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Walleye Predation on Hatchery Releases of Kokanees and Rainbow Trout in Lake Roosevelt, Washington

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Abstract.—Recruitment failures of stocked kokanees (lacustrine sockeye salmon *Oncorhynchus nerka*) in Lake Roosevelt have led to examination of various limiting factors. We evaluated the predatory impacts of piscivores on hatchery-released and net-pen-released kokanees and rainbow trout *O. mykiss* from the Sherman Creek Hatchery in 1999 and 2000. We used an angler tournament to mark walleyes *Stizostedion vitreum* for an abundance estimate, and then used gillnetting and electrofishing to collect recaptures and monitor the diet of walleyes. A bioenergetics model was used to quantify consumption, and estimates were extrapolated to walleye abundance to determine a percent loss of hatchery fish. Kokanees averaged 22–100% of the diet contents of walleyes ($>$300 mm total length), whereas rainbow trout averaged 0–25%, depending on location and timing following release. In 1999, we estimated that 16,610 walleyes consumed 15% of the hatchery kokanees within 41 d of release; however, our diet information did not correspond spatially with our population estimate. In 2000, we corrected our spatial bias and estimated that the population of 12,233 walleyes consumed 9.4% of the hatchery kokanees and 7.3% of the hatchery rainbow trout within 41 d of release. We conclude that the walleye population in northern Lake Roosevelt was effectively ‘‘swamped’’ by the biomass of salmonids released at the Sherman Creek Hatchery. However, piscivores may still limit kokanee recruitment, depending on long-term predation rates for the reservoir-wide walleye population.

Fish predators can affect prey fish populations in freshwater systems by selecting specific species and size-classes (Forney 1974; Stewart et al. 1981; Lyons and Magnuson 1987; Rieman et al. 1991; Hartman and Margraf 1993; Knight and Vondracek 1993; Yule and Luecke 1993). Predation of hatchery-released fishes may also hinder stocking efforts by management agencies (Stein et al. 1981; Baldwin et al. 2000; Yule et al. 2000). High densities of stocked fish can stimulate a predator feeding response and, in some instances, may result in an abrupt shift in piscivore diet (McMillan 1984; Vigg et al. 1991; Collis and Beaty 1995; Shiveley et al. 1996; Baldwin et al. 2000; Fayram and Sibley 2000). Depletion of fish prey is common for introduced fish assemblages in reservoir settings, where drawdown increases vulnerability of prey fish (McMillan 1984; McMahon and Bennett 1996).

Bioenergetics modeling can be used to quantify the effect of predators on prey populations (Stewart et al. 1983; Ney 1990; Yule and Luecke 1993; Beauchamp et al. 1995; Hartman and Brandt 1995; Baldwin et al. 2000). Researchers apply basic biological data on growth, diet, and thermal experience to computer models that simulate species-

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and size-specific physiology to allow estimation of consumption. Individual fish consumption is then expanded to abundance and mortality estimates to quantify population-level effects (Stewart et al. 1981; Hartman and Brandt 1995; Baldwin et al. 2000).

The objective of our study was to assess the impact of predators on hatchery and net-pen releases of rainbow trout *Oncorhynchus mykiss* and kokanee (lacustrine sockeye salmon *O. nerka*) in Lake Roosevelt, Washington. After determining the diet, growth, thermal experience, and abundance of piscivores in the vicinity of the Sherman Creek Hatchery (SCH), we used a bioenergetics model to identify which species and age-classes had the greatest potential to impact hatchery releases. We estimated the abundance of the dominant piscivore in the system, the walleye *Stizostedion vitreum*, then expanded individual consumption to the population of walleyes to determine their effect on stocked salmonids.

Study Area

Franklin D. Roosevelt Lake (Lake Roosevelt) is a Columbia River reservoir created in 1941 by the construction of Grand Coulee Dam (GCD) at river kilometer 960 (Figure 1). The reservoir covers approximately 33,000 ha at a full pool elevation of 393 m above mean sea level and is managed as a national recreation area by the National Park Service. The dam was built for hydropower generation, flood control, and water storage for irrigation in the Columbia Basin Reclamation Project. The annual hydrologic regime commonly includes spring drawdowns of 12–20 m, with a maximum operational limit of 25 m. The reservoir extends 241 km upstream from GCD, is generally 1–3 km wide, and has a maximum depth of 122 m. Water retention times are short (12–80 d), and the zooplankton community is more typical of a large river than a lake or reservoir (R. Black, Eastern Washington University, personal communication).

The fish community of Lake Roosevelt has changed since inundation. Northern pikeminnow *Ptychocheilus oregonensis* were the primary fish captured in historical gill-net surveys, comprising 65% of the total sample in 1948 (Gangmark and Fulton 1949), 54% in 1976 (Stober et al. 1977), and 15% from 1980 to 1983 (Beckman et al. 1985). In recent studies, however, northern pikeminnow have generally comprised less than 5% of the individuals captured in gill nets (Cichosz et al. 1997, 1999). Burbot *Lota lota* were rarely mentioned in historical surveys but consistently comprise 5–15% of individuals captured in recent gill-net surveys (Cichosz et al. 1997, 1999; Baldwin et al. 1999; Lake Roosevelt Fisheries Evaluation Project [LRFEP], unpublished data). In recent gill-net and electrofishing surveys, the fish community in Lake Roosevelt has been dominated by largescale suckers *Catostomus macrocheilus*, lake whitefish *Coregonus clupeaformis*, and walleyes (Peone et al. 1990; Cichosz et al. 1997, 1999).

Walleyes were first detected in Lake Roosevelt in the early 1950s, and by the early 1980s, walleyes comprised 30% of the total fish relative abundance (Beckman et al. 1985). Kokanee and rainbow trout stocking programs were expanded in 1988 to provide a fishery for limnetic planktivores that would experience minimal distribution overlap with walleyes (Scholz et al. 1986). The rainbow trout stocking program has been successful in providing a fishery (Cichosz et al. 1997, 1999); however, low angler harvest of kokanee and sparse returns of adult kokanees to egg collection sites led to investigations of limiting factors (Cichosz et al. 1997, 1999; Tilson and Scholz 1998; McLellan et al. 2001). Many walleyes spawn in the Spokane River arm of Lake Roosevelt and then migrate north towards Canada (Hall et al. 1985; McLellan et al. 2002). The walleye postspawn migration overlaps temporally and spatially with hatchery kokanee releases at the SCH. One potential limiting factor for hatchery salmonid success in Lake Roosevelt includes piscivory by walleyes or other piscivores, including northern pikeminnow and burbot.

Grand Coulee Dam is a barrier to historic anadromous salmon and steelhead runs. Mitigation for losses of historical salmon migrations into this portion of the Columbia River have resulted in hatchery kokanee and rainbow trout stocking programs. The SCH, the Spokane Tribal Hatchery, and the Lake Roosevelt Net-Pen Program have released approximately 750,000 kokanees and 500,000 rainbow trout annually since 1988. Hatchery and net-pen releases occur from late May to mid-July, depending on reservoir operations, temperature, and fish health. Kokanees have been released at the SCH with the intention of collecting eggs from returning age-3 spawners. The number of age-3 spawners returning to egg collection sites has never been adequate for egg takes, so other strategies such as net-pens and yearling releases have been employed in an attempt to improve survival.

Sherman Creek Hatchery is located 163 km upstream of GCD and 95 km from the confluence

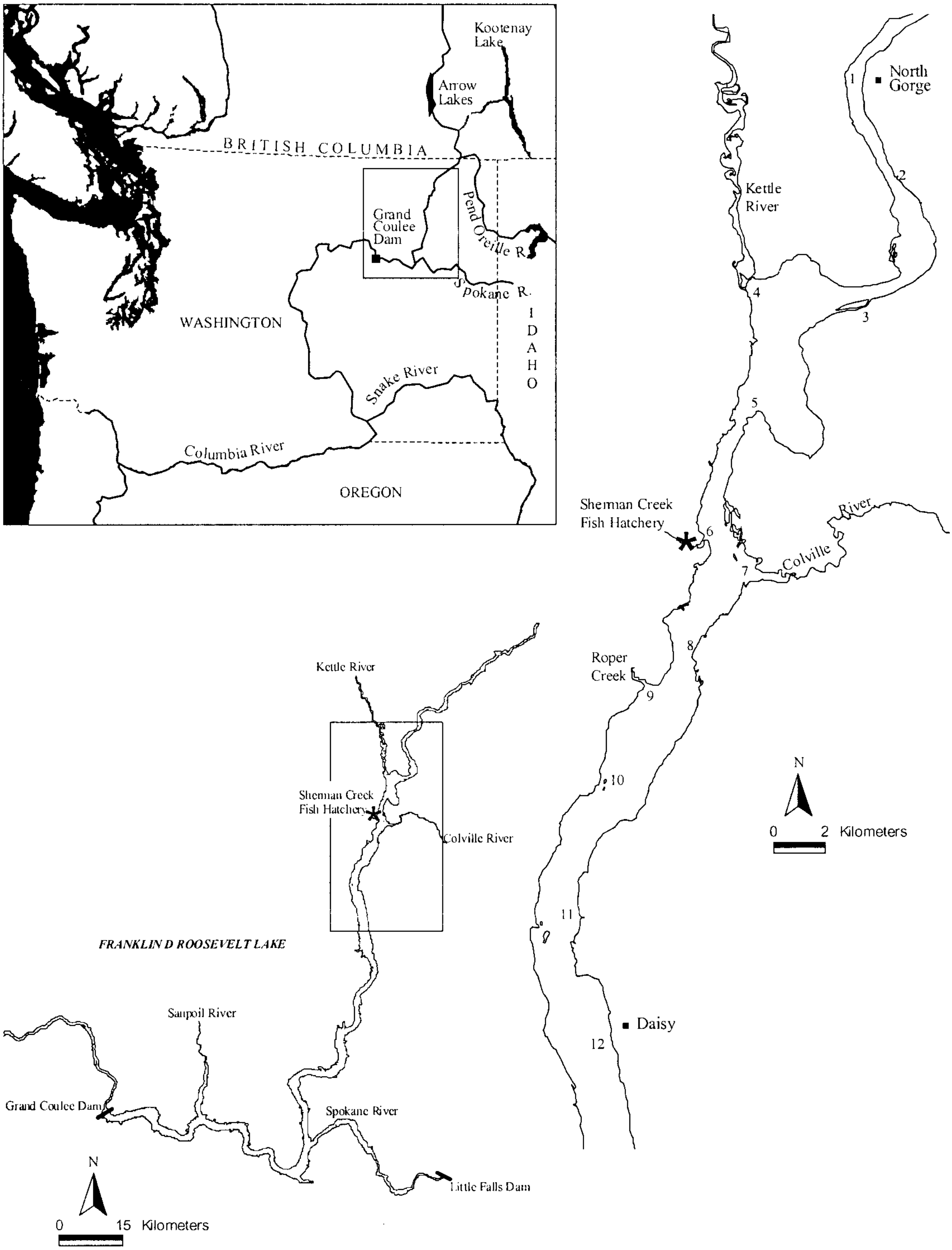

FIGURE 1.—Map showing Lake Roosevelt, Washington, on the Columbia River, the location of the study area within Lake Roosevelt, and electroshocking and gill-net sampling locations in 1999 and 2000. Numbers correspond to boat ramp locations, bays, or creek mouths in the following order: (1) North Gorge, (2) Evans, (3) Marcus Island, (4) Kettle River, (5) Kettle Falls, (6) Sherman Creek, (7) Colville River, (8) Rickey Point, (9) Roper Creek, (10) French Rocks, (11) Barnaby Island, and (12) Daisy.

TABLE 1.—Hatchery salmonid release information for the study area within Lake Roosevelt, Washington, during 1999 and 2000. Mean fish length and SD were determined with 100 fish from the three raceways at the Sherman Creek Hatchery (SCH). Fish lengths marked with an asterisk were calculated from the number of fish per pound (Piper et al. 1982).

Date	Species	Release facility	Location	Number released	Biomass released (kg)	Mean length (mm) (± SD)
Jun 28, 1999	Kokanee	SCH	SCH	279,847	12,451	155 (27)
Jul 29, 1999	Kokanee	SCH	SCH	88,775	4,030	167*
Jun 14, 2000	Rainbow trout	Net-pen	Kettle Falls	37,428	3,657	208*
Jun 14, 2000	Kokanee	Net-pen	Kettle Falls	197,975	4,563	133*
Jun 26, 2000	Kokanee	SCH	SCH	295,610	13,932	172 (25)
Jul 14, 2000	Rainbow trout	Net-pen	Kettle Falls	29,233	1,491	166*

with the Spokane River (Figure 1). At full pool, a 200-m stretch of stream and ~4-ha cove separate the hatchery from the main reservoir. Fish that disperse from the cove have been recovered in tributary mouth habitats such as the Colville River, in shallow embayments throughout the reservoir, and at various depths in the main stem (Tilson and Scholz 1998; Baldwin et al. 1999; LRFEP, unpublished data).

Methods

Predator collection and diet analysis.—The 1999 study included both pelagic and littoral gillnetting near the Sherman Creek embayment and Colville River arm of Lake Roosevelt (Figure 1). Sampling occurred on nine occasions over a 40-d period, beginning 1 d prior to the release of about 280,000 kokanees (12,500 kg) from SCH on June 28 (Table 1). A second group of about 89,000 (4,000 kg) fish was released on July 29 (day 33 of the study; Table 1). Kokanees were not fed for 1 d prior to release, and were forced out of the raceways on the day of release; however, thousands of kokanees were observed in the stream for several weeks following release.

Horizontal gill nets included floating, midwater, and bottom nets with 6-m long by 2.6-m deep panels and with mesh sizes ranging from 25 to 102 mm in 13-mm increments. Two of the horizontal gill nets had mesh sizes ranging from 51 to 102 mm to minimize bycatch of hatchery kokanee. Littoral gill nets were oriented perpendicular to the shoreline in water depths from 2 to 12 m. The smallest mesh size was set closest to shore. Nets were set on nine occasions: June 27, 28, 29, and 30; July 5, 12, 20, and 29; and August 6. On each occasion, three nets were set outside the mouth of Sherman Creek Cove (27 total net-nights), two nets were set in Colville River Bay (18 total net-nights), and two to three nets were set in the offshore main stem (22 total net-nights). Offshore gill nets were set at various depth strata, in water depths ranging from 23 to 45 m (maximum depth within the sampling area). Nets were generally set between 1800 and 1900 hours and retrieved between 2300 and 0200 hours, so piscivore diets represented the crepuscular and night feeding periods. All walleyes, northern pikeminnow, and burbot were measured to the nearest millimeter and weighed to the nearest 5 g, and their stomachs were removed and preserved in 95% ethanol until laboratory examination.

The 2000 study area was expanded to a 55-km stretch of the reservoir from Daisy to North Gorge. This area better represented the spatial heterogeneity of walleye diets following the hatchery release, and coincided with the boundaries of the abundance estimate. The 2000 study period was 31 d and began 1 d prior to a release of approximately 296,000 kokanees from the SCH on June 26. Other groups of kokanee were released prior to, during, and immediately following the study (Table 1). Twelve collection sites were used, but only seven were sampled on a particular night. Sherman Creek (site 6) and Colville River (site 7) were sampled each night, but all other sites were sampled alternately as odd- or even-numbered sites. Electrofishing surveys were conducted nine times between June 25 and July 25 (June 25, 26, 27, 28, and 29; and July 10, 11, 24, and 25). Our goal was to collect five nonempty walleye stomachs from each site, but this goal was not achievable at all sample sites due to empty stomachs and low catch rates.

Sites were sampled between 1600 and 2400 hours by use of a Smith-Root boat electrofisher with the DC voltage adjusted to produce 3–5 A and with a pulse frequency of 120 pulses/s. Piscivores were collected and measured to the nearest millimeter, and stomach contents were removed by gastric lavage for walleyes larger than 275 mm (Light et al. 1983). On occasions when a stomach appeared to still contain items after lavaging, the fish was sacrificed and the stomach was removed. Stomachs from 30 systematically selected walleyes (1 out of every 10 fish) were removed to determine gastric lavage efficacy.

Gill nets were used to increase sample size and supplement electrofishing data on July 10 and July 24, 2000. The horizontal gill nets previously described were used at Sherman Creek and at one downstream site and one upstream site. The upstream site was in Singer Bay (between sites 4 and 5) on both occasions, and the downstream sites were Martin Beach (between sites 9 and 10) on July 10 and Barnaby Island (site 11) on July 24.

Stomach contents were examined under a dissecting microscope in the laboratory and sorted by taxon to the nearest order for invertebrates and the nearest family, genus, or species for fish. Fish prey were identified with diagnostic bone keys (Hansel et al. 1988) and known example specimens taken from Lake Roosevelt. The blotted-dry wet weight of each prey category for individual predators was recorded to the nearest 0.01 g (Baldwin et al. 2000). The total length (TL), standard length (SL), or vertebral column length (VCL) was recorded to the nearest millimeter for all nondigested prey fish. The SLs or VCLs of partially digested kokanees were converted to TLs with the following regression equations developed by Yule and Luecke (1993):

$$\text{kokanee TL} = 1.05 \cdot \text{SL} + 26.8 \quad (n = 30,\ r^2 = 0.95), \quad \text{and}$$

$$\text{kokanee TL} = 1.49 \cdot \text{VCL} - 19.3 \quad (n = 46,\ r^2 = 0.99).$$

We developed the following similar equations for rainbow trout in this study from the diet of Lake Roosevelt piscivores:

$$\text{rainbow trout TL} = 1.03 \cdot \text{SL} + 14.1 \quad (n = 12,\ r^2 = 0.89), \quad \text{and}$$

$$\text{rainbow trout TL} = 1.23 \cdot \text{VCL} + 21.0 \quad (n = 12,\ r^2 = 0.82).$$

We used several statistical methods to define predator length–prey length relationships between walleyes and their salmonid prey. Tests were considered significant if P-values were less than 0.05. The ratio of prey length to predator length was determined by dividing prey fish length by predator length. The maximum values for the length ratio represented the point of gape limitation for walleyes feeding on salmonids. We compared the length distribution of kokanees in the raceways before release to the length distribution of kokanees in walleye stomachs with a Kolmogorov–Smirnov test (SAS Institute 1999). The null hypothesis (H_0) was that the lengths of kokanees in the raceways and in the diet of walleyes did not differ. We used a simple linear regression model to determine whether larger walleyes selectively chose larger salmonids (SAS Institute 1999; H_0 = no change in prey size with increased predator size). Analysis of variance (ANOVA) was performed on the regression points to determine whether the slope varied significantly from zero (SAS Institute 1999; H_0 = slope was equal to zero). We compared the slopes of the predator length–prey length regression lines by use of the equations provided in Zar (1984) to determine whether data could be pooled for the two years (H_0 = no difference between years).

In 2000, we compared the proportions of two different kokanee stocks in the diet contents of walleyes. Kokanee from Lake Whatcom, Washington, and from Meadow Creek, British Columbia, were reared in identical fashion, implanted with coded wire tags, and released as a mixed group from the SCH. We used a 2 × 2 contingency table analysis to compare the number of tags recovered from walleye stomachs to the number released for each stock. The H_0 was that there was no difference in the rate of tag recovery from the two stocks of kokanee.

Walleye abundance.—A mark–recapture study was used to estimate walleye abundance in the 55-km stretch of Lake Roosevelt from Daisy to North Gorge. Walleyes were initially collected and marked on June 19 and 20, 1999, and June 24 and 25, 2000, in conjunction with the Governor's Cup Walleye Tournament (GCWT) in Kettle Falls, Washington. The tournament boundaries were Daisy on the downstream end and North Gorge on the upstream end. Weather during the 1999 tournament was clear and calm on June 19 and partly cloudy and calm on June 20, with surface water temperatures at Kettle Falls ranging from 14°C to 16°C, respectively. The weather was partly cloudy and calm on June 24, 2000, and sunny and calm on June 25, 2000, with 13°C surface water temperatures at Kettle Falls.

Tournament rules and organization were designed to minimize walleye mortalities and maximize tagging opportunities for our study. Participants were required to have aerated and recirculating live-wells, and were only allowed to hold five walleyes at a time (even though state regulations allowed eight). Anglers were penalized one fish (out of total of 10) for scoring a dead walleye. A walleye was considered dead if it was unable to maintain an upright position in the live-well. Tournament regulations were modified to allow anglers to score all fish, with the 10 longest (heaviest) being used for tournament prizes. The modification was meant to increase the probability that anglers would provide all captured fish for marking and to reduce the chance that anglers would engage in ''high-grading,'' or holding fish in the live-wells for long periods until bigger fish were caught. A length–weight regression was used to estimate weights for tournament prizes, thereby avoiding additional handling during weigh-in. Weigh boats were located approximately every 3 km between Daisy and North Gorge to minimize holding time in and traveling distance of anglers' live-wells, and to ensure that releases were relatively close to the capture locations. Walleyes were not usually held in contestants' live-wells for more than 1 h, and were typically held for a shorter duration. When catch rates were high, anglers filled their live-wells quickly and thus scored them often. When catch rates were low, either the weigh boats would move to the contestants to score fish, or the contestants would bring one to four walleyes to a weigh boat to avoid the penalty of keeping mortalities in their live-wells.

Fish were tagged and released at the weigh boat following scoring for the tournament. Fish were first placed in an aerated live-well and held while the remaining fish were scored from an individual boat. Biologists on the weigh boats affixed each fish with an individually numbered, 20-mm-long, monofilament T-anchor Floy tag (model FD 94), and immediately released them. Tags were inserted at the posterior base of the first dorsal fin, as described by Guy et al. (1996). Walleyes were usually held for 10 min or less, but no longer than 20 min, during marking.

Walleyes were recaptured during the predation gill-net sampling at Sherman Creek between June 27 and August 9, 1999, and during gill-net and electrofishing sampling between June 25 and July 25, 2000. Due to low numbers of walleyes recaptured on each sampling day (low recapture probabilities), data from June 27–30, 1999, and June 26–28, 2000, were pooled to form single recapture occasions for each year (Menkens and Anderson 1988).

We used the computer program CAPTURE and model M_t-Chao to estimate walleye abundances, standard errors, 95% confidence intervals (CIs), and capture probabilities for both years (Otis et al. 1978; White et al. 1982; Chao 1989; Rexstad and Burnham 1991). Model M_t-Chao was used because it reduces to the Lincoln–Petersen estimator when there are two sampling occasions and performs well when capture probabilities are low (Chao 1989; Mitro and Zale 2002). In 1999 and 2000, walleyes shorter than 305 mm and 304 mm, respectively, were excluded from the analysis because they were smaller than the fish tagged during the marking periods and thus were not represented in the abundance estimates. Recaptures of fish marked during the recapture period were ignored during analysis. Precision of the estimate was measured by calculating a coefficient of variation (CV), which was defined as the ratio of the standard error of the estimate to the estimate (Hightower and Gilbert 1984). We evaluated heterogeneity due to gear selectivity by comparing the length frequency distributions of fish captured during the mark and recapture occasions in 1999 and 2000 with a Kolmogorov–Smirnov test (SAS Institute 1999; H_0 = no difference between the lengths of walleyes caught during the mark and recapture occasions). Angler-related mortality (harvest), emigration, and immigration were assumed to be minor and were evaluated with volunteer angler tag returns.

Piscivore consumption estimates.—We used the Wisconsin bioenergetics model (Hanson et al. 1997) to generate daily consumption estimates for each age-class of walleyes from ages 3 to 7 over the 41-d modeling period in 1999 (June 27 to August 6) and the 31-d modeling period in 2000 (June 25 to July 25). Model inputs specific to Lake Roosevelt included diet (Table 2), growth (Table 3), and thermal experience (Table 4). Literature values, provided in the model software manual, were used for prey caloric densities (Hanson et al. 1997). We modeled the average wet weight proportions of each diet item or category on each sampling day (Table 2). Sample sizes were too small to facilitate age-specific diets, so we used the average diet of all walleyes over 300 mm on each sampling day for ages 3–7. In 1999, diet proportions for walleyes over 300 mm were applied on nine occasions, whereas in 2000, diet proportions were applied on five occasions; the model extrapolated diet proportions between sampling dates. To achieve adequate sample sizes (10–20 fish), we combined days 2 and 3, days 4 and 5, days 16 and 17, and days 30 and 31 (Table 2). In

TABLE 2.—Mean wet weight diet proportions used to model consumption by walleyes in Lake Roosevelt, Washington, in 1999 and 2000. Caloric densities (J/g) for each prey group are shown in brackets. Sample size (*n*) of nonempty stomachs is provided.

Modeling day	*n*	Proportion of diet (%) Kokanee [5,500 J/g]	Rainbow trout [5,500 J/g]	Other fish [4,186 J/g]	Invertebrates [3,000 J/g]
		1999 (300–620-mm walleyes)			
1	4	0.00		0.25	0.75
2	16	0.94		0.00	0.06
3	14	1.00		0.00	0.00
4	31	1.00		0.00	0.00
9	44	0.95		0.00	0.05
17	32	0.95		0.00	0.05
24	12	0.75		0.00	0.25
33	12	1.00		0.00	0.00
41	14	0.83		0.10	0.07
		2000 (275–299-mm walleyes)			
1–31	26	0.04	0.04	0.73	0.20
		2000 (300–644-mm walleyes)			
1	9	0.34	0.22	0.44	0.01
2–3	33	0.55	0.13	0.11	0.22
4–5	33	0.40	0.09	0.31	0.20
16–17	28	0.69	0.10	0.11	0.10
30–31	12	0.25	0.00	0.66	0.09

2000, we used the diet of walleyes 275–299 mm in length to represent the diet of age-2 fish. The sample size was not large enough to determine the diets on multiple dates for 275–299-mm walleyes, so all samples were pooled to provide one diet estimate throughout the study. Walleyes smaller than 300 mm were excluded from model consumption extrapolations because they were not represented in the abundance estimate.

Walleye growth was determined by estimating the mean length at age from scale analysis and then adjusting for the duration of the study period. We used a 4-year (1996–1999) sample of scales that we assumed represented average walleye growth in Lake Roosevelt (LRFEP, unpublished data). We estimated growth from June 15 (formation of the annulus) to October 15 (fall gill-netting and electrofishing). Mean lengths of each

TABLE 3.—Population characteristics of walleyes in Lake Roosevelt, Washington, in 1999 and 2000. Age frequency was estimated from standardized, reservoir-wide gill-net and electrofishing surveys. Mean length was back-calculated to the nearest annulus from scale-aged walleyes captured in 1999–2000 ($n = 2{,}693$). Growth was modeled for 41 d in 1999 and 31 d in 2000 and was based on the mean monthly growth rate from July to October, 1996–2000. The proportion *P* of maximum consumption as predicted by the bioenergetics model is provided for each cohort.

Year and age-class (years)	Age frequency	Mean length (mm)	SD length (mm)	Model Start weight (g)	End weight (g)	*P*
1999						
2						
3	0.45	333	46	307	356	0.31
4	0.36	398	48	537	599	0.30
5	0.11	458	59	826	898	0.29
6	0.05	510	69	1,157	1,238	0.29
7+	0.02	558	83	1,524	1,613	0.28
2000						
2		261	42	144	169	0.65
3	0.48	333	46	307	343	0.33
4	0.32	398	48	537	582	0.32
5	0.09	458	59	826	879	0.32
6	0.07	510	69	1,157	1,216	0.31
7+	0.04	558	83	1,524	1,589	0.31

TABLE 4.—Mean water temperatures from the upper 12 m of water, averaged across three sites in northern Lake Roosevelt, Washington, in 1999 and 2000.

Study date	Modeling day	Water temperature (°C)
1999		
Jun 27	1	13.3
Jun 30	4	13.8
Ju1 12	16	15.2
Ju1 25	29	16.3
Aug 6	41	17.1
2000		
Jun 25	1	14.4
Jul 5	11	15.4
Jul 25	31	17.6

age-group (ages 2–7) were converted to weights with a log-transformed length–weight regression (SAS Institute 1999). We then estimated the mean daily growth rate from June 15 to October 15 and applied it to the number of days in the study period.

Thermal experience was estimated by averaging water temperature measurements from the top 12 m at three water quality sites collected by the LRFEP during biweekly water quality sampling. Mean water temperature of the entire water column was not used because very few walleyes were captured in deep offshore nets, where water temperatures were slightly cooler.

Age-specific consumption estimates were adjusted to their relative frequency from reservoir-wide gill-net and electrofishing surveys in 1999 (LRFEP, unpublished data; Table 3). Consumption rates were expanded to piscivore abundance estimates to determine the biomass of each fish prey species consumed. Percent loss of each species was calculated by summing the estimated number of fish consumed during the study interval by the number stocked.

Salmonid growth during the study period was determined by applying a daily growth rate to the mean size at release. Daily growth for rainbow trout and kokanee was estimated with the bioenergetics model, beginning with the size at stocking and ending with the mean capture size in fall gill-net surveys (LRFEP, unpublished data).

In 2000, kokanees and rainbow trout were released from net-pens prior to our study (June 14), and these fish were present in the diet of walleyes on our first day of sampling. To estimate walleye consumption of these fish, we back-calculated consumption for the 10th day before the start of our study (June 25) to the first day (June 14) by use of the diet, growth, and thermal experience from June 25. Although not ideal, this method provides a conservative estimate because diet proportions were likely higher and temperatures were definitely lower during the pre-study period.

Results

Predator Collection and Diet Analysis

Walleyes represented 89% and 94% of piscivore relative abundance in 1999 and 2000, respectively (Table 5). Burbot comprised 8% of piscivore relative abundance in 1999, but less than 1% in 2000. Northern pikeminnow comprised 3% of piscivore relative abundance in 1999 and 5% in 2000 (Table 5). Salmonid prey were present in burbot (1999) and northern pikeminnow (2000) diets, but the sample size of nonempty stomachs was too small to facilitate further analysis.

Walleyes sampled in 1999 were larger and from a more limited geographic range than in 2000. In 1999, 281 walleyes were captured, with lengths ranging from 196 to 620 mm and a mean length of 432 mm (SD = 82; Figure 2). Most walleyes were captured in the Sherman Creek mouth (n = 233; 27 net-nights) and the Colville River mouth (n = 44; 18 net-nights). Only four walleyes were captured in the 22 net sets from the offshore mainstem sites. In 2000, 585 walleyes were captured, with lengths ranging from 115 to 644 mm and a mean length of 326 mm (SD = 83; Figure 2). Most walleyes (46%) were captured in the Colville River mouth (site 7), whereas only 3% came from the Sherman Creek mouth (site 6; Figure 1). Sites 1–5 (upstream) provided 10% of the total walleye catch and sites 8–12 (downstream) provided 40% (Figure 1).

Salmonids were an important diet item for walleyes after hatchery releases during 1999 and 2000. In 1999, kokanee constituted 75–100% of the walleye (>300 mm) diet by weight, and were present in 142 of 175 (81%) nonempty stomachs (Table 2). Thirty-four percent of walleye stomachs were empty in 1999 (Table 5). In 2000, kokanees and rainbow trout comprised 25–79% of large (300–644 mm) walleye diets and 8% of small (275–299 mm) walleye diets (Table 2). Salmonid prey fish were present in 72 of 115 nonempty large walleye stomachs and 4 of 26 small walleye stomachs. The lavage technique was successful in removing all diet items in 90% (27 out of 30) of the walleyes randomly subsampled for lavage efficacy.

The walleye population removed more small than large salmonids; however, larger walleyes

TABLE 5.—Total catch of piscivores sampled in Lake Roosevelt, Washington, that were longer than 300 mm in 1999 or longer than 275 mm in 2000. Percentages of fish with empty stomachs are provided in parentheses. Northern pikeminnow (NPM) and burbot consumption were not modeled due to small sample sizes of those predators.

Sampling date and abundance	Modeling day	Number caught (% empty stomachs) Walleyes	Northern pikeminnow	Burbot
1999				
Jun 27	1	13 (69)		1 (0)
Jun 28	2	22 (27)	3 (67)	2 (0)
Jun 29	3	16 (13)	2 (100)	1 (100)
Jun 30	4	39 (21)	1 (100)	2 (100)
Jul 5	9	63 (30)	2 (100)	5 (40)
Jul 13	17	54 (43)	1 (100)	6 (67)
Jul 20	24	20 (40)		5 (80)
Jul 29	33	18 (33)		1 (100)
Aug 6	41	26 (46)		
Total		271 (34)	9 (89)	23 (61)
Relative abundance		0.89	0.03	0.08
2000				
Jun 25	1	27 (48)		1 (100)
Jun 26	2	18 (44)		
Jun 27	3	124 (77)	4 (100)	
Jun 28	4	90 (79)	7 (14)	1 (0)
Jun 29	5	37 (41)	1 (100)	
Jul 10	16	50 (60)	7 (14)	
Jul 11	17	15 (40)		1 (100)
Jul 24	30	32 (56)	3 (67)	
Jul 25	31	10 (60)		1 (100)
Total		403 (65)	22 (41)	4 (75)
Relative abundance		0.94	0.05	0.01

tended to consume larger salmonid prey. The length distribution of kokanees consumed by walleyes was significantly smaller than that of kokanees measured in the raceways before release during both 1999 (Kolmogorov–Smirnov test; $\chi^2 = 12.6$, df = 2, $P = 0.004$) and 2000 ($\chi^2 = 34.3$, df = 2, $P < 0.001$; Figure 3). The sample size of measurable rainbow trout in walleye diet samples was too small ($n = 6$) to facilitate statistical comparison between the size eaten (mean 147 mm; SD = 49) and the size released (208 mm). The mean predator length–prey length ratio was 0.32 in 1999 and 0.33 in 2000. The maximum predator length–prey length ratios of 0.53 in 1999 and 0.54 in 2000 indicate that gape limitation occurred at approximately 50% of the predator's body length (Figure 4). Results of the predator length–prey length ratio were pooled between years because the slopes of the regressions were not significantly different ($t = -0.118$, df = 251, $P > 0.50$). Prey length increased with predator length as described by the following relationship:

$$\text{kokanee length} = \text{walleye length} \times (0.20) + 50.58$$

The slope of the regression line was significant (ANOVA; $F = 66.10$, df = 1, 254, $P < 0.001$), but the relationship was weak ($r^2 = 0.21$; Figure 4).

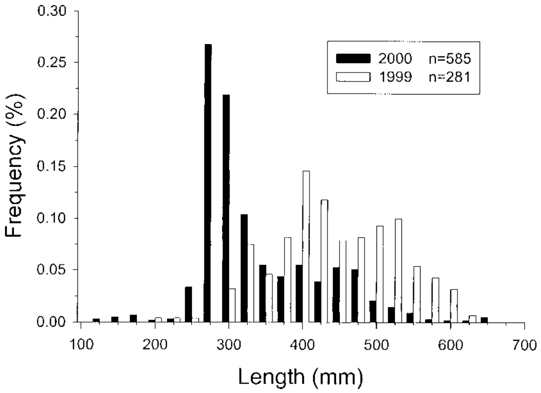

FIGURE 2.—Length frequency of walleyes collected in Lake Roosevelt, Washington, with experimental mesh gill nets in 1999 (white bars) and electrofishing and experimental mesh gill nets in 2000 (black bars).

The two different strains of kokanee experienced similar rates of predation by walleyes, as indicated by coded wire tag recoveries. Twenty coded wire tags were recovered from 94,518 ko-

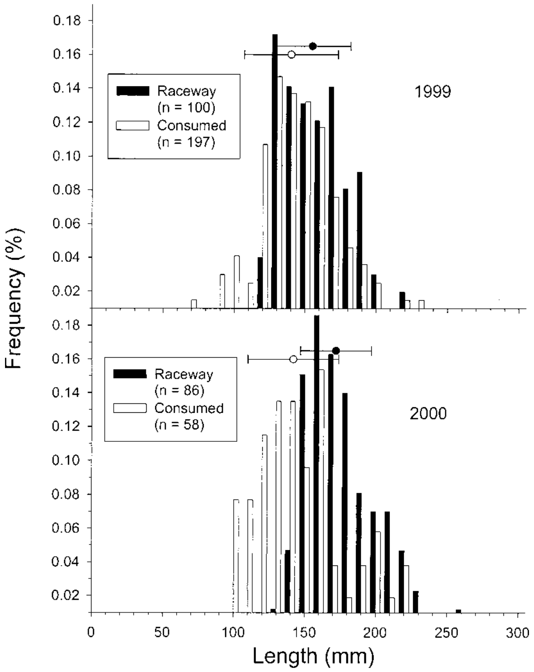

FIGURE 3.—Length frequency (bars) and mean total length (circles; ±SD) of kokanees released from the Sherman Creek Hatchery raceways (black) and kokanees consumed by walleyes (white) in Lake Roosevelt, Washington, during 1999 and 2000.

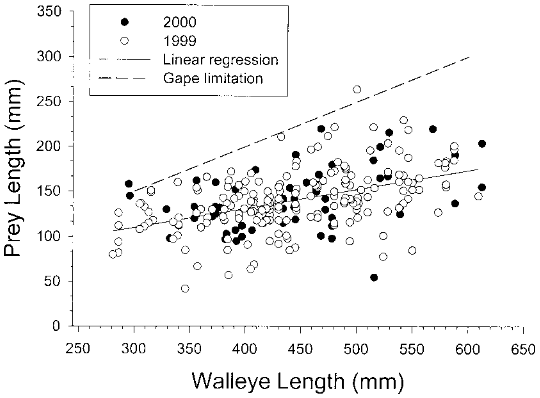

FIGURE 4.—Relationship between walleye length and salmonid prey length in Lake Roosevelt, Washington, during 1999 and 2000. The regression (solid line) represents pooled data from both years, and is defined by the following equation: salmonid length = walleye length · (0.20) + 50.58 (r^2 = 0.21). The dashed line shows a linear relationship of walleye length · 0.50 and represents walleye gape limitation.

TABLE 6.—Walleyes captured between Daisy and North Gorge in Lake Roosevelt, Washington, in 1999 and 2000. Captures (*C*) are the number of unmarked fish, recaptures (*R*) are the number of marked fish, and the totals are the pooled values used to generate the abundance estimates. Asterisks denote dates not included in the abundance estimates due to pooling.

Sampling date	*C*	*R*
1999		
Marking period		
Jun 19	734	
Jun 20	760	
Total	1,494	
Recapture period		
Jun 27	25	3
Jun 28	21	1
Jun 29	13	2
Jun 30	32	2
Total	91	8
Jul 5*	60	1
Jul 6*	5	1
Jul 7*	10	1
Jul 13*	48	2
Jul 20*	20	0
Jul 29*	16	0
Aug 4*	1	0
Aug 5*	2	0
Aug 6*	27	2
2000		
Marking period		
Jun 24	404	
Jun 25	301	
Total	714	
Recapture period		
Jun 26	12	1
Jun 27	84	5
Jun 28	50	1
Total	146	7
Jun 29*	18	0
Jul 10*	32	3
Jul 11*	14	0
Jul 24*	12	0
Jul 25*	10	0

kanees of Lake Whatcom origin, whereas 24 coded wire tags were recovered from 105,432 kokanees of Meadow Creek origin. The proportions of Lake Whatcom and Meadow Creek kokanees recovered from walleye stomachs did not differ significantly (χ^2 = 0.06, df = 1, $P > 0.75$).

Walleye Abundance

In 1999, 1,494 walleyes (≥305 mm) were tagged and released during the GCWT. Between June 27 and June 30, 91 walleyes were captured during the predation gill-net sampling, eight of which were recaptures (Table 6). The estimated number of walleyes 305 mm TL or larger was

16,610 (SE = 5,266, CV = 0.32, 95% CI = 9,296–30,864). Capture probabilities during mark and recapture occasions were 0.09 and 0.01, respectively.

In 2000, 714 walleyes (≥304 mm) were tagged and released during the GCWT. A total of 146 walleyes were collected between June 26 and June 28 during the electrofishing and gill-net sampling between Daisy and North Gorge. Of the 146 walleyes, seven were recaptures (Table 6). The estimated number of walleyes 304 mm TL or larger was 12,233 (SE = 3,932, CV = 0.32, 95% CI = 6,747–22,834). Capture probabilities during mark and recapture occasions were 0.06 and 0.01, respectively.

Anglers voluntarily returned tags or tag information from 22 walleyes that were originally marked at the 1999 tournament and caught between July 3 and July 30, 1999. Of those 22 returns, nine (40.9%) were captured outside of the study area. All fish caught by anglers outside of the study area were within 10 km of the study area.

Anglers reported catching six walleyes that had been tagged during the 2000 tournament, between June 25 and July 21, 2000. One of the six was caught during the abundance estimate period (June 25) within the study area and was released. Another (16.7%) of the six returns was caught 6 km outside of the study area. The fish that emigrated from the study area in 2000 was caught after the abundance estimate period (July 21).

Size selectivity of walleyes varied significantly among gear types used during mark and recapture periods of the abundance estimate. The length distribution of walleyes captured by angling was significantly different than that of walleyes collected by gillnetting in 1999 (Kolmogorov–Smirnov test; $\chi^2 = 36.7$, df = 2, $P < 0.0001$) and electrofishing in 2000 ($\chi^2 = 33.5$, df = 2, $P < 0.0001$; Figure 5).

Piscivore Consumption

Estimates of consumption by walleyes, expressed as a proportion of maximum consumption (P_{max}) were generally low and decreased slightly from ages 3 to 7. The values of P_{max} were similar in 1999 and 2000 for walleyes aged 3–7, ranging from 0.28 to 0.31 in 1999 and from 0.31 to 0.33 in 2000 (Table 3). In 2000, age-2 walleyes had a higher P_{max} value (0.65) than did walleyes aged 3–7; however, due to their shorter total length, age-2 walleyes did not have access to as many stocked salmonids as did larger walleyes (Table 3).

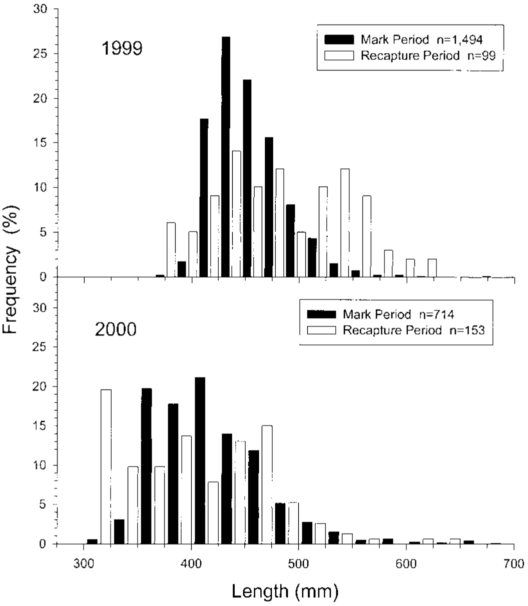

FIGURE 5.—Length frequency of walleyes captured in Lake Roosevelt, Washington, during the mark–recapture studies in 1999 and 2000. Walleyes were captured by angling during the marking periods on June 19 and 20, 1999, and June 24 and 25, 2000 (black bars). Walleyes were recaptured by gillnetting in 1999 (June 27–30) and by electrofishing in 2000 (June 26–28) (white bars).

Individual walleye consumption of kokanees ranged from 3.0 to 12.4 g/d in 1999 and from 0.1 to 8.8 g/d in 2000, depending on walleye age and day of the study. The total daily consumption of kokanees by individual walleyes increased with age, but cumulatively, age-3 and age-4 walleyes (mean lengths 333 mm [SD = 46] and 398 mm [SD = 48], respectively) had the greatest impact on hatchery releases (Figure 6) because of their high relative abundances (Table 3).

In 1999, walleyes consumed 200 kg of kokanees per 1,000 individuals 305 mm and larger. Maximum consumption of kokanees by walleyes occurred on day 33 (6 kg/1,000 walleyes; Figure 7), when diet proportions were 100% kokanee following the second hatchery release (Table 2). With a population estimate of 16,610 walleyes (95% CI = 9,296–30,864), a total of 3,316 kg of kokanees were consumed from two releases totaling 16,481 kg, for a loss of 20% (not adjusted for kokanee growth during the study period). Kokanee growth during the study was 0.9 g/d (27 g/month; 26 mm/month), starting with a mean release size of 166 mm and 45 g. Therefore, the cumulative number of kokanees lost to predation was 54,073 (30,263–

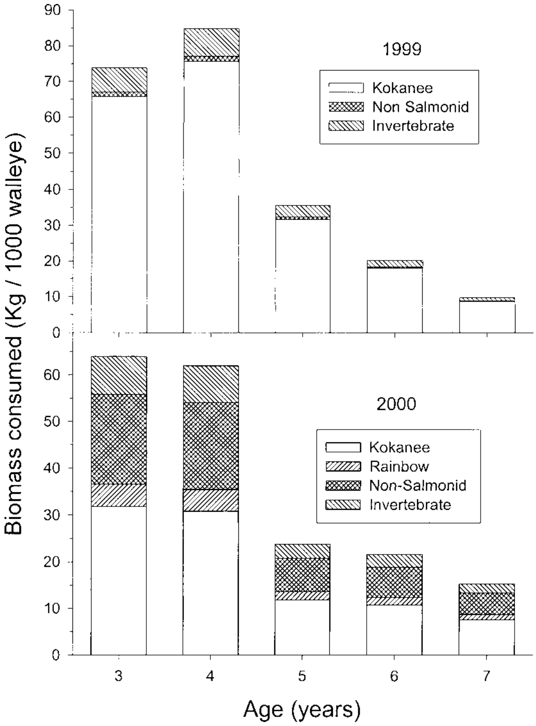

FIGURE 6.—Age-specific consumption of various prey types per 1,000 walleyes in Lake Roosevelt, Washington, from June 27 to August 6, 1999, and from June 14 to July 25, 2000. The 1,000 walleye predators were adjusted to the age-class structure of 3–7-year-old walleyes. Age-7 and older walleyes were modeled as one cohort and reported as age 7+.

100,477) or 15% (8–27%) of the hatchery releases within the study area.

In 2000, walleyes consumed 93 kg of kokanees and 14 kg of rainbow trout per 1,000 individuals 304 mm and larger. Maximum consumption of kokanees occurred on day 17 (4.2 kg/1,000 walleyes) and maximum consumption of rainbow trout on day 1 (1.2 kg/1,000 walleyes; Figure 7). With a population estimate of 12,233 walleyes (95% CI = 6,747–22,834), a total of 1,357 kg of kokanees and 313 kg of rainbow trout were consumed. In 2000, we used growth rates of 0.9 g/d and 1.7 g/d for kokanees and rainbow trout, respectively. Therefore, kokanee numerical losses totaled 34,076 (95% CI = 18,794–63,607), translating to a 9.4% (95% CI = 5.2–17.5%) loss; and rainbow trout numerical losses totaled 4,839 (95% CI = 2,669–9,033), translating to a 7.3% (95% CI = 4.0–13.6%) loss.

Discussion

Predatory impacts of native and nonnative piscivores on native salmonids has been studied extensively in the lower Columbia River basin (Vigg et al. 1991; Tabor et al. 1993; Collis and Beaty 1995; Zimmerman 1999); however, resident fish predator–prey interactions in the upper Columbia River basin have not been investigated. The kokanee stocking program in Lake Roosevelt was not meeting harvest and spawner return goals, and predation was identified as a potential limiting factor (Tilson and Scholz 1998; Cichosz et al. 1999). Reservoir-wide diet studies and bioenergetics modeling revealed inconsistent patterns in predatory impact that resulted in a broad range (0–73%) of possible impacts to hatchery releases (Baldwin et al. 1999).

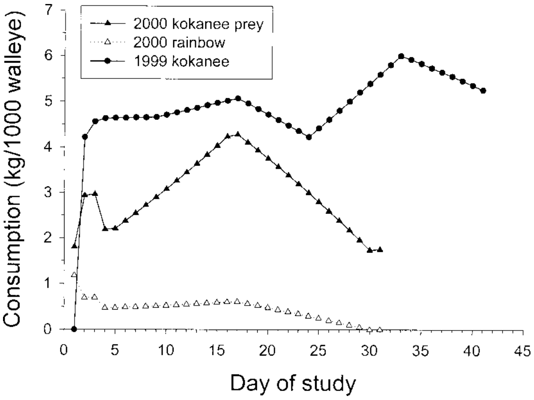

FIGURE 7.—Daily consumption of kokanees and rainbow trout by walleye predators in Lake Roosevelt, Washington, in 1999 and 2000. The 1,000 walleye predators are adjusted to the age-class structure of walleyes aged 3 and older.

In 1999, our study was limited because our diet information came from a small portion (3–5 reservoir kilometers) of the geographic range of the abundance estimate (55 reservoir kilometers). Consumption estimates were then expanded to total walleye abundance; however, data collected by LRFEP (July 7–9; *n* = 16) suggested that walleye diets contained much smaller proportions of kokanee (7%) when taken from various locations throughout the study area (LRFEP, unpublished data). This conclusion led us to a different approach for 2000 that allowed us to sample from a broader area. The proportion of kokanee in the diets declined in 2000, but so did the population estimate (by 36%), thereby reducing the impact from 15% to 9.4%. We believe the sampling biases from our 1999 study overestimated the impact of walleyes. However, both years are an underestimate of total predation due to some consumption by walleyes smaller than 300 mm and by other predators, such as burbot and northern pikeminnow, that could not be quantified. Despite the limitations of the 1999 study, it was helpful in understanding our sampling biases and annual abundance fluctuations. The 1999 study also increased the sample size of salmonids consumed by walleye predators for the predator–prey relationships.

Closed population models, including M_t-Chao, have three basic assumptions: (1) the population in the study area remains closed throughout the study, (2) the marked fish do not lose their tags, and (3) all fish in the population have an equal chance of being captured during each sampling occasion (Otis et al. 1978; Seber 1982; White et al. 1982; Pollock et al. 1990).

In short-term studies, open populations can sometimes be estimated with closed models because recruitment and mortality can essentially be ignored, as long as there is no significant immigration or emigration (Pollock et al. 1990). Due to the short time period of our estimates, natural mortality and recruitment (growth to a taggable size; 305 mm in 1999 and 304 mm in 2000) were assumed to be negligible. The most likely causes for violations of the closure assumption would have been angler-related mortalities, emigration, or immigration. Based on voluntary angler tag returns of zero for 1999 and one tag for 2000 (the fish was released), there was limited angler harvest during our study. Additionally, angler harvest was low because 45% of the walleyes marked at the 1999 tournament and 48% of the walleyes tagged during the 2000 tournament were within a protective slot limit of 406–508 mm.

Short-term delayed mortality resulting from capture by live-release tournament angling could have biased our abundance estimates. Hooking mortality has been demonstrated to be negligible when walleyes are released immediately after being caught (Fletcher 1987; Payer et al. 1989; Schaefer 1989); however, several studies have demonstrated that short-term delayed mortality of tournament-caught walleyes can be substantial (Goeman 1991; Fielder and Johnson 1994; Hoffman et al. 1996). Increased mortality was generally related to poor weather conditions (high winds and rough water), high water temperatures, high bag limits, non-recirculating live-wells, and lack of penalties for dead fish. We believe short-term delayed mortality at the GCWT was negligible due to the tournament structure, optimal temperatures, and good weather conditions. The GCWT was designed to minimize mortalities and was very similar to the modified tournament structure that would have resulted from the combined recommendations of Goeman (1991), Fielder and Johnson (1994), and Hoffman et al. (1996).

The main concerns regarding violations of the population closure assumption were due to emigration and immigration. Some emigration occurred during both years, as indicated by angler tag returns; however, we minimized the effect of this by reducing our abundance estimate temporally. This suggested that our abundance estimate was low; however, immigration was not evaluated. If mortality, emigration, and immigration all occurred, then abundance was overestimated (Otis et al. 1978; Pollock et al. 1990).

We assumed zero tag loss due to the short time period of the estimate. McLellan (1998) held 24 walleyes (391 mm to 506 mm) that were tagged in the same manner as this study for 60 d in laboratory streams and observed no tag loss.

There are three types of unequal capture probabilities: time, behavior, and heterogeneity, which can act independently or in combination in a population (Otis et al. 1978; White et al. 1982; Pollock et al. 1990). The model we selected, M_t-Chao, accounts for unequal capture probabilities due to time effects. By changing gear types between the marking and recapture occasions, we eliminated a behavioral response (Pollock et al. 1990). Violation of the assumption of equal catchability due to heterogeneity may have also biased our abundance estimates. If capture probabilities are heterogeneous in each sample, but independent from sample to sample, then the estimate is not biased (Pollock et al. 1990). The different gear types used in the mark and recapture periods had significantly different size selection in both years, but the size selection was independent, so we contend that our estimates were unbiased by heterogeneity.

For both years, the modeling period extended past the end of the recapture period for the abundance estimate. The cutoff date for recaptures was selectively chosen to reduce violation of assumptions of the mark–recapture models. We assumed that during the latter half of each predation study, our abundance estimate did not change, even though we had some evidence of walleyes moving into and out of the study area. We believe that any error incurred from walleye movement during the study period would not change the abundance estimate to the point of substantially altering the estimated impacts on hatchery releases.

Physical conditions vary annually in Lake Roosevelt (Cichosz et al. 1997, 1999); the timing of reservoir refill, temperature, turbidity, and water retention times are all dependent on spring runoff patterns and corresponding flood control rule curves. The number of walleyes in the study area in any given year may depend on these conditions.

Although percent impacts on kokanees and rainbow trout were similar in 2000, the Sherman Creek and Kettle Falls rainbow trout releases only represented 16% of the reservoir-wide net-pen program. In contrast, 77% of hatchery-reared kokanees were released in this area in 2000. Therefore, impacts on the overall hatchery program were better represented for kokanee than for rainbow trout.

During both years, consumption of kokanee peaked in the middle to end of the study period. The proportion of salmonids in the diet of walleyes remained relatively high, and water temperatures increased, thereby increasing the foraging ability and digestive efficiency of walleyes (Swenson and Smith 1973). If walleyes continued to feed on hatchery-released salmonids until fall, the impact of predation could have increased two- to threefold.

The length frequency of walleyes was considerably different between years, due primarily to gear selectivity (Hamley 1975; Rudstam et al. 1984; Henderson and Wong 1991). This difference had little effect on the predator length–prey length relationship and did not increase the mean prey length consumed.

Management options based on our results would include the release of larger hatchery salmonids, use of different release sites that have lower densities of walleyes, or reduction in total walleye abundance and the mean size of walleyes in the population through regulation changes. Release of larger fish might increase rainbow trout survival, but rearing kokanees to larger sizes would likely increase the rate of precocity, thereby reducing the number of age-3 fish recruiting to the fishery and returning to egg collection sites (Patterson 1998). Kokanees have been released from other areas in the reservoir, including the Spokane River below Little Falls Dam, Seven Bays near the confluence with the Spokane River, and Lincoln (near Hawk Creek) without substantially better returns than the northern release sites (Tilson and Scholz 1998; McLellan et al. 2001). A change in the walleye regulation has already been submitted to the Washington Department of Fish and Wildlife that would allow harvest of walleyes between 406 and 508 mm (the previously protected slot limit). Because harvest of smaller walleyes would not be restricted, this regulation should contribute to increased survival of stocked salmonids.

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