns 1992).

The intense feeding by small and large bull trout on *Daphnia* in late August and September appears to be the main reason for the reduction in abundance of the largest *Daphnia*. Generally, *Daphnia*

populations in most north temperate lakes decline after the late-summer chlorophyll-*a* maximum and production of ephyppia (Hall 1964). However, this is not the case in alpine lakes, where adult *Daphnia* overwinter (Wilhelm et al. 1998; McNaught et al. 1999). The overwinter survival of *Daphnia* adults is probably a function of a low metabolic rate resulting from the cold summer lake temperatures. The low predation on *Daphnia*, coupled with ephyppia production early in the open-water season while bull trout feed on chironomid pupae, pro-

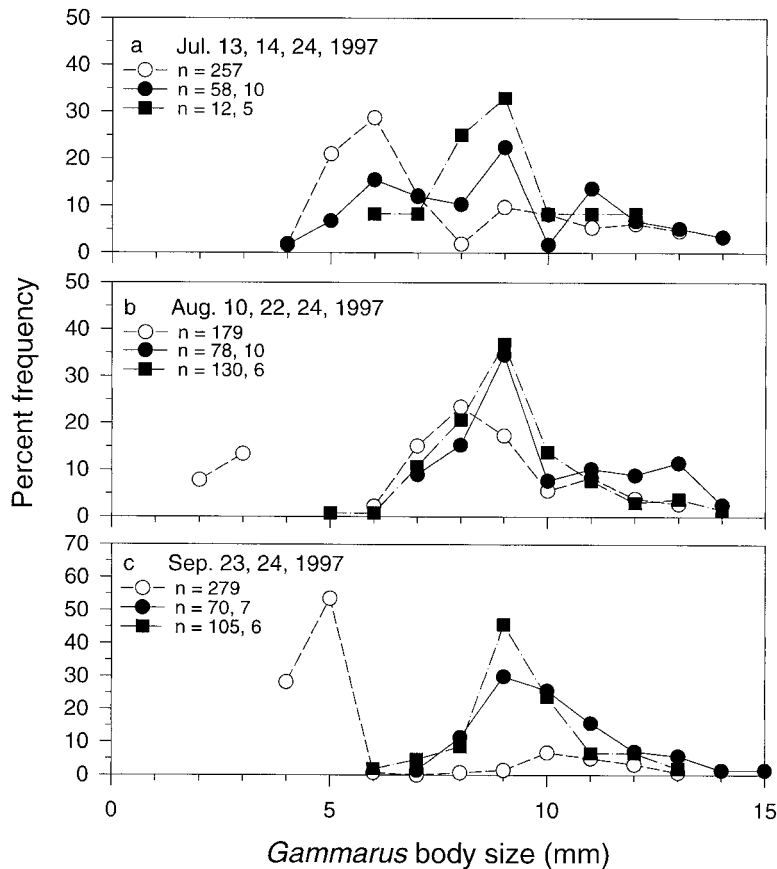


FIGURE 8.—A comparison of seasonal size distributions of *Gammarus* in bull trout stomachs (●, fish \leq 250 mm, and ■, fish $>$ 250 mm) with those in Harrison Lake (○) in 1997; n = number of *Gammarus* measured (first number) or number of stomachs containing *Gammarus* (second number). Young of year were not included in analysis but are shown for completeness.

notes the year-to-year persistence of the *Daphnia* population. The intense predation on *Daphnia* late in the open-water season therefore probably has little influence on population dynamics the following year.

The spatial segregation of bull trout by size in Harrison Lake, with large fish in the pelagic zone and small fish in the nearshore littoral zone (Wilhelm 1998), also benefits the *Daphnia* population. Large bull trout either cannot retain *Daphnia* less than 2 mm or elect not to consume them (Figures 6a, 7c-f). *Daphnia* commence reproduction and ephippial production between 1.5 and 2.0 mm. Therefore, many *Daphnia* can reproduce before they become vulnerable to size-selective fish predation in the pelagic zone. Although small *Daphnia* were consumed by small fish, the latter were excluded from the pelagic zone due to the risk of cannibalism by large fish.

The low predation on *Gammarus* in early summer also coincided with their critical reproductive period. Oviparous females were present from ice-out until approximately the first week in August, when they released their young. Because bull trout predation was focused on chironomid pupae and adults during this time, many female *Gammarus* successfully released their young. The timing of the switch by bull trout from chironomids to amphipods likely varies between years and is probably determined by the rate of warming after ice-out, because this would determine the duration of chironomid emergence (see Figure 3b). The effect of a change in timing of the prey switch on the *Gammarus* population is unknown.

The presence of chironomid pupae in Harrison Lake and their selection by bull trout in July is a key feature allowing *Daphnia* and *Gammarus* to survive in Harrison Lake. Chironomid pupae in

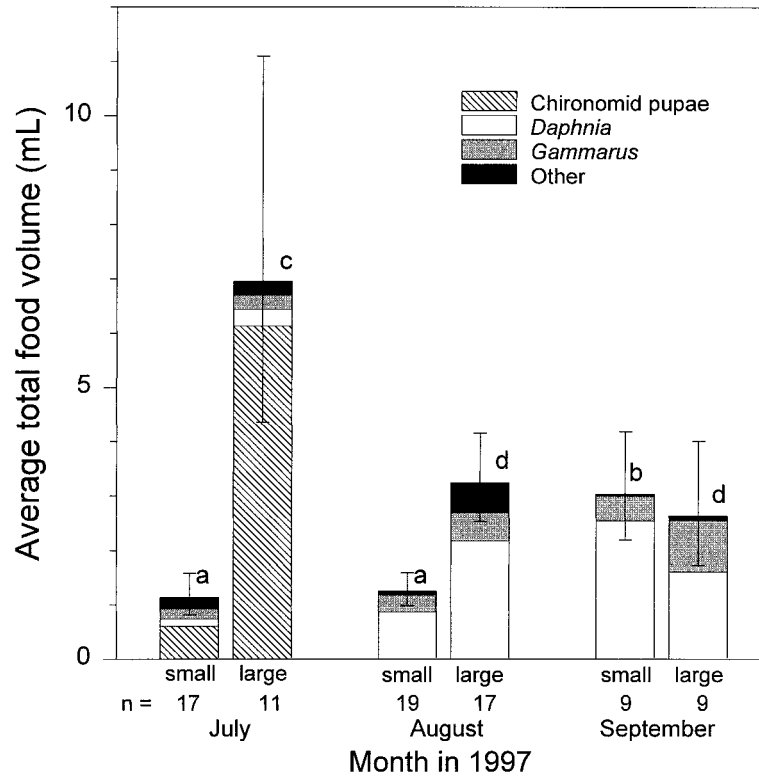


FIGURE 9.—Average total food volume in the stomach of small (≤ 250 mm FL) and large (> 250 mm FL) bull trout for each sampling month. Volumes are log back-transformed means, and error bars represent 95% confidence intervals; n = the number of fish for each sample date and size-group. Within a size-group, bars topped with the same letter indicate similar mean volumes; size-classes were analyzed separately.

Harrison Lake are either entirely black or opaque white and approximately 10–15 mm in length, making them highly visible and easy targets for the bull trout. Their high abundance in bull trout stomachs suggests they are energetically rewarding. In comparison, the smaller, unpigmented *Daphnia* are present at low densities in early July, which may make them less appealing and beneficial as prey than the larger chironomid pupae. Although *Gammarus* are present in the lake year round, they must be selected from bottom depressions filled with organic debris (Wilhelm 1998). This makes them more difficult to capture than large chironomid pupae.

Dietary Overlap

The diet similarity between large and small bull trout in Harrison Lake was striking because, in general, different size-classes of *Salvelinus* spp. in the same lake consume different prey (Rawson 1961; Martin 1966; Johnson 1980; Power 1980; Gerstmeier 1985; Fraley and Shepard 1989). How-

ever, our prey-size analyses indicated that the overlap may be less important than suggested by the similarity index because each bull trout size-class concentrated on a different *Daphnia* size. This finding suggests that significant diet overlap values from indices, such as the Schoener's similarity index, generated by the reliance of predators on one or two prey species, should be further examined to determine if apparent overlaps can be separated based on prey size.

The predominance of a few prey species in the diet of each bull trout size-class also suggests a high potential for competition within size-classes. The lack of widespread specialized feeding beyond the common food items might have been the result of the absence of other abundant prey types. However, the specialization of several large bull trout in August (Figure 4d) indicates that, like other salmonids, bull trout may concentrate on specific prey species (Bryan and Larkin 1972). This selectivity may be the result of a local concentration of prey items that a particular fish may have dis-

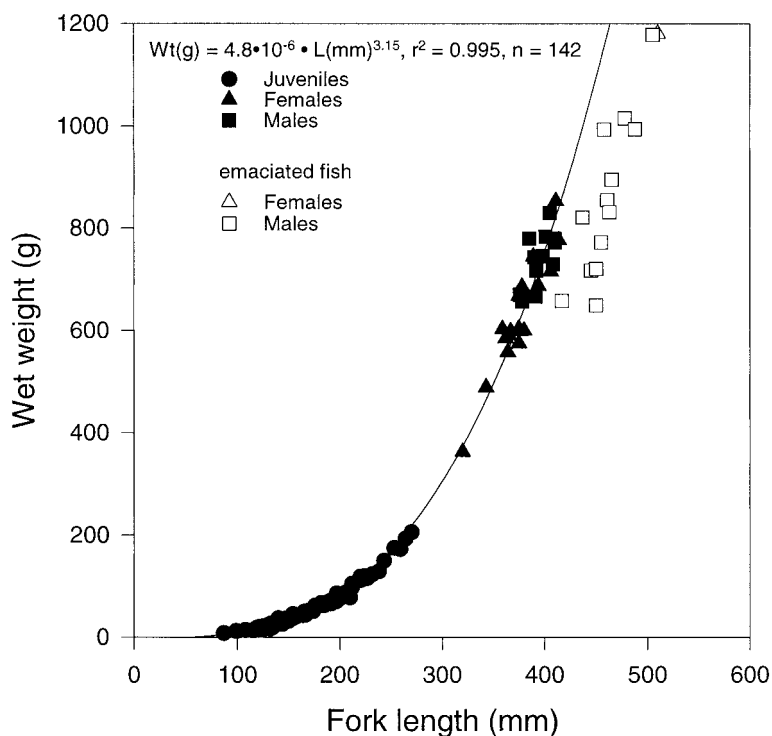


FIGURE 10.—Bull trout length–weight regression for individuals captured in Harrison Lake in 1997; n = the number of fish used in the regression. Emaciated fish were not included in the regression. Sex classification of the emaciated fish is unreliable.

covered by chance. Bull trout diet studies from lower-elevation lakes suggest that they are generalists and prey opportunistically on abundant prey items (Leathe and Graham 1982; Donald and Alger 1993; Mushens and Post 1997). Therefore, the lack of other abundant prey items in Harrison Lake combined with the decline in the amount of food in the stomachs of large bull trout over the course of the open-water season (Figures 4–9) suggests that large fish were food limited and supports the argument of high intra-size-class competition for the food that is available. Furthermore, the upper size limit reached by bull trout in this lake, compared to lakes where prey fish are available also suggests that the population is food limited (see below).

Seasonal Food Volume

In contrast to small fish, food intake in large bull trout declined in August and September in 1997 compared with July. We do not have caloric values for the consumed food, but considering that the prey species and volumes were nearly identical to those of the small fish in September, we suggest

that large bull trout may be food limited. This decrease in food quantity may explain the presence of many large emaciated individuals. Large bull trout probably obtain adequate food during the chironomid hatch early in the summer, allowing them to grow or maintain weight. But they appear to be incapable of capturing the smaller prey that are available in late August and September. Similar feeding maxima occurring shortly after ice-out or early in the open-water season have been reported for salmonids in arctic and alpine environments (Johnson 1980; Dawidowicz and Gliwicz 1983; Hofer and Medgyesy 1997).

Cannibalism on small bull trout could alleviate the food limitation faced by large fish. However, the low rate of cannibalism that we observed from stomach analyses in Harrison Lake suggests it is either infrequent or occurs under ice in winter. Vulnerability to cannibalism may increase after freeze-up, when more than 1 m of ice would displace small fish from their shallow-water (<15 cm deep) lake refuges if they did not emigrate to the stream outflow. We do not know if large bull trout switch to cannibalism or even feed during the ice-

covered period, when water temperatures fall below 1.5°C throughout the water column. Winter diet data for lake trout *Salvelinus namaycush* suggest little under-ice feeding, with yearly minimum gut fullness occurring just before ice break-up (Martin 1954). A similar pattern may also occur in bull trout.

The poor condition of some large bull trout could also be caused by spawning the previous fall. Weight loss after spawning by adfluvial bull trout in Lower Kananaskis Lake, Alberta, ranges between 8% and 17% (Mushens and Post 1997), whereas Johnson (1980) reported a weight loss of up to 26% after spawning in populations of Arctic char *S. alpinus*. If we assume a similar weight loss due to spawning, it would account for only 6 of the 14 emaciated adults we captured. The remaining eight individuals, which were 30–40% underweight, may represent a postreproductive senescing portion of this unexploited population.

Bull Trout Size and Diet

Salmonids generally change diet as they grow, switching from planktivory to piscivory if forage fish are available (Rawson 1961; Martin 1966; Nilsson and Pejler 1973; Langeland 1978; Leathe and Graham 1982; Boag 1987). Thus, larger bull trout would be more expected in lakes with forage fish than in lakes without them, where bull trout subsisted on invertebrates. This relationship was the basis for Donald and Alger's (1993) model of increasing maximum trout size with increasing lake food web complexity. Bull trout generally reach 440 mm FL in Harrison Lake where forage fish are absent and the occurrence of cannibalism is presumed to be low. Similarly, in Pinto Lake, another bull trout-only lake, maximum size was approximately 500 mm FL (Carl et al. 1989). In contrast, bull trout exceed 600 mm FL in Flathead Lake, Montana, and Lower Kananaskis Lake, Alberta, where prey fish are present (Leathe and Graham 1982; Mushens and Post 1997; Stelfox 1997). Preliminary diet data from Lower Kananaskis Lake show that bull trout less than 450 mm FL fed mainly on large invertebrates, including the opossum shrimp *Mysis relicta* (Mushens and Post 1997). Therefore, the absence of forage fish suggests a "trophic bottleneck" as defined by Heath and Roff (1996) and indicates that a maximum size of 400–500 mm FL can be expected for bull trout restricted to an invertebrate diet.

Unlike nonnative salmonids, which frequently decimate the native invertebrate fauna in lakes where they are stocked (Gliwicz 1980; Pechlaner

1984; Parker and Schindler 1995; Parker et al. 1996; McNaught et al. 1999), native bull trout coexist with their invertebrate prey, including large crustacean species. We have shown that a self-sustaining bull trout population can exist in an alpine lake with three invertebrate prey species. That these three prey species are common in other high-elevation lakes bodes well for potentially establishing bull trout populations in other mountain lakes.

Acknowledgments

We thank T. Johnson, S. Clare, R. Vinebrooke, C. Wilson, and R. Whittington for assistance in the field. This research was carried out with permission of the Canadian Parks Service and under the University of Alberta Animal Care Protocol 607129. Funding for this research was provided by a Friends of Banff National Park Research Grant, an NSERC operating grant (89673) to D. W. Schindler, and the Biodiversity Grants Program (University of Alberta–Alberta Conservation Association). Author F.M.W. was supported by NSERC, Izaak Walton Killam Memorial, and University of Alberta Dissertation scholarships. Helpful comments on earlier drafts of the manuscript were provided by J. C. Holmes, D. Beauchamp, and an anonymous reviewer.

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