Modeling Seasonal Trophic Interactions of Adfluvial Bull Trout in Lake Billy Chinook, Oregon

Pelton Round Butte Hydroelectric Project

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ABSTRACT

We examined the trophic interactions of bull trout *Salvelinus confluentus* in Lake Billy Chinook, Oregon, using a bioenergetics model combined with data on annual growth, seasonal diet, distribution, and thermal experience to determine the seasonal and size-specific prey requirements of bull trout and the influence of bull trout predation on some of their major prey species in the reservoir. Per capita consumption estimates were expanded to “population-level” estimates of consumption, based on estimates of size structure and abundance of the bull trout population.

Bull trout became progressively more piscivorous with increasing size, and fish were the primary prey of predators ≥ 450 mm fork length (FL). Kokanee *Oncorhynchus nerka* and other salmonids (predominantly bull trout and rainbow trout *O. mykiss*) represented the largest fraction of fish prey in the diet, although cyprinids (mostly longnose dace *Rhinichthys cataractae*), cottids, and catostomids were also consumed. Most predation on kokanee occurred in autumn, and secondarily in winter–spring. Predation by bull trout ≤ 450 mm FL was greatest on smaller bull trout and rainbow trout in the reservoir during June and summer, whereas predation by bull trout ≥ 450 mm FL on salmonids other than kokanee was most prevalent during winter–spring. Bull trout of all sizes were capable of eating fusiform fishes up to 50% of their own total length.

Given the size structure observed in Lake Billy Chinook, for every 1,000 bull trout ≥ 200 mm FL, model simulations indicated that 971 kg of kokanee, 56 kg of bull trout, 29 kg of rainbow trout, 108 kg of mountain whitefish, 364 kg of unidentified salmonids (but not kokanee), 520 kg of other fishes, and 1,668 kg of benthic invertebrates were consumed in the reservoir annually. This translated into annual, size-specific numerical losses of 13,876 kokanee (9,362 age-0, 398 age-1, and 4,116 ages 2–3), 5,273 bull trout (4,446 age-0 and 827 age-1), 4,335 rainbow trout (3,872 age-0 and 462 age-1), 3,172 mountain whitefish (2,031 age-0, 453 age-1, and 688 ages 2–3), plus an estimated 10,224 unidentifiable salmonids (assuming that the size distribution reflected the sizes of identifiable salmonids) and 56,715 other fishes (predominantly longnose dace). Cannibalism removed 3–6% of the age-0 bull trout and 1–2% of the age-1 bull trout for every 1,000 predators ≥ 200 mm FL, based on the range of juvenile bull trout abundances generated from data in 1990, 1991, and 1993. Based on two methods for estimating age-specific kokanee abundance, predation removed 1% age-0, <1% age-1, and 4–9% of the age 2–3 kokanee per 1,000 age 3–7 bull trout. Because back-calculations of age-specific abundance from spawning ground surveys suggested that the abundance of bull trout ≥ 200 mm FL included at least 3,600–8,400 piscivores, the estimated population-level predation losses represented potentially large fractions of the bull trout (19–44% age-0 and 7–16% age-1) and kokanee (5–11% age-0, 1–2% age-1, 13–74% ages 2–3) populations. Thus, cannibalism and prey supply are potentially important factors limiting the abundance and production of bull trout in Lake Billy Chinook.

INTRODUCTION

Bull trout *Salvelinus confluentus* were recently listed as a threatened species under the Endangered Species Act. Among the reasons cited for this listing were habitat degradation and fragmentation, interactions with nonnative fishes, and overexploitation by sport fisheries. Fluvial populations are often most affected by habitat alteration, whereas adfluvial bull trout may be more affected by biotic interactions in lakes or reservoirs due to a generally higher incidence of nonnative species in lentic waters (Donald and Alger 1993). To determine which factors limit a specific population, stage-specific growth and survival can be quantified and compared to past performance by the same population when it was in healthy condition, or compared to healthier neighboring stocks which can provide a reference for expected growth or mortality rates. Lake Billy Chinook currently supports a relatively healthy population of adfluvial bull trout and thus could serve as a useful reference population, but recent fluctuations in spawner counts and coincident changes in the forage base have raised concerns about this population and its role in the structure and function of the reservoir food web.

Kokanee *Oncorhynchus nerka* and other salmoniformes are important prey for adfluvial bull trout populations during lake residence (Jeppson and Platts 1959; Bjornn 1961; Fraley and Shepard 1989). Major fluctuations in these prey populations can alter the diet composition, distribution, and growth of bull trout with consequent changes in adult fecundity or survival and juvenile recruitment. Kokanee are also an important sport fish in Lake Billy Chinook (Thiesfeld et al. 1999) and many other lakes and impoundments in western states (Paragamian 1995; Rieman and Maiolie 1995). Declines in kokanee, particularly mortality from bull trout predation, have been a serious concern in this system, but the magnitude and duration of this loss has not been quantified. By quantifying the temporal-, spatial-, and size-related processes involved in predation, managers can identify which segments of the bull trout population would be most affected by reductions in the kokanee forage base, and conversely, impose the greatest control over the population dynamics of kokanee. How vulnerability to predation changes along dimensions of time, space, and size of potential predators and prey determines whether these interactions will allow stable, desirable production levels of both bull trout and kokanee.

The objectives of this study were to describe and quantify the seasonal and size-specific food habits of bull trout in Lake Billy Chinook, relate diet and consumption rates to the seasonal availability of major prey in the reservoir, determine if food supply or cannibalism regulated growth or survival of any age class, and if so, identify when the critical interactions occurred and which sizes of predators and prey were involved.

STUDY SITE

Lake Billy Chinook was formed during 1964 when Round Butte Dam impounded the Deschutes River just below the confluence of the Metolius, Deschutes, and Crooked rivers. Passage of anadromous and fluvial fishes was terminated in 1968 (Thiesfeld et al. 1999). The reservoir is located on the east side of the Cascade Mountains in central Oregon, USA, at an elevation of 593 m. The reservoir is very productive, with annual mean concentrations of 62 *u*g/L total phosphorus, 145 *u*g/L total nitrogen, and 19 *u*g/L Chlorophyll-a; the water residence time in this 1,619-ha reservoir is only 0.2 years (Raymond et al. 1997). The canyons of the three river channels form steep, relatively narrow arms of the reservoir, with the Metolius Arm extending 21 km to the west, the Deschutes Arm 13 km south-southwest, and the Crooked Arm 10 km south of the dam (Figure 1). Most of the bull trout and kokanee production is generated from the Metolius River, which is primarily spring-fed and provides relatively stable flows and cold temperatures throughout the year (Buchanan and Gregory 1997). Transition zones form below the inlets of the three rivers; these zones are thermally unstratified, with temperatures very similar to the rivers. The transition zones extend for several 100 m into the reservoir before these cold water masses plunge to depths with water of similar temperature and density.

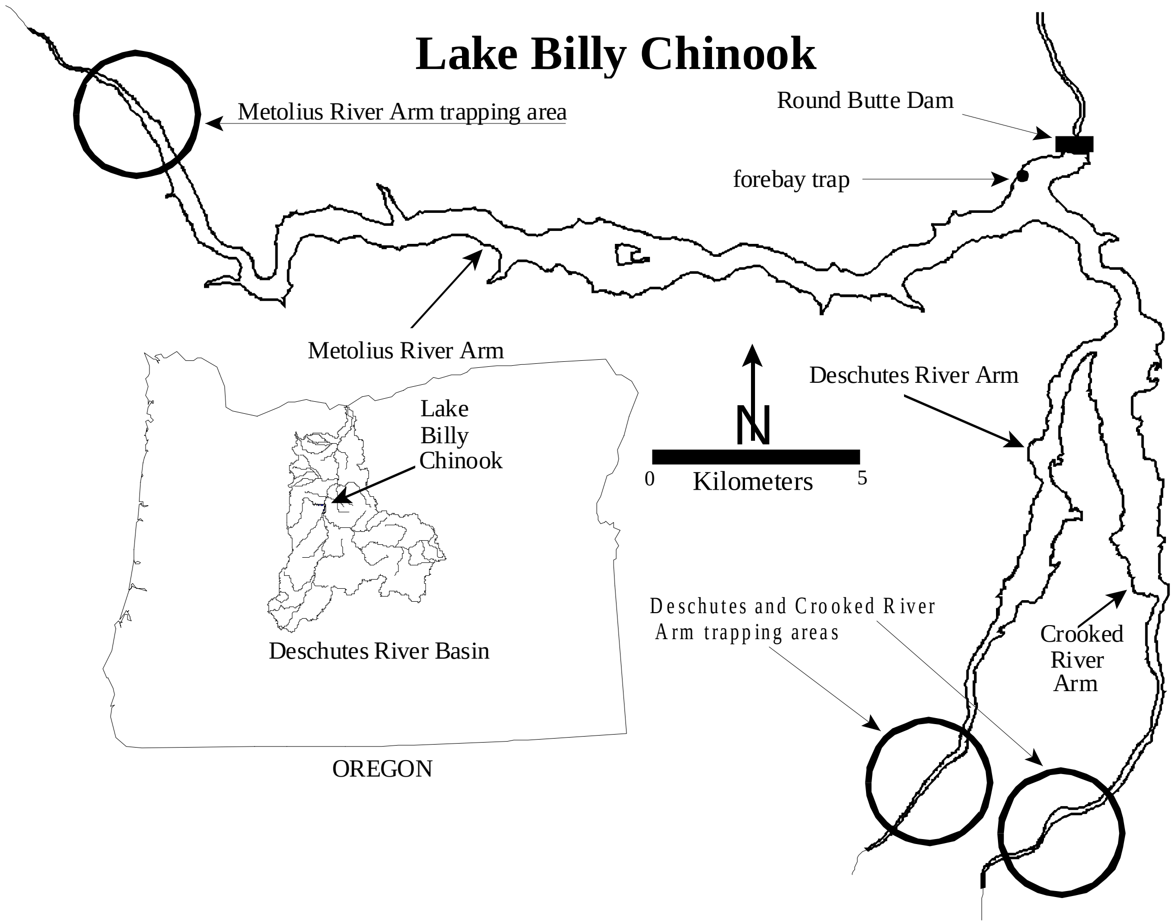

Figure 1. Map of Lake Billy Chinook and the location of sampling sites.

METHODS

Bioenergetics modeling provides an efficient method for quantifying predation on a daily time scale for individuals or populations of predators. This approach can incorporate changes in food habits, temperature, and size structure of prey and predator populations. Thus the biomass of all prey consumed can be estimated over appropriate predation periods, apportioned according to the observed prey composition of bull trout, and converted to numbers of prey consumed to examine the effects of predation on the demographics of prey populations. Seasonal consumption demand by different age/size classes of bull trout for each relevant prey category were simulated with a bioenergetics model (Hanson et al. 1997) using estimates of diet composition, annual growth, thermal history, and distribution obtained from existing data as inputs for the model simulations.

Bioenergetics Model Simulations

Model Parameters

A bioenergetics model, parameterized for lake trout (Stewart et al. 1983), was used as a surrogate model for bull trout. Whenever parameter values are borrowed from models developed for other species, the accuracy of the simulation results may become suspect. Because lake trout and bull trout are closely related species and exhibit similar distribution and behavior patterns (i.e., become large and highly piscivorous, inhabiting cold regions of primarily oligotrophic and mesotrophic lakes) in lakes, their physiological responses should be similar. Despite these similarities, we were concerned that the temperature effect on consumption rates might differ considerably between species. Experimentally-derived maximum consumption rates for juvenile bull trout over 7.5^{o}–12^{o} (T. McMahon, Montana State University, Bozeman, personal communication), which represented most of the thermal conditions experienced by bull trout in Lake Billy Chinook, were only 0–6% below those estimated by the lake trout model over the same range of temperatures. Although no comparisons are currently available for larger sizes of bull trout and lake trout, these preliminary data lend some reassurance that the lake trout model represented a reasonable surrogate model for bull trout.

Consumption rates were estimated for all age classes of bull trout residing in the transition and reservoir zones. For each age cohort, simulations began on 1 April (simulation day 1) and ended on 31 March the following year. Bull trout $<$ 450 mm FL (ages 1–4) were assumed to remain in the reservoir or transition zones throughout the year. Bull trout $\geq$ 450 mm FL were assumed to mature and migrate to riverine environments for staging and spawning during June–September (Ratliff et al. 1996; Thiesfeld et al. 1996).

Diet Composition

Seasonal, size-specific diet compositions used in bioenergetic simulations were derived from analysis of 288 nonempty stomachs out of a total 308 stomachs (20 empty). Stomach samples were generally not taken from bull trout captured in the river zone, so our analysis and simulation modeling concentrated on food habits in the transition and reservoir regions. Because we wanted to focus on piscivory in the reservoir and transition zones, and isolate our analyses from the uncertainty about food habits during stream residence, we assigned a diet of 100% invertebrates to adult bull trout while they occupied the rivers during the summer.

Stomach samples were obtained from bull trout sampled in the transition and reservoir zones using Merwin traps, angling, and short-duration (2-h) gill net sets (Figure 2). Stomach contents were removed from live fish using gastric lavage and were preserved in 10% buffered formalin. Stomach contents were examined under dissecting microscopes. Prey fishes were identified to species when possible using diagnostic bones, and were categorized as kokanee, bull trout, rainbow trout *O. mykiss*, mountain whitefish *Prosopium williamsoni*, cyprinids (primarily longnose dace *Rhinichthys cataractae* with some redside shiners *Richardsonius balteatus* and chiselmouth *Acrocheilus alutaceus*), catostomids (largescale suckers *Catostomus macrocheilus*), cottids, and larval fishes. We could generally discriminate between the digested remains of Salmoniformes and other prey fishes, and kokanee were readily distinguishable from other salmoniformes. Salmoniformes that could not be identified to species were categorized as "other salmonids." Fish prey that could not be identified to any lower taxonomic level were categorized as "unidentified fish." When possible, standard lengths of prey fishes were measured to the nearest millimeter. Insects, crayfish, and other invertebrates were combined into a general invertebrate category. All prey categories were blotted dry and weighed to the nearest 0.01 g.

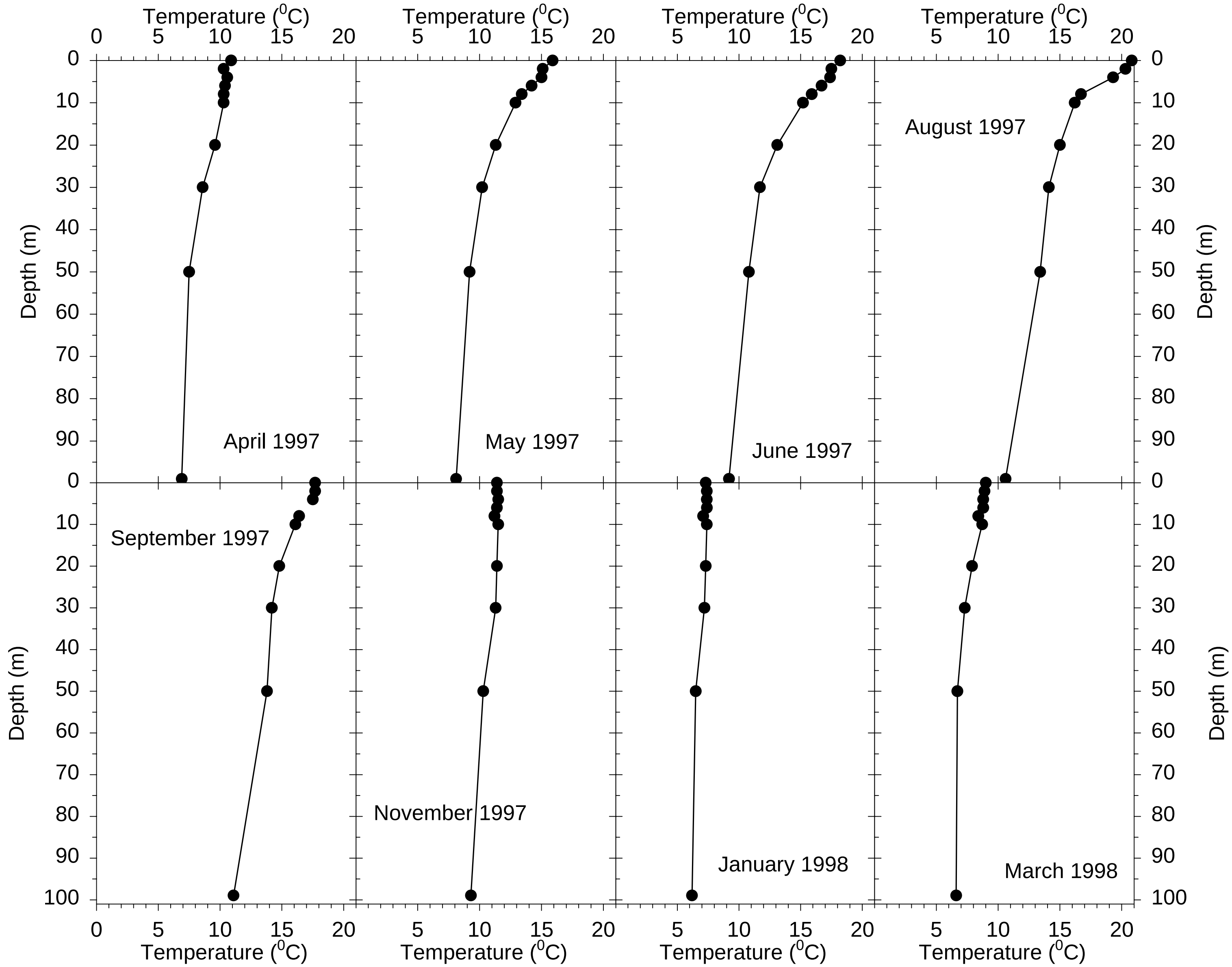

Figure 2. Temporal sequence of vertical temperature profiles measured near the forebay in Lake Billy Chinook during 1997–1998.

The average proportional biomass contribution of each prey category was computed for each season (winter–spring, summer, autumn) and size/age class of bull trout in the reservoir (ages 0-2, 75–200 mm FL; age 3, 200–300 mm FL; age 4, 300–450 mm FL; age 5, 450–600 mm FL; and ages 6 and older, 600–900 mm FL). For bioenergetic simulations, nonsalmoniform fishes were combined into an “other fish” category, and all invertebrates, including crayfish, were combined. Unidentified fish were reallocated to the identifiable prey fish categories in proportion to ratio of the weight contribution of each identifiable fish species to the total weight of all identifiable fish prey for each combination of season and predator size category.

Predator Growth

Consumption was modeled to fit annual growth increments reported by Pratt (1991) for ages 3–7 assuming that annuli were formed on 1 April. Length-at-age was converted to weights with a length-weight regression using bull trout collected during 1989–1997 by all capture methods and during all seasons ($r^2 = 0.965$, $N = 114$, ranging 150–850 mm FL).

$$Wt(g) = 0.00000326\ FL^{3.2253}$$

These weights were used as initial and final weights of an annual growth increment for each age class in the bioenergetic simulations (Table 1). Because sample sizes were too small to estimate seasonal growth rates for each age cohort, seasonal contributions to the annual growth increment were controlled by the thermal experience of bull trout in the reservoir. For age 5 and older adults, spawning was modeled as an average 8% loss of body mass on 7 September (simulation day 160).

Thermal Experience

Thermal experience differed among size classes of bull trout due to size-specific seasonal distribution patterns in the river, transition, and reservoir zones (Table 2). The river and transition zones remained cool (5.1^o–9.2^oC) and unstratified throughout the year, whereas temperatures in the reservoir during May–September ranged 15^o–21^oC in the epilimnion and 8^o–15^oC in the hypolimnion (Figure 2).

Table 1. Body weights and size classes of bull trout used in model, and back-calculated age-specific abundances of bull trout to reflect the relative abundance of each size class of piscivorous (age 3–7) bull trout in the reservoir. Abundances are presented for 1,000 age 3–7 bull trout and for populations based on spawner estimates from 1993 and 1994.

Age	Body weights (g) used in model simulations: Initial	Body weights (g) used in model simulations: Final	Size class (mm)	Abundance for 1,000 age 3–7 bull trout	Back-calculated abundance from spawner surveys in 1993	Back-calculated abundance from spawner surveys in 1994
1	2	5	75–200	2,064	7,472	17,327
2	5	87	75–200	1,032	3,736	8,664
3	87	311	200–300	516	1,868	4,332
4	311	1,176	300–450	258	934	2,166
5	1,176	3,592	450–600	129	467	1,083
6	3,592	8,257	600–900	65	233	541
7	8,257	10,009	600–900	32	117	271
Abundance of age 3–7 bull trout:				1,000	3,619	8,393
Abundance of spawners (age 5–7):				226	817	1,895
Abundance of age 1–7 bull trout:				4,096	14,827	34,384

Table 2. Thermal experience used in bioenergetic simulations. Thermal experience for each cohort was based on catch per effort and average depth captured for each predator size class.

Month	day	Predator Size (mm): 75–200	200–300	300–450	450–600	600–900
April	1	7.0	7.7	7.0	7.0	7.0
May	31	7.7	8.3	7.7	7.7	7.7
June	62	8.7	11.9	8.7	8.7	8.7
July	92	9.2	9.2	9.2	9.2	9.2
August	123	9.0	9.0	9.0	9.0	9.0
September	154	8.0	8.0	8.0	8.0	8.0
October	184	6.6	13.9	11.5	12.9	12.9
November	215	6.3	13.8	11.5	11.0	11.0
December	245	5.1	13.8	11.5	8.9	8.9
January	276	5.1	6.2	5.1	5.1	5.1
February	307	5.7	6.5	5.7	5.7	5.7
March	335	6.3	7.1	6.3	6.3	6.3
April	365	7.0	7.7	7.0	7.0	7.0

Consumption Estimates

Seasonal predation rates on kokanee, bull trout, and other prey were estimated from bioenergetics model simulations of the prey biomass consumed per individual predator from each age or size class in the transition and reservoir zones of Lake Billy Chinook. These size-specific, individual consumption rates were expanded to population-level predation rates in two ways. First, because most adfluvial bull trout in Lake Billy Chinook enter the reservoir at age 3 (≥ 200 mm FL; Table 3), the observed size and age structure of bull trout reported by Pratt (1991) was used to construct a reservoir population of 1,000 age 3–7 bull trout.

Table 3. Seasonal, size-specific catch-per-unit-effort (CPUE) of bull trout in the river, transition, and reservoir zones of Lake Bill Chinook during 1997–1998.

		Reservoir zone		
Size class	**Season**	**Reservoir**	**River**	**Transition**
75–200	Win–Spr	0.003	3.944	0.072
	June	0.000		0.110
	Summer	0.000	1.000	0.048
	Autumn	0.000	0.500	0.000
200–300	Win–Spr	0.016	0.000	0.019
	June	0.024		0.026
	Summer	0.000	0.000	0.068
	Autumn	0.007	0.000	0.000
300–450	Win–Spr	0.014	0.056	0.022
	June	0.009		0.029
	Summer	0.000	8.000	0.067
	Autumn	0.017	0.000	0.000
450–900	Win–Spr	0.008	0.444	0.001
	June	0.000		0.000
	Summer	0.000	8.000	0.000
	Autumn	0.003	0.000	0.000

An annual survival rate of 47% ($-Z = -0.7368$) was estimated by regressing $\log_e$ counts of each age class (ages 3–7) against age ($r^2 = 0.98$) for age samples reported by Pratt (1991). Based on these results, we arbitrarily used an annual survival rate of 50% ($-Z = -0.69315$) to construct age-specific abundance of the bull trout population in the reservoir such that $N_{3\text{-}7} = 1{,}000$. This was accomplished by iteratively fitting the abundance of age-3 bull trout ($N_3 = 516$) which satisfied the expression:

$$\Sigma N_t e^{-Z(t-3)} = 1{,}000 \quad (\text{for } t = 3 \text{ to } 7).$$

Because all age 5–7 bull trout appeared to spawn in Metolius River tributaries each year, we used estimates of the total spawning population during 1993 (817 spawners) and 1994 (1,895 spawners) from Ratliff et al. (1996) to calculate the total abundance of age 3–7 bull trout in the reservoir (Table 1). Thus, seasonal and annual predation rates could be generated for an arbitrary population of 1,000 age 3–7 bull trout (FL $\geq$ 200 mm), and for a range of bull trout population sizes back-calculated from estimated spawner abundances from two recent years.

Numerical predation losses of kokanee and bull trout were estimated by dividing the consumed biomass of kokanee, bull trout, and other prey fishes by the reconstructed mean weight of these prey in stomachs from each season and age class of predator. Prey fish weights were reconstructed where possible from standard, fork, or total lengths of prey measured from stomach samples and a length-weight regression for kokanee which we used as a surrogate for all salmonid prey fishes ($r^2 = 0.994$, $N = 419$, range 34–334 mm; S. Thiesfeld, Oregon Department of Fish and Wildlife, Madras, Oregon):

$$Wt(g) = 0.00000368\ TL(mm)^{3.166}$$

Prey sizes in the stomachs were compared against the size distribution of kokanee (Thiesfeld and Chilcote 1997, Thiesfeld and Dale 1998) and bull trout (Ratliff et al. 1996) available in the reservoir during each season. We assumed that all adult bull trout ($\geq$ 450 mm) left the reservoir to spawn in tributaries of the Metolius River from July through September and returned to the reservoir in October (Ratliff et al. 1996). This assumption was supported by an absence of adult bull trout in summer samples from the reservoir compared to 23 adults captured during autumn through spring (Table 3; Figure 3).

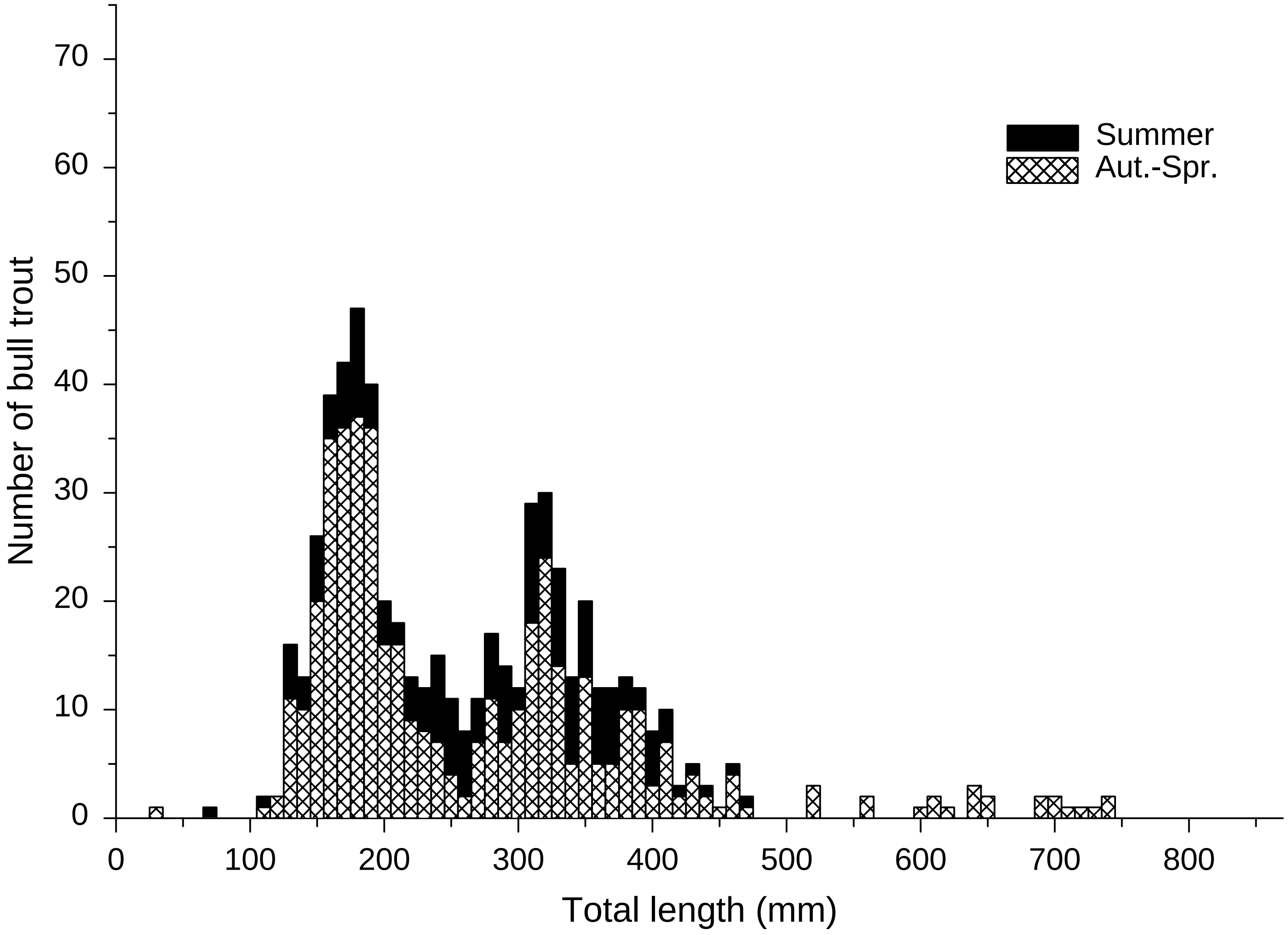

Figure 3. Length frequency of bull trout captured in Lake Billy Chinook during summer versus autumn through spring. The lack of adult fish in summer samples reinforces the assumption that all adults leave the reservoir every summer to spawn in the Metolius River and tributaries.

Predation Impacts on Kokanee and Bull Trout

To evaluate how predation losses might affect the dynamics of kokanee and bull trout populations, we generated rough approximations of age-specific abundance for both species using existing hydroacoustic survey data for kokanee (Thiesfeld et al.1999) and creel and spawner survey data for bull trout (Ratliff et al. 1996).

We estimated the abundance of age-4 (300–450 mm) bull trout by dividing estimated annual harvest (only the fish kept in Table 9 from Ratliff et al. 1996) by exploitation rates that were determined from tag recoveries in the fishery during 1990, 1991, and 1993 (computed from data in Table 10 and Figure 15 in Ratliff et al. 1996). Using an estimated annual survival of 50% as described above, we generated the abundance of younger and older age classes of bull trout from

$$N_t = N_4 e^{-Z(t-4)},$$

where Z = 0.69395. This approach was based on the simplifying assumptions that survival was constant among age classes and that recruitment was constant among years. In reality, younger (ages 0–1) bull trout probably experience lower survival rates than older age classes; thus, by assuming a constant survival rate for all ages, the back-calculated abundances would underestimate the actual abundances of the younger age classes. Night snorkeling surveys of age 1–3 bull trout in the major rearing tributaries of the Metolius River during 1992–1994 exhibited relatively constant densities overall and no consistent trends in density among tributaries; thus the assumption of relatively constant recruitment among years seemed reasonable, at least over the period of those surveys.

Age-specific abundance of kokanee was computed two ways. The first method used the estimated 46,920 age-3 spawners and the summer hydroacoustic estimate of 750,000 age-0 kokanee (Thiesfeld and Dale 1998; Thiesfeld et al. 1999) to compute an annual instantaneous mortality rate by:

$$-Z = \log_e(46{,}920/750{,}000)/3 = -0.92388$$

which equates to an annual survival rate of S = 40%. The second method related the hydroacoustic estimate of ages 1–3 kokanee (250,000) to age-0 kokanee (750,000). Because N_0 = 750,000 and ΣN_t = 250,000 for ages t = 1–3, and

$$N_t = N_0 e^{-Zt},$$

then

$$250{,}000 = \Sigma(e^{-Zt} * 750{,}000) \text{ for } t = 1 \text{ to } 3.$$

Rearranging and iteratively solving for Z, we obtained Z = 1.3863 which translates into an annual survival rate of S = 25%. The two alternative annual survival rate estimates were applied to the estimated 750,000 age-0 kokanee during summer to generate two sets of age-specific kokanee abundance for comparison to the estimated annual predation losses imposed by 1,000 age 3–7 bull trout on each age class of kokanee.

RESULTS

Seasonal and Size-specific Distribution of Bull Trout

The river, transition zone, and reservoir were sampled for all size classes (40–740 mm FL) of bull trout throughout the year, except that samples from the Metolius River were lacking during June. An analysis of size-specific catch-per-unit-effort (CPUE) from Merwin traps and supplemental angling data by season and region indicated that all sizes of bull trout were concentrated in either the river or transition zones during summer and in the reservoir during autumn (Table 3). Adults (> 470 mm FL) were found exclusively in the river during the summer, and 96–100% of the bull trout < 200 mm FL were sampled in the river throughout the year. Bull trout occupied all three zones during winter–spring and June, but CPUE was considerably lower in the reservoir than in the river or transition zones (Table 3).

Seasonal and Size-specific Food Habits

Bull trout became progressively more piscivorous with increasing size, and predators ≥ 450 mm ate predominantly fish prey (Table 4). Kokanee or other salmonids represented the largest fraction of fish prey in the diet, although cyprinids (mostly longnose dace), cottids, and catostomids, were also consumed. Most predation on kokanee occurred in autumn, and secondarily in winter–spring, whereas other salmonids were more prevalent in the diet during winter–spring and summer. Adult bull trout (FL ≥ 450 mm) migrated up the Metolius River in summer, and thus did not consume kokanee or other lacustrine prey from June through September. Unlike the adults, immature bull trout remained in the reservoir during the summer, when salmonids represented 24–43% of their diet. Cannibalism on smaller bull trout was only detected in stomachs of bull trout ≤ 450 mm FL and was confined to the winter–spring and summer periods, but represented up to 10% of the identifiable prey in the diet.

Predator-Prey Size Relationships

Bull trout of all sizes were capable of eating fusiform prey fishes up to 50% of their own total length (Figure 4). Bull trout consumed a broad size range of kokanee and mountain whitefish. Bull trout > 250 mm fed primarily on age-1 kokanee (150–250 mm FL, averaging 59.7 g) during winter–spring, and on age-0 kokanee (80–125 mm FL, averaging 10.5 g) during summer. In autumn, the 300–450 mm bull trout continued to feed on age-0 kokanee (80–125 mm FL, averaging 10.5 g), while adult bull trout (FL ≥ 450 mm) consumed ages 2–3 subadult and adult kokanee (250–350 mm FL, averaging 316 g). Small bull trout (FL < 300 mm) ate age-0 mountain whitefish in winter–spring (30–60 mm, 0.2–0.8 g) and summer (50–70 mm, 1.5 g). Subadult bull trout (300–450 mm) consumed intermediate-sized (144 mm, 25 g) mountain whitefish during summer, and bull trout ≥ 450 mm consumed larger mountain whitefish (240–260 mm, 142 g) during winter–spring. The sizes of other prey fishes were less variable in stomach samples. The mean total length (SD, N) and weight of other prey fishes were 110 mm (38 mm, N = 19) 9.0 g for bull trout, 98 mm (24 mm, N = 8) and 6.4 g for rainbow trout, 106 mm (22 mm, N = 12) for cyprinids (predominantly longnose dace), and 107 mm (44 mm, N = 3) for largescale suckers.

Table 4. Seasonal diet composition of bull trout by predator size in the transition zone and reservoir regions of Lake Billy Chinook during 1997–1998. Diet composition is expressed as the proportional mean contribution of each prey category to the total wet weight of prey items in each stomach.

Predator size (mm)	Season	Kokanee	Bull trout	Rainbow trout	Mountain whitefish	Other salmonid	Cyprinid	Cottid	Catostomid	Unknown fish	Larval fish	Inverts.	Crayfish	N
75–200	Win–Spr	0.000	0.000	0.000	0.005	0.002	0.000	0.000	0.000	0.008	0.063	0.922	0.000	96
	June	0.000	0.000	0.250	0.122	0.170	0.000	0.000	0.000	0.000	0.000	0.458	0.000	4
	Summer	0.000	0.214	0.000	0.000	0.000	0.000	0.000	0.257	0.000	0.000	0.529	0.000	2
	Autumn	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	2
200–300	Win–Spr	0.033	0.024	0.000	0.000	0.009	0.033	0.000	0.000	0.018	0.000	0.883	0.000	31
	June	0.100	0.100	0.100	0.079	0.100	0.120	0.000	0.000	0.000	0.000	0.401	0.000	10
	Summer	0.000	0.000	0.000	0.000	0.000	0.064	0.000	0.000	0.147	0.000	0.789	0.000	10
	Autumn	0.000	0.000	0.000	0.000	0.000	0.000	0.133	0.000	0.133	0.000	0.734	0.000	7
300–450	Win–Spr	0.021	0.066	0.022	0.000	0.037	0.044	0.018	0.000	0.062	0.038	0.636	0.056	46
	June	0.092	0.217	0.134	0.000	0.032	0.090	0.000	0.071	0.059	0.000	0.305	0.000	17
	Summer	0.065	0.043	0.030	0.043	0.062	0.045	0.003	0.000	0.056	0.000	0.646	0.007	31
	Autumn	0.213	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.083	0.000	0.579	0.000	8
450–600	Win–Spr	0.000	0.000	0.000	0.167	0.332	0.154	0.167	0.000	0.000	0.000	0.180	0.000	6
	June	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.750	0.000	0
	Summer	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.750	0.000	0
	Autumn	0.500	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.000	0.000	2
600–900	Win–Spr	0.286	0.000	0.000	0.071	0.429	0.000	0.000	0.000	0.071	0.000	0.143	0.000	14
	June	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.750	0.000	0
	Summer	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.750	0.000	0
	Autumn	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1

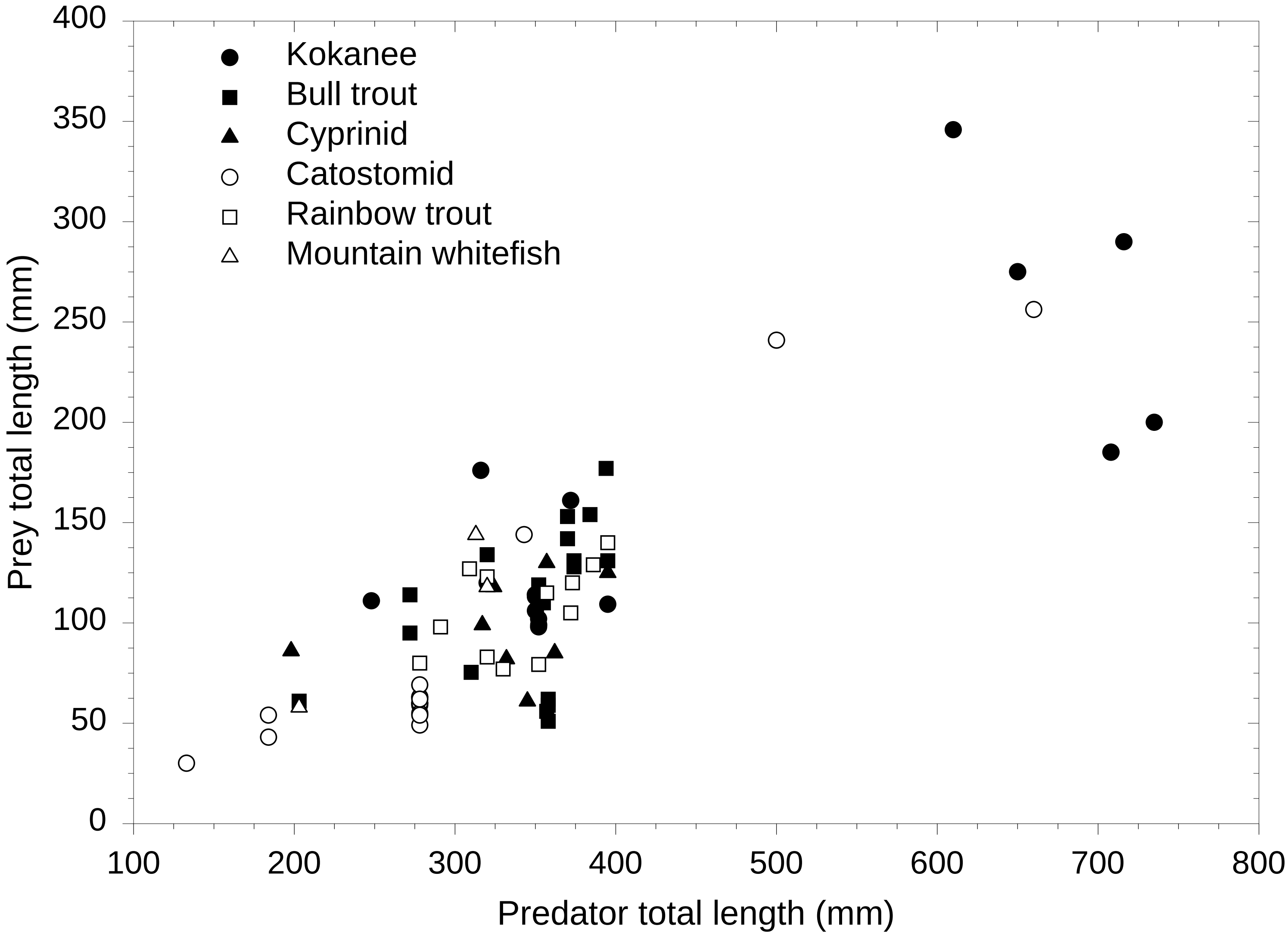

Figure 4. The length of prey fishes found in stomachs of bull trout of different lengths in Lake Billy Chinook.

Bioenergetic Model Estimates of Consumption

Model simulations indicated that bull trout consumption of prey fishes and invertebrates varied seasonally, and that the total biomass consumed per individual increased with body size (Table 5). In general, per capita predation by bull trout ≤ 300 mm FL on kokanee and bull trout was heaviest during summer and winter–spring, and was heaviest on rainbow trout, mountain whitefish, and other salmonids during summer. The 300–450-mm FL bull trout were large enough to feed on kokanee throughout the year, and their heaviest per capita predation occurred during autumn, followed by summer. The 300–450-mm FL bull trout also exhibited considerable per capita predation on younger bull trout, rainbow trout, and other salmonids during winter–spring and summer, and preyed heavily on other fishes throughout the year. When residing in the

Table 5. Seasonal per capita prey consumption (g/season) by each size class of bull trout.

Predator size (mm)	Season	Kokanee	Bull trout	Rainbow trout	Mountain whitefish	Other salmonid	Other fish	Inverts.
200–300	Win–Spr	18.6	13.4	0.0	0.0	5.3	23.7	435.6
	June	9.1	9.0	8.9	7.1	9.0	10.8	38.7
	Summer	0.3	0.3	0.3	0.2	0.3	57.2	212.3
	Autumn	0.0	0.0	0.0	0.0	0.0	158.3	440.3
300–450	Win–Spr	59.8	134.2	45.3	0.0	72.8	213.2	1,152.4
	June	28.1	67.1	41.0	0.0	9.9	50.2	91.5
	Summer	81.3	55.7	40.1	53.2	77.5	61.3	684.1
	Autumn	461.0	2.6	1.9	2.6	3.8	271.0	1,026.9
450–600	Win–Spr	143.4	0.0	0.0	709.9	1,411.3	1,356.1	760.4
	June	0.0	0.0	0.0	0.0	0.0	209.1	606.9
	Summer	0.0	0.0	0.0	0.0	0.0	703.8	2,111.4
	Autumn	3,798.1	0.0	0.0	0.0	0.0	36.6	109.8
600–900	Win–Spr	3,557.4	0.0	0.0	784.8	4,842.8	0.0	1,466.7
	June	0.0	0.0	0.0	0.0	0.0	529.7	1,598.9
	Summer	0.0	0.0	0.0	0.0	0.0	1,823.7	5,471.1
	Autumn	9,220.4	0.0	0.0	0.0	0.0	93.3	279.9
Total		17,377.6	282.3	137.5	1,557.7	6,432.6	5,598.0	16,486.8

reservoir, adult bull trout fed heavily on kokanee, mountain whitefish, and other unidentifiable salmonids during winter–spring, and preyed very heavily on predominantly adult and subadult kokanee during autumn. We did not detect any predation by adult bull trout on smaller bull trout or rainbow trout throughout the year; however, some of the large biomass of unidentifiable salmonids consumed during winter–spring could have included these species.

Although per capita predation on kokanee was heaviest by older bull trout, the total magnitude of predation by each size class of piscivore depends on the product of individual predation rates and the relative or absolute abundance of individuals within each size class. To account for the size-specific and seasonal abundance of piscivores in the reservoir, population-level predation rates were computed for 1,000 predators (ages 3–7; length > 200 mm) exhibiting the size structure observed in Lake Billy Chinook (Table 6). For every 1,000 bull trout in Lake

Table 6. Seasonal prey consumption (kg/season) by each cohort for 1000 age 3–7 (FL > 200 mm) bull trout.

Predator size (mm)	Season	Kokanee	Bull trout	Rainbow trout	Mountain whitefish	Other salmonid	Other fish	Inverts.
200–300	Win–Spr	6.2	4.4	0.0	0.0	1.7	7.7	143.8
	June	3.9	3.9	3.9	3.1	3.9	4.7	16.8
	Summer	0.1	0.1	0.1	0.1	0.1	22.1	82.0
	Autumn	0.0	0.0	0.0	0.0	0.0	51.8	144.1
300–450	Win–Spr	9.6	22.1	7.5	0.0	12.0	35.0	189.3
	June	6.1	14.6	8.9	0.0	2.1	10.9	19.9
	Summer	15.7	10.8	7.8	10.3	15.0	11.9	132.3
	Autumn	75.4	0.5	0.3	0.5	0.7	44.3	168.2
450–600	Win–Spr	10.5	0.0	0.0	60.0	119.3	114.3	64.1
	June	0.0	0.0	0.0	0.0	0.0	22.7	66.0
	Summer	0.0	0.0	0.0	0.0	0.0	68.1	204.4
	Autumn	312.2	0.0	0.0	0.0	0.0	3.2	9.5
600–900	Win–Spr	151.4	0.0	0.0	33.9	209.2	0.0	63.2
	June	0.0	0.0	0.0	0.0	0.0	28.8	86.9
	Summer	0.0	0.0	0.0	0.0	0.0	88.3	264.9
	Autumn	379.3	0.0	0.0	0.0	0.0	4.0	12.1
Total		970.5	56.4	28.5	107.8	364.1	517.9	1,667.8

Billy Chinook, model simulations indicated that 971 kg of kokanee, 56 kg of bull trout, 29 kg of rainbow trout, 108 kg of mountain whitefish, 364 kg of unidentified salmonids that were not kokanee, 518 kg of other fishes, and 1,668 kg of benthic invertebrates were consumed in the reservoir annually. Predation on age-0 kokanee was greatest by 300–450-mm bull trout, and predation on subadult and adult kokanee was greatest by bull trout $\geq$ 450 mm in autumn and by bull trout $\geq$ 600 mm in winter. Cannibalism on age-0 bull trout was greatest by 200–450-mm bull trout during winter through the summer, whereas age-1 bull trout were cannibalized by 300–450-mm bull trout during autumn through spring. When predation rates were converted from biomass to size-specific numerical losses, model simulations indicated that 1,000 bull trout $\geq$ 200 mm, annually consumed 13,876 kokanee (9,362 age-0, 398 age-1, and 4,116 ages 2–3), 5,273 bull trout (4,446 age-0 and 827 age-1), 4,335 rainbow trout (3,872 age-0 and 462 age-1), and 3,172 mountain whitefish (2,031 age-0, 453 age-1, and 688 age-2–3). In addition, another estimated 10,224 unidentifiable salmonids (assuming that the size distribution was similar to the sizes of identifiable salmonids), and 56,715 other fishes (predominantly longnose dace) were also consumed annually (Table 7).

The estimated predatory impact per unit 1,000 age 3–7 bull trout was highest on age-0 bull trout and age-0 and adult kokanee. Based on the range of juvenile bull trout abundances generated from data in 1990, 1991, and 1993, cannibalism removed 3.2–5.8% age-0 and 1.2–2.2% age-1 bull trout per 1,000 predators each year (Table 8). Based on the two methods for estimating age-specific kokanee abundance, predation removed 1.2% age-0, 0.1–0.2% age-1, and 3.5–8.8% of the age 2–3 kokanee per 1,000 age 3–7 bull trout (Table 9). Based on the spawner counts for bull trout, we estimated that 3,620 and 8,395 age 3–7 bull trout resided in the reservoir in 1993 and 1994, respectively. Given these estimates of piscivore abundance, the resulting population-level predation rates imposed by the entire population of age 3–7 bull trout would increase by a factor of 3.6–8.4. This translates into a loss of 11.4–49.1% age-0 and 4.2–18.3% age-1 bull trout per year during 1990, 1991, and 1993 due to cannibalism, and predation losses to kokanee of 5–11% age-0, 1–2% age-1, and 13–74% ages 2–3 subadults and adults.

Table 7. Seasonal numerical prey consumption by each cohort for 1,000 age 3–7 bull trout.

Predator size (mm)	Season	Kokanee	Bull trout	Rainbow trout	Mountain whitefish	Other salmonid	Other fish
200–300	Win–Spr	131	1,372	0	0	1,292	455
	June	358	432	507	2,020	1,570	863
	Summer	8	12	7	11	10	1,295
	Autumn	0	0	0	0	0	14,997
300–450	Win–Spr	268	827	1,580	0	426	2,211
	June	657	1,410	1,752	0	244	905
	Summer	1,118	1,170	456	410	1374	696
	Autumn	7,221	50	33	43	84	12,831
450–600	Win–Spr	109	0	0	469	1,935	7,229
	June	0	0	0	0	0	1,438
	Summer	0	0	0	0	0	4,307
	Autumn	777	0	0	0	0	917
600–900	Win–Spr	1,579	0	0	218	3,287	0
	June	0	0	0	0	0	1,820
	Summer	0	0	0	0	0	5,583
	Autumn	1,651	0	0	0	0	1,169
Total		13,876	5,273	4,335	3,172	10,224	56,715
Age-specific predation losses:							
	Age-0	9,362	4,446	3,872	2,031		
	Age-1	398	827	462	453		
	Age 2–3	4,116	0	0	688		

Table 8. Predation losses as a percentage of each age class for bull trout. Percentage losses were computed per 1,000 age 3–7 bull trout for age-0 and -1 bull trout, based on back-calculated age-specific abundances. The abundance of age-4 bull trout was calculated from the harvest, exploitation rate, and percentage of age-4 bull trout in the harvest. Abundances of younger ages were back-calculated, assuming an annual survival rate of 50% (see text).

Year	Bull trout harvest	Exploitation rate	Estimated abundance	Percentage of age-4 bull trout in the harvest	Abundance of age-4 bull trout	Abundance of age-1 bull trout	Abundance of age-0 bull trout	Predation rate per 1,000 age 3-7 bull trout	
								on age-1	on age-0
1990	863	0.15	5,868	90%	5,282	42,252	84,505	2.0%	5.3%
1991	880	0.11	7,920	60%	4,752	38,016	76,032	2.2%	5.8%
1992	1,087	0.05	23,914						
1993	246	0.02	12,546	70%	8,782	70,258	140,515	1.2%	3.2%

Year	Predation rate per 3,600 age 3–7 bull trout		Predation rate per 8,400 age 3–7 bull trout	
	on age-1	on age-0	on age-1	on age-0
1990	7.0%	18.9%	16.4%	44.2%
1991	7.8%	21.1%	18.3%	49.1%
1993	4.2%	11.4%	9.9%	26.6%

Table 9. Predation losses as a percentage of each age class for kokanee. Percentage losses were computed per 1,000 age 3–7 bull trout for kokanee with annual survival rates of 40% and 25% (see text).

Age class	Abundance assuming 40% annual survival	Losses per 1,000 predators	Losses as % of age class	Age class	Abundance assuming 25% annual survival	Losses per 1,000 predators	Losses as % of age class
0	750,000	9,362	1.2%	0	750,000	9,362	1.2%
1	297,733	398	0.1%	1	187,500	398	0.2%
2	118,193	4,116	3.5%	2	46,875	4,116	8.8%
3	46,920			3	11,719		
Lifetime loss per year class:		13,876				13,876	

	3,600 bull trout > 200 mm FL			8,400 bull trout > 200 mm FL		
		40% Survival:	25% Survival:		40% Survival:	25% Survival:
Age class	Losses per 3,600 predators	Losses as % of age class	Losses as % of age class	Losses per 8,400 predators	Losses as % of age class	Losses as % of age class
0	33,703	4.5%	4.5%	78,640	10.5%	10.5%
1	1,434	0.5%	0.8%	3,346	1.1%	1.8%
2–3	14,818	12.5%	31.6%	34,575	29.3%	73.8%
Lifetime loss:	49,954			116,560		

DISCUSSION

Our modeling simulations suggest that the bull trout population in Lake Billy Chinook could be limited both by predation and food supply. Predation on kokanee and cannibalism by bull trout can remove significant fractions from both of these populations. Thus, depletion of the kokanee population could both reduce growth rates of bull trout and increase mortality due to cannibalism. Due to the rapid growth of kokanee, smaller bull trout (FL < 450 mm) were generally only capable of eating age-0 kokanee, but could feed on age 0–1, and perhaps age-2 bull trout and other salmonids. Larger bull trout could generally eat all available sizes of kokanee. Thiesfeld et al. (1999) found a positive correlation between condition factor in bull trout and kokanee abundance during 1990–1998 and demonstrated that intermediate-sized predators (356–508 mm FL) were more responsive to the abundance and size structure of available kokanee than the larger bull trout. Under the current prey availability and environmental conditions, cannibalism, particularly by immature (300–450 mm FL) bull trout, may be important in regulating the population dynamics of bull trout.

Most salmoniformes recruiting to the reservoir experienced prolonged and significant predation risk from larger bull trout. Bull trout fed on relatively large prey fishes in Lake Billy Chinook, demonstrating the ability to consume salmonids and other fusiform prey $\leq$ 50% of their own body length. This was consistent with results for piscivorous lake trout in Flaming Gorge Reservoir (Yule and Luecke 1993), Flathead Lake (Beauchamp 1996) and Yellowstone Lake (Ruzycki and Beauchamp 1997).

The extent to which the availability of alternative prey influences cannibalism, or predation on other species of interest, cannot be determined directly without comprehensive, long term data on diet composition and the relative abundance of the major prey fishes in the basin. In other lakes with complex fish assemblages, bull trout feed heavily on coregonids, salmonids, percids, and nongame species like cyprinids, catostomids, and cottids (Leathe and Graham 1982, Fraley and Shepard 1989, Donald and Alger 1993). In Lake Billy Chinook, the opportunity for considerable prey-switching through time and over the ontogeny of bull trout can be inferred by the variety of fish species contributing simultaneously to the diet of particular size classes of bull trout. For instance, rainbow trout and bull trout co-occurred seasonally in relatively similar proportions in the diet of bull trout < 450 mm. These prey species may buffer each other from the full brunt of bull trout predation, with the more abundant species absorbing the majority of the predation. Other fishes (predominantly longnose dace) represent a consistent and substantial fraction of the fish biomass consumed throughout the year by immature bull trout and during winter–spring by smaller adult bull trout (450–600 mm). Mountain whitefish and unidentified salmonids offer the only alternatives to kokanee for large bull trout, and only provide a potential buffer for kokanee during winter–spring.

These results have important implications for evaluating the feasibility of re-establishing anadromous salmonids in and above the reservoir. How predation might influence the dynamics of reintroduced salmonids will depend on the relative sizes of potential predators and prey, the extent of their temporal-spatial overlap, and the environmental conditions that prevail during their overlap.

Cannibalism and predation by sympatric piscivores have rarely been reported for other adfluvial bull trout populations (Johnson 1975, Leathe and Graham 1982, Donald and Alger 1993), and has never before been quantified. This is not surprising, because data from other adfluvial populations have generally come from fairly large, complex systems like Flathead Lake, Montana (surface area = 500 km^2), where cannibalism, even if significant, would likely represent an extremely small fraction of the prey available and consumed. Thus the probability of detecting ecologically significant levels of cannibalism, or predation by other piscivores, without an intensive, highly-directed sampling program, would be remote. The patterns we observed in Lake Billy Chinook should be useful for designing appropriate sampling programs for adfluvial populations in larger, more challenging systems.

Several important uncertainties remain regarding the role of predation and food supply on the production of bull trout and other salmonids during the riverine phases of their life history. Because juvenile bull trout spend up to 3 years in the Metolius River or its tributaries before migrating to the reservoir, the potential impact of cannibalism on smaller conspecifics or predation on other fishes could affect recruitment of bull trout, kokanee, rainbow trout, and mountain whitefish. This uncertainty can be remedied by directed sampling of the diet and distribution of bull trout in the Metolius River, tributaries, and in the reservoir during migrations of juvenile salmonids and for 1–2 months in the reservoir following the migration.

Improved information on thermal physiology, thermal experience, and the overlap of bull trout and prey fishes in time and space also warrant additional examination. The bioenergetics model used lake trout parameters for temperature-dependent functions for respiration costs and maximum consumption. Both bull trout and lake trout demonstrate strong adaptations to cold temperatures, but segregation by elevation within areas of geographic overlap (Donald and Alger 1993) suggests that bull trout exhibit more optimal physiological responses at lower temperatures than lake trout. If true, then predation estimates during winter–spring and autumn would likely increase, and summer consumption rates in the reservoir would decline relative to the simulation results presented here. However, the predation estimates would likely change less than 10% overall. The close correspondence between predicted consumption from the lake trout model and preliminary experimental results for juvenile bull trout (T. McMahon, personal communication) suggests that only minor errors should result from using a lake trout model as a surrogate for bull trout over the range of temperatures experienced in Lake Billy Chinook.

Information on the actual thermal experience of bull trout and their spatial-temporal overlap with prey fishes in the reservoir could be acquired efficiently by sonically tracking bull trout over diel periods during different seasons and life history stages. The availability of 6- and 12-month tags suitable for subadult and adult bull trout, and the high probability of reacquiring fish periodically through the year make this a feasible option. Sonic tracking would provide depth and relative location information, which are important for determining thermal experience, and for decisions about how to apply diet data to potential spatial stratification designs (e.g., do diets differ nearshore versus offshore, or between regions in the reservoir). Bull trout may cover enough distance and traverse a variety of habitats sufficiently that we can assume that their diet is integrated over many potential spatial strata. This has important implications for modeling predation and can only be acquired efficiently from boat-based sonic tracking data.

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APPENDIX 1.

SEASONAL PREY ENERGY DENSITIES (J/g) USED IN THE BIOENERGETICS MODEL SIMULATIONS FOR BULL TROUT

Appendix 1. Seasonal prey energy densities (J/g) used in the bioenergetics model simulations for bull trout.

Predator size (mm)	Season	Kokanee	Bull trout	Rainbow trout	Mountain whitefish	Other salmonid	Other fish	Inverts.
0–200	Win–Spr	5,241	5,766	5,769	5,464	5,796	5,021	4,184
	June	5,241	5,766	5,765	3,996	5,765	5,021	4,184
	Summer	5,241	5,764	5,764	3,952	5,764	5,021	4,184
	Autumn	5,241	5,948	5,769	4,018	5,764	5,021	4,184
200–300	Win–Spr	5,631	5,885	5,772	4,033	5,782	5,021	4,184
	June	6,257	5,854	5,829	9,020	5,889	5,021	4,184
	Summer	10,139	5,768	5,767	4,178	5,770	5,021	4,184
	Autumn	5,426	5,773	5,772	4,672	5,775	5,021	4,184
300–450	Win–Spr	5,233	5,764	5,764	4,923	5,764	5,021	4,184
	June	5,233	5,764	5,764	5,173	5,764	5,021	4,184
	Summer	25,545	5,764	5,764	3,952	5,764	5,021	4,184
	Autumn	15,086	5,764	5,764	20,661	7,503	5,021	4,184
450–600	Win–Spr	5,233	5,790	5,790	3,952	5,764	5,021	4,184
	June	5,976	5,790	5,790	11,458	5,825	5,800	4,184
	Summer	5,976	5,790	5,790	11,458	5,825	5,800	4,184
	Autumn	10,965	5,790	5,790	11,458	5,825	5,021	4,184
600–900	Win–Spr	5,233	5,790	5,790	13,050	5,764	5,021	4,184
	June	5,976	5,790	5,790	13,050	5,825	5,800	4,184
	Summer	5,976	5,790	5,790	13,050	5,825	5,800	4,184
	Autumn	6,647	5,790	5,790	13,050	5,825	5,021	4,184