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[Article]

Using Bioenergetics Modeling to Estimate Consumption of Native Juvenile Salmonids by Nonnative Northern Pike in the Upper Flathead River System, Montana

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Abstract.—Introductions of nonnative northern pike *Esox lucius* have created recreational fisheries in many waters in the United States and Canada, yet many studies have shown that introduced northern pike may alter the composition and structure of fish communities through predation. We estimated the abundance of nonnative northern pike (2002–2003) and applied food habits data (1999–2003) to estimate their annual consumption of native bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisi* juveniles in the upper Flathead River system, Montana. Population estimates were generally consistent among years and ranged from 1,200 to 1,300 individuals. Westslope cutthroat trout were present in the diet of younger ($\leq$600 mm) and older ($>$600 mm) northern pike during all seasons and bull trout were found only in larger northern pike during all seasons but summer. Bioenergetics modeling estimated that the northern pike population annually consumed a total of 8.0 metric tons (mt) of fish flesh; the highest biomass was composed of cyprinids (4.95 mt) followed by whitefishes *Prosopium* spp. (1.02 mt), bull trout (0.80 mt), yellow perch *Perca flavescens* (0.41 mt), westslope cutthroat trout (0.34 mt), and other fishes (centrarchids and cottids; 0.14 mt). Numerically, the northern pike population consumed more than 342,000 fish; cyprinids and catostomids comprised approximately 82% of prey fish (278,925), whereas over 13,000 westslope cutthroat trout and nearly 3,500 bull trout were eaten, comprising about 5% of the prey consumed. Our results suggest that predation by introduced northern pike is contributing to the lower abundance of native salmonids in the system and that a possible benefit might accrue to native salmonids by reducing these predatory interactions.

Introductions of exotic species threaten the biodiversity of native faunas throughout the world (Mack et al. 2000). The extinction of many rare and endangered plant and animal species are often a direct result of anthropogenic introductions of exotic species into novel environments (Allan and Flecker 1993). Invasive species may negatively affect native biota through competitive exclusion, niche displacement, hybridization, introgression, predation, and ultimately extinction (Mooney and Cleland 2001).

In North America, freshwater fish are probably the most threatened group of vertebrates other than amphibians (Ricciardi and Rasmussen 1999). A review of the literature by Miller et al. (1989) found that exotic species introductions (illegal and intentional) were a factor in 68% of fish extinctions in North America, and the rates of introductions have increased dramatically in the last 50 years (Fuller et al. 1999), affecting nearly every major watershed in the United States (Courtenay et al. 1984). Fisheries management programs have transplanted popular sport fishes, such as northern pike *Esox lucius* (McMahon and Bennett 1996), brown trout *Salmo trutta* (Taylor et al. 1984), brook trout *Salvelinus fontinalis* (Holton 1990), rainbow trout *Oncorhynchus mykiss* (Hitt et al. 2003), and lake trout *S. namaycush* (Bowles et al. 1991), to provide recreational opportunities, while other aquatic organisms have been transplanted to enhance fish growth (e.g., opossum shrimp *Mysis relicta*; Northcote 1991; Spencer et al. 1999). Additionally, international

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commerce has facilitated the movement of species via ballast water in ships (e.g., the zebra mussel *Dreissena polymorpha*) and aquarium releases, and illegal translocations of species persistently confound fisheries management programs (Fuller et al. 1999). Regardless of the cause of species introductions, the establishment and proliferation of invasive species often results in the decline and potential extinction of native species, with invasive predators having the most dramatic effects on community structure and species persistence (Mooney and Cleland 2001).

The northern pike is a top-level piscivore usually found in warm, slow-moving water within meandering and vegetated rivers or warm weedy bays of lakes (Scott and Crossman 1973). Northern pike have a circumpolar distribution in the Northern Hemisphere, and in North America the native distribution of northern pike extends from Alaska south to Nebraska and east to Missouri (Scott and Crossman 1973). However, northern pike have been widely introduced (both illegally and legally) outside their native range, yet many studies have shown that introduced northern pike may alter the composition and structure of fish communities through predation (McMahon and Bennett 1996).

Northern pike were illegally introduced and have become a sport fishery in the upper Flathead River upstream from Flathead Lake, Montana. This lake-influenced section of the upper Flathead River also is used by native subadult bull trout *S. confluentus* and westslope cutthroat trout *O. clarkii lewisi* for rearing and overwintering, and as a migratory pathway to Flathead Lake (Shepard et al. 1984; Muhlfeld et al. 2000; Muhlfeld and Marotz 2005). However, populations of bull trout and westslope cutthroat trout have declined throughout their historic range, including the upper Flathead River system, owing primarily to habitat degradation and fragmentation and interactions with nonnative species (Liknes and Graham 1988; Rieman et al. 1997; Shepard et al. 2005). The spatial and temporal overlap may increase the probability of predation by northern pike on juvenile salmonids. Therefore, understanding the potential predatory effects of introduced northern pike on native juvenile salmonids is critical for implementing effective management programs for conservation and recovery of existing bull trout and cutthroat trout populations.

Bionenergetics modeling is a valuable tool for assessing the trophic level dynamics in fish communities (Hansen et al. 1993; Ney 1993). These models have been used to estimate predator–prey relationships and food consumption (Stewart et al. 1981; Beauchamp et al. 1989; Ruggerone and Rogers 1992). Systemwide consumption of juvenile bull trout and westslope cutthroat trout is of extreme importance to fisheries management for protection and conservation of critical populations and life histories, Endangered Species Act concerns, and public pressures to provide quality fisheries. The goal of this study was to determine the potential predatory effects of northern pike on native juvenile salmonids in an interconnected river and lake system. The specific objectives were to (1) estimate northern pike abundance, (2) quantify the seasonal diets of northern pike, and (3) estimate the annual consumption of juvenile salmonids by the northern pike population.

Study Area

We estimated the predation rates, diets, and growth of northern pike throughout the upper Flathead River system in Montana. The current known distribution of northern pike in the upper Flathead River system extends from Flathead Lake upstream to the confluence of the Stillwater and Flathead rivers (Muhlfeld et al. 2000). Thus, the study area included the lower section of the main-stem Flathead River from the mouth of the Stillwater River to the north end of Flathead Lake, Flathead County, Montana (Figure 1). This 32-km section of the river is a low-gradient (<0.4-m/km) sinuous channel that contains deep, slow-run habitat in the main channel (maximum depth = 27.5 m) with connected slough habitats in lateral areas of the floodplain. The reach is characterized by sand, silt, and gravel substrates and dominated by rooted and floating aquatic vegetation in the summer, especially in the sloughs. This river portion is influenced by seasonal backwater effects (vertical fluctuations of approximately 3 m) caused by the impoundment of Flathead Lake by Kerr Dam at the outlet. Flathead Lake is held near full pool capacity for water storage and recreation from June through September, so water levels increase during the summer months, transforming the lower river from a lotic to a lentic aquatic environment. The main-stem Flathead River is also influenced by water releases from Hungry Horse Dam, which is located 69 km upstream in the South Fork Flathead River. Dam operations have essentially reversed the natural hydrograph resulting in the storage of spring meltwater during spring and summer and releasing water in the fall and winter when flows were historically low.

Native fishes in the lower river include northern pikeminnow *Ptychocheilus oregonensis*, largescale sucker *Catostomus macrocheilus*, longnose sucker *C. catostomus*, peamouth *Mylocheilus carinus*, redside shiner *Richardsonius balteatus*, bull trout, westslope cutthroat trout, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *P. coulteri*, and sculpins *Cottus* spp. Nonnative fishes found in the upper

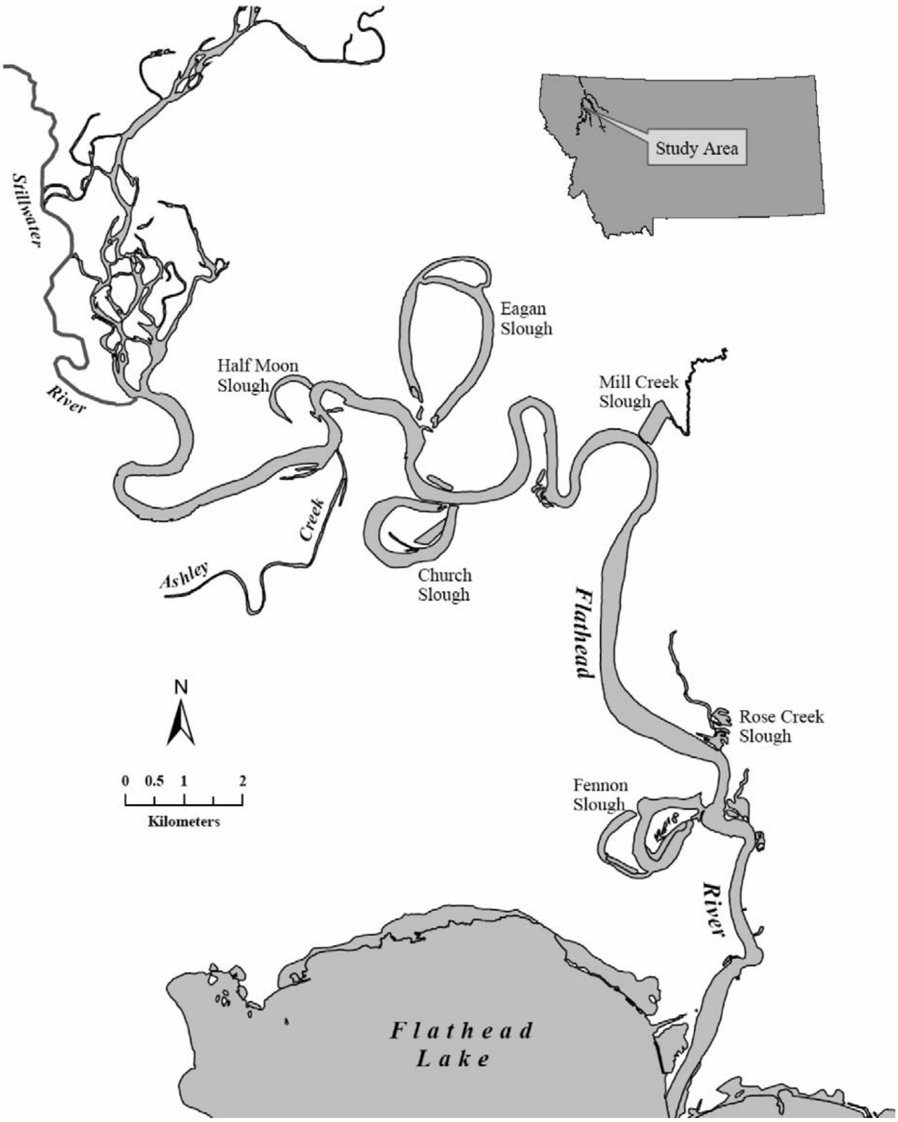

FIGURE 1.—Map of the study area in the upper Flathead River, Montana.

Flathead River include lake trout *S. namaycush*, lake whitefish *Coregonus clupeaformis*, kokanee *O. nerka*, yellow perch *Perca flavescens*, northern pike, largemouth bass *Micropterus salmoides*, pumpkinseed *Lepomis gibbosus*, and black bullhead *Ameiurus melas*.

Methods

Northern pike sampling.—Passive trapping and angling were used to estimate the abundance and growth of northern pike, whereas diet data were collected from angler-caught fish. Fyke traps were deployed from 4 April to 31 October 2002 throughout the river and sloughs; ice formation precluded sampling during late fall and winter. An equal number of traps were initially set in the river and sloughs and as flows increased during spring runoff we moved them to the sloughs, which are known spawning areas for pike in the Flathead River system (Muhlfeld et al. 2000). The 2002 catch data revealed significantly higher catch rates for all fishes, including northern pike, during spring high flows (April–June), with catch rates declining dramatically in the summer and fall months (<5% of the total annual catch). Thus, subsequent trapping efforts were focused during late winter and

TABLE 1.—Notation in the capture–recapture methods (Evans and Bonett 1994) used to estimate northern pike in the upper Flathead River systerm. Northern pike captured in period 1 and recaptured in period 2 are represented by F_{11}, while those not recaptured in period 2 are represented by F_{12}. Northern pike captured in period 2, but not in period 1 are represented by F_{21}; F_{22} is the number of fish not seen in periods 1 or 2. Column and row totals are indicated by asterisks.

Period 1 capture status	Captured in period 2	Not captured in period 2	Row totals
Captured in period 1	F_{11}	F_{12}	F_{1*}
Not captured in period 1	F_{21}	F_{22} (unknown)	F_{2*}
Column totals	F_{*1}	F_{*2}	N

spring in 2003 (4 February–2 July). The average number of nets deployed was 12 per day (range, 9–13 nets/d).

Northern pike were measured to total length (TL; mm), weighed (g), marked with individually numbered spaghetti tags at the base of the dorsal fin, and released near their capture location. Each tag was printed with a return address that included a $5.00 reward statement to increase the probability of tag returns from anglers. A few pike were not tagged owing to their small body size or the belief that they would not survive. All recaptured pike were measured and released.

Custom fyke nets were fabricated to passively capture northern pike. The square mesh size of the fyke nets was 25 mm and the traps were constructed with two rectangular conduit frames (1.2 m × 1.8 m) at the mouth to prevent the net from rolling on the river bottom. Behind the frames were three fiberglass hoops (1.2 m diameter) that funneled fish into a holding area. We also built an escape hatch for river otters *Lutra canadensis* that opened from the holding area and extended 2.4 m up to a 0.6-m polyvinyl chloride frame with floats on the water surface. One lead (3-cm mesh) was attached to the center of the trap mouth and extended 20 m to the shoreline. Leads were stretched perpendicular to the shoreline to capture fish moving in either direction.

Survival and abundance.—We estimated the survival of northern pike age 3 and older using the Chapman–Robson estimator (Everhart and Youngs 1981). Age-3 fish were used as the coded age-0 up to age-7 fish. Annual survival was estimated at 0.5997 and used among all the age-classes to obtain population abundance for each of the cohorts. Thus, we assumed that age-1 and age-2 northern pike had the same survival rates as the age-3 and older cohorts.

Lincoln–Petersen population estimates of northern pike were obtained by using mark–recapture methods to compute population abundance. The mark–recapture data obtained from both angler and trap-net catches provided statistically robust data for several estimates. We used a modified Lincoln–Petersen estimator (Evans and Bonett 1994) based on the framework shown in Table 1.

The Evans–Bonett (1994) estimator is

$$N = (F_{1*} + 1)(F_{*1} + 1)/(F_{11} + 0.5) - 1.5,$$

the variance was estimated as

$$\frac{(F_{1*} + 1)(F_{*1} + 1)(F_{21} + 0.5)(F_{12} + 0.5)}{(F_{11} + 0.5)^3},$$

and the SE is the square root of the variance.

Using these data we computed several population estimates generally from April through August for 2002 and 2003. Period 1 for each subsequent month in a year consisted of all of the previous months for that year—that is, all of the time when fish were caught and marked before the month of interest. Also, we adjusted the number of marked northern pike available for recapture based on the estimated survival ($S = 0.5997$; e.g., for 2003, those “captured in period 1” numbers are F_{1*}, and 60% of the 2002 tagged fish are 2002 tagged fish in the recapture count, F_{11}). This approach leads to more stable estimates of northern pike numbers in April and May because 2002 marked fish were recaptured in those months.

Additional demographic data for northern pike were needed to estimate at the population level, including age–length and length–weight relationships. Laine et al. (1991) reported that scales are a valid (accurate and precise) technique to assess age-class structure of northern pike. Therefore, we developed a length-at-age relationship based on scales that were aged by an outside expert (Rodney Pierce, Minnesota Department of Natural Resources, Grand Rapids). Seven age-classes were identified from the scale reading with about equal numbers of fish from each age-class being represented. We back-calculated the TL (mm) at age from the equation

$$\text{mean TL(mm)} = 98.462 \cdot \text{age} + 294.01 \quad (r^2 = 0.98, n = 38)$$

and used the following weight–length equation to compute the mean weight at age:

$$W = 6.99 \times 10^{-6} \cdot \text{TL}^{3.01} \quad (r^2 = 0.94).$$

Seasonal diets.—Anglers collected stomachs from northern pike from 1999 to 2003 to assess the seasonal variability in diet. Stomachs were collected from harvested fish by volunteer anglers who removed the entire stomach from the body cavity. Stomach samples were not collected from pike captured in fyke traps

TABLE 2.—Seasonal comparison of the mean total lengths (mm) and weights (g) of prey consumed by northern pike in the upper Flathead River system, Montana. Lengths were measured or estimated from bony parts; weights were derived from weight–length equations (see footnotes).

			Prey category					
Northern pike size-class	Season	Sample size and variable	Westslope cutthroat trout[a]	Bull trout[b]	Whitefishes[c]	Minnows and suckers[d]	Other fishes[e]	Yellow perch[f]
≤600 mm	Fall	*n*						
		Length (SD)						
		Weight						
	Winter	*n*			4	27		11
		Length (SD)			193 (91)	61 (129)		118 (53)
		Weight			62	20		17
	Spring	*n*			3	34		1
		Length (SD)			244 (23)	94 (39)		93
		Weight			131	7		8
	Summer	*n*	1			15		
		Length (SD)	189			110 (39)		
		Weight	61			12		
>600 mm	Fall	*n*	4	2	7	91		
		Length (SD)	163 (138)	263 (55)	165 (59)	149 (51)		
		Weight	38	152	38	33		
	Winter	*n*	4	3	87	101	3	6
		Length (SD)	185 (94)	308 (51)	197 (75)	123 (61)	94 (3)	153 (31)
		Weight	57	235	66	17	1	40
	Spring	*n*	2	1	15	17	2	
		Length (SD)	106 (12)	308	211 (57)	105 (52)	128 (18)	
		Weight	10	235	83	10	3	
	Summer	*n*			3	46	1	6
		Length (SD)			199 (28)	143 (51)	181	164 (82)
		Weight			69	28	71	50

[a] $W = 0.00000491 \cdot \mathrm{TL}^{3.11565}$ (Montana Fish, Wildlife and Parks, unpublished data).

[b] $W = 0.000036944 \cdot \mathrm{TL}^{2.733684}$ (Muhlfeld and Marotz 2005).

[c] $W = 0.0000051 \cdot \mathrm{FL}^{3.1574}$ (Carlander 1969).

[d] $W = 0.0000014 \cdot \mathrm{TL}^{3.39}$ (redside shiner; Bennett et al. 1983).

[e] $W = 0.00000164 \cdot \mathrm{TL}^{2.94}$ (Bennett et al. 1983).

[f] $W = 0.000002 \cdot \mathrm{TL}^{3.34}$ (Carlander 1997).

because diets could be biased towards prey items captured in the trap (Bowen 1996). Stomach samples were preserved in 10% formalin and labeled according to location and date of capture and length and sex of the pike. Prey items were later identified to the lowest practical taxonomic level, enumerated, and weighed by trained technicians in the Department of Fish and Wildlife at the University of Idaho, Moscow. Fish were identified directly to species or indirectly using bone keys and species lists. Body length measurements of prey fishes were taken when possible or key bony parts (i.e., cleithra, opercles, and dentary and pharyngeal teeth) were measured using ocular micrometers and later converted to body lengths using previously determined proportions or regressions for the same or similar species (D. Bennett, unpublished data). Weights of these prey fishes were then determined by applying weight–length equations from the literature for the species or a similar species at the closest geographical location (bull trout and westslope cutthroat trout, upper Flathead River, Montana: Muhlfeld and Marotz 2005; C. Muhlfeld, unpublished data; whitefishes: Carlander 1969; yellow perch: Carlander 1997; redside shiner: Bennett et al. 1983; other fishes: Bennett et al. 1983; Table 2). Although invertebrates occasionally occurred in the stomachs of pike, they comprised an insignificant percent composition by weight of the overall diet (0.07% of the total diet weight) and were, therefore, omitted from the analysis. The biomass of unidentifiable items was not used in the determining diet proportions. Diet analysis was conducted for northern pike less than or equal to 600 mm (smaller) and those larger than 600 mm (larger), which closely coincided with ages 1–3 and ages 3–7, respectively.

Bioenergetics modeling.—We used the computer model Fish Bioenergetics 3.0 (Hanson et al. 1997) with the coefficients developed by Bevelhimer et al. (1985) to estimate the total annual consumption of fish flesh. Six inputs were needed to estimate prey consumption: water temperature, seasonal diet proportions, energy density of prey, mortality, initial and final weights for each growth cohort, and population abundance of northern pike. Simulations were run from day 1 (January 1) through day 365 (December 31) for each of seven age-cohorts and summed to obtain annual estimates of consumption for the smaller and larger cohorts of northern pike. The

TABLE 3.—Population abundance, SEs of the estimates, number of recaptures from which estimates were computed, and 95% confidence intervals (CIs) for northern pike made from mark–recapture estimates in the Flathead River system, Montana.

Year	Month(s)	Abundance	SE (%)	Recaptures	±95% CI
2002	May	1,229	445 (36.2)	6	339–2,119
	Jun	628	105 (16.7)	22	418–838
	Jul–Aug	1,245	338 (27.1)	10	569–1,921[a]
2003	Apr	1,342	1,816 (135.3)	0	0–4,974
	May	5,146	7,182 (139.5)	0	0–19,510
	Jun	1,145	412 (36.0)	6	321–1,969
		Combined estimate[b]			
	Apr	1,993	542 (27.2)	11	909–3,077
	May	2,854	1,702 (59.6)	2	0–6,258
	Jun	2,644	963 (36.4)	6	718–4,570

[a] Population estimate used to compute consumption.

[b] 2002 tag data adjusted for mortality.

age-1 cohort was started with the estimated population abundance and as fish became older, mortality affected their abundance. We used the internal energy density values of the program for northern pike and did not account for energy used during spawning, which may have negatively biased our estimates slightly.

We delineated seasons based on historic temperature and flow data in the Flathead River valley (U.S. Geological Survey [http://waterdata.usgs.gov/mt/nwis/rt]) and classified them as winter (1 December–31 March), spring (1 April–30 June), summer (1 July–15 September), and fall (16 September–30 November). Hourly water temperatures were recorded throughout the study period in the river and sloughs using Hobo thermometers, and we used the beginning and ending monthly mean temperatures in the bioenergetics model. Water temperatures increased from less than 1°C in January to a high of 21.2°C in early August, then declined steadily until early November, when they were about 4°C (Tables 3, 4).

Six dietary categories were included in the simulations: westslope cutthroat trout, bull trout, coregonids, cyprinids and catostomids (combined), yellow perch, and other fishes (e.g., centrarchids and cottids). Energy values for prey fish were obtained from the literature and assumed to be constant throughout the year (Cummins and Wuycheck 1971; Vidergar 2000). Coregonids (5,989 J/g dry weight) were the highest in energy density values followed by bull trout (5,776 J/g), cutthroat trout (5,764 J/g) and cyprinids and catostomids (5,770 J/g). Other fishes (5,439 J/g) and yellow perch (4,186 J/g) were the lowest in prey energy densities. We estimated the number of prey eaten from the computed biomass consumed, which was divided by the mean weight of prey consumed for that season and dietary group. Because of sample size concerns, we assumed that the diet of northern pike up to 600 mm was representative of that of age-1–3 fish and that the diet of northern pike greater than 600 mm was representative of that of age-4–7 fish.

Results

We collected 367 northern pike from the upper Flathead River system in 2002 and 189 in 2003. These fish ranged from 200 to 1,045 mm long in 2002 and from 283 to 960 mm long in 2003. During 2002, 70% of the fish were longer than 500 mm, whereas in 2003 only 45% were longer than 500 mm.

Northern Pike Abundance

The population estimates were generally consistent among years, ranging from 1,200 to 1,300 individuals; however, estimates based on tag numbers from the previous year were about twice as high as those based on estimated mortality rates (Table 3). We used the estimate of 1,245 individuals (95% confidence interval [CI] = 569–1,921) from July and August 2002 because it was more similar to other estimates, had the second lowest SE, and had the second smallest CI (Table 3). Also, several estimates included zero in the lower 95% CI and one estimate from May 2003 was estimated arithmetically but not considered valid because no recaptures were made and these estimates had large standard errors.

Seasonal Diet

We collected and analyzed 284 northern pike stomachs; 56 (19.7%) of those stomachs were empty. The highest number of empty stomachs occurred in spring ($n = 25$), followed by winter ($n = 18$), summer ($n = 11$), and fall ($n = 2$). Overall, a higher proportion of the diet biomass of larger northern pike consisted of native salmonids as compared with smaller northern pike (Tables 4, 5). Westslope cutthroat trout ($n = 11$) and bull trout ($n = 6$) were dietary items in winter, spring, and fall by the large size-class of northern pike,

TABLE 4.—Diet proportions and water temperatures used in simulations for northern pike ≤600 mm (age 1 to age 3).

				Prey category					
Simulation day	Calendar date	Season	Water temperature (°C)	Cutthroat trout	Bull trout	Whitefish	Minnows and suckers	Other fishes	Yellow perch
1	1 Jan	Winter	0.7	0	0	0.1860	0.6294	0	0.1846
31	31 Jan	Winter	1.4	0	0	0.1860	0.6294	0	0.1846
32	1 Feb	Winter	1.5	0	0	0.1860	0.6294	0	0.1846
59	28 Feb	Winter	2.0	0	0	0.1860	0.6294	0	0.1846
60	1 Mar	Winter	1.5	0	0	0.1860	0.6294	0	0.1846
90	31 Mar	Winter	8.3	0	0	0.1860	0.6294	0	0.1846
91	1 Apr	Spring	6.5	0	0	0.4282	0.4513	0	0.1205
120	30 Apr	Spring	12.3	0	0	0.4282	0.4513	0	0.1205
121	1 May	Spring	13.0	0	0	0.4282	0.4513	0	0.1205
151	31 May	Spring	13.1	0	0	0.4282	0.4513	0	0.1205
152	1 Jun	Spring	13.5	0	0	0.4282	0.4513	0	0.1205
181	30 Jun	Spring	19.5	0	0	0.4282	0.4513	0	0.1205
182	1 Jul	Summer	20.1	0.3556	0	0.0115	0.6156	0	0.0172
212	31 Jul	Summer	20.6	0.3556	0	0.0115	0.6156	0	0.0172
213	1 Aug	Summer	21.2	0.3556	0	0.0115	0.6156	0	0.0172
243	31 Aug	Summer	19.2	0.3556	0	0.0115	0.6156	0	0.0172
244	1 Sep	Summer	19.1	0.3556	0	0.0115	0.6156	0	0.0172
258	15 Sep	Summer	18.0	0.3556	0	0.0115	0.6156	0	0.0172
259	16 Sep	Fall	17.9	0	0	0	1	0	0
273	30 Sep	Fall	12.9	0	0	0	1	0	0
274	1 Oct	Fall	12.7	0	0	0	1	0	0
304	31 Oct	Fall	3.8	0	0	0	1	0	0
305	1 Nov	Fall	3.8	0	0	0	1	0	0
334	30 Nov	Fall	2.2	0	0	0	1	0	0
335	1 Dec	Winter	1.9	0	0	0.1860	0.6294	0	0.1846
365	31 Dec	Winter	0.7	0	0	0.1860	0.6294	0	0.1846

TABLE 5.—Diet proportions and water temperatures used in simulations for northern pike >600 mm (age 4 to age 7).

				Prey category					
Simulation day	Calendar date	Season	Water temperature (°C)	Cutthroat trout	Bull trout	Whitefish	Minnows and Suckers	Other Fishes	Yellow Perch
1	1 Jan	Winter	0.7	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
31	31 Jan	Winter	1.4	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
32	1 Feb	Winter	1.5	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
59	28 Feb	Winter	2.0	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
60	1 Mar	Winter	1.5	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
90	31 Mar	Winter	8.3	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
91	1 Apr	Spring	6.5	0.0161	0.5478	0.1532	0.2232	0.0250	0.0347
120	30 Apr	Spring	12.3	0.0161	0.5478	0.1532	0.2232	0.0250	0.0347
121	1 May	Spring	13.0	0.0161	0.5478	0.1532	0.2232	0.0250	0.0347
151	31 May	Spring	13.1	0.0161	0.5478	0.1532	0.2232	0.0250	0.0347
152	1 Jun	Spring	13.5	0.0161	0.5478	0.1532	0.2232	0.0250	0.0347
181	30 Jun	Spring	19.5	0.0161	0.5478	0.1532	0.2232	0.0250	0.0347
182	1 Jul	Summer	20.1	0	0	0.0731	0.8171	0.0502	0.0596
212	31 Jul	Summer	20.6	0	0	0.0731	0.8171	0.0502	0.0596
213	1 Aug	Summer	21.2	0	0	0.0731	0.8171	0.0502	0.0596
243	31 Aug	Summer	19.2	0	0	0.0731	0.8171	0.0502	0.0596
244	1 Sep	Summer	19.1	0	0	0.0731	0.8171	0.0502	0.0596
258	15 Sep	Summer	18.0	0	0	0.0731	0.8171	0.0502	0.0596
259	16 Sep	Fall	17.9	0.0621	0.0309	0.0874	0.7849	0	0.0348
273	30 Sep	Fall	12.9	0.0621	0.0309	0.0874	0.7849	0	0.0348
274	1 Oct	Fall	12.7	0.0621	0.0309	0.0874	0.7849	0	0.0348
304	31 Oct	Fall	3.8	0.0621	0.0309	0.0874	0.7849	0	0.0348
305	1 Nov	Fall	3.8	0.0621	0.0309	0.0874	0.7849	0	0.0348
334	30 Nov	Fall	2.2	0.0621	0.0309	0.0874	0.7849	0	0.0348
335	1 Dec	Winter	1.9	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605
365	31 Dec	Winter	0.7	0.0897	0.2048	0.4314	0.2115	0.0022	0.0605

TABLE 6.—Estimated annual biomass (metric tons) of prey eaten by northern pike in the upper Flathead River system.

	Prey category						
Season	Whitefish	Minnows and suckers	Cutthroat trout	Other fishes	Yellow perch	Bull trout	Total
			Northern pike ≤600 mm				
Winter	0.0534	0.1806	0	0	0.0530	0	0.2869
Spring	0.3418	0.3603	0	0	0.0962	0	0.7983
Summer	0.0187	0.9955	0.5751	0	0.0278	0	1.6170
Fall	0	0.5973	0	0	0	0	0.5973
Total	0.4139	2.1336	0.5751	0	0.1770	0	3.2995
			Northern pike >600 mm				
Winter	0.1880	0.0922	0.0391	0.0009	0.0264	0.0892	0.4358
Spring	0.1921	0.2799	0.0202	0.0313	0.0435	0.6867	1.2536
Summer	0.1647	1.8416	0	0.1132	0.1344	0	2.2538
Fall	0.0669	0.6005	0.0475	0	0.0266	0.0237	0.7651
Total	0.6116	2.8141	0.1067	0.1455	0.2309	0.7996	4.7083

whereas only westslope cutthroat trout were eaten by small northern pike in the summer. Bull trout were the principal dietary item of large northern pike by weight during the spring. During winter, native salmonids ranged in dietary proportions (weight) from 9% to 20% in the large northern pike, whereas in the spring they ranged from 2% to 55%. The dietary proportion of cyprinids and catostomids was the most consistent among seasons and peaked in the summer (81.7%) for large northern pike and was the only identifiable item in small northern pike in the fall. Coregonids were most abundant in the diets of both size-classes of northern pike during both winter and spring, comprising up to 43% of the dietary biomass. Other fishes were only present in the diet of large northern pike and peaked at about 5% of the diet biomass. Yellow perch peaked in dietary abundance in the winter for small northern pike (18%), but were of less importance to large northern pike (maximum, 6%).

We found a significant relationship between the length of northern pike and that of the fish in the diet when all prey fishes were considered; when only salmonid prey were considered, however, the relationship was not significant ($t = -0.02$, $P = 0.986$) and highly variable ($r^2 = 0.125$). Overall, the length of all fish in the diet of northern pike was significantly proportional to body length ($t = 5.11$, $P < 0.01$), as were prey eaten in the spring ($t = 3.57$, $P < 0.01$, $n = 136$) and winter ($t = 3.35$, $P < 0.01$, $n = 99$) but not those eaten in the summer ($t = 0.17$, $P = 0.864$, $n = 40$) or fall ($t = 1.22$, $P = 0.232$, $n = 35$).

Prey size varied among seasons and between the larger and smaller size-classes of northern pike (Table 2). Bull trout (308 mm) was the largest of all prey fish in the stomachs followed by coregonids (199 mm), cutthroat trout (189 mm), and cyprinids and catostomids (153 mm). Estimated mean lengths from the prey fish varied widely among diet categories and seasons. Yellow perch and cyprinids and catostomids were consistently lowest in mean weight.

Estimated Consumption

We estimated that the northern pike population in the upper Flathead River system annually consumed 8.0 metric tons (mt) of fish flesh (Table 6). The highest biomass was composed of cyprinids (4.9 mt), followed by coregonids (1.02 mt), bull trout (0.8 mt) and westslope cutthroat trout (0.68 mt). Estimated consumption of other fishes (0.14 mt) was the lowest of all prey eaten.

The prey biomass consumed by large northern pike was about 50% higher than that consumed by small northern pike (Table 6). The consumption of westslope cutthroat trout was higher for large northern pike than for small ones, and only large northern pike consumed bull trout.

The estimated number of fish eaten was about 342,000 (Table 7), with bull trout and cutthroat trout accounting for 5% of the prey consumed. Cyprinids and catostomids (278,925) comprised the highest number of prey fish, accounting for nearly 81.5% of all prey numbers consumed. Yellow perch were second, with an estimated 20,506 being consumed, and westslope cutthroat trout were third, with over 13,000 being consumed; bull trout comprised the lowest number of prey eaten (3,457).

Peak prey consumption by weight occurred in the summer for both size-classes of northern pike (Tables 6, 7). Cyprinid and catostomid consumption was high in the summer for both size-classes of northern pike. The consumption of bull trout by large northern pike was nearly 10 times as high in the spring as in the winter and fall, whereas westslope cutthroat trout were consumed by small northern pike in the summer and by large fish in the fall, winter, and spring.

TABLE 7.—Estimated numbers of prey fishes eaten annually by northern pike in the upper Flathead River system.

	Prey category						
Season	Whitefish	Minnows and suckers	Cutthroat trout	Other fishes	Yellow perch	Bull trout	Total
			Northern pike ≤600 mm				
Winter	861	9,028	0	0	3,116	0	13,004
Spring	2,610	51,466	0	0	12,019	0	66,095
Summer	270	82,956	9,428	0	557	0	93,210
Fall	0	18,100	0	0	0		18,100
Total	3,741	161,549	9,428	0	15,692	0	190,409
			Northern pike >600 mm				
Winter	2,848	5,421	686	947	659	380	10,941
Spring	2,314	27,986	2,015	10,441	967	2,922	46,646
Summer	2,386	65,773	0	1,594	2,687	0	72,441
Fall	1,759	18,196	1,250	0	591	156	21,952
Total	9,308	117,376	3,951	12,982	4,905	3,457	151,979

Discussion

Introductions of nonnative northern pike have created recreational fisheries in many waters in the United States and Canada, including the upper Flathead River system in Montana. However, many studies have shown that introduced northern pike may alter the composition and size structure of fish communities through predation (McMahon and Bennett 1996). Understanding the predatory impacts of northern pike on native and recreational fisheries is critical for developing effective recovery and management programs to balance recreation and native species recovery efforts, especially for a threatened species like the bull trout. Before our work, however, few studies have estimated the consumption of migratory bull trout and westslope cutthroat trout by nonnative pike in an interconnected river–lake system using the bioenergetics approach. Our bioenergetics model estimated that the northern pike population annually consumed more than 13,000 westslope cutthroat trout and nearly 3,500 bull trout, which is probably contributing to the reduced abundance of native salmonids in the system.

Westslope cutthroat trout were present in the diet of younger and older northern pike during all seasons, and bull trout were found only in larger northern pike during all seasons except summer. Furthermore, bull trout dominated the dietary biomass of northern pike in the spring and represented a significant proportion of the biomass in winter. However, analysis of the pike stomachs revealed that cyprinids and catostomids accounted for the majority of their diet in the summer and fall for both the large and small northern pike. In winter, coregonids were the dominant food items of large northern pike and in the spring for small northern pike. Yellow perch were not a major food item and consumption peaked at about 18% by weight, which is lower than the levels reported in other published studies (Diana 1979, 1983). Northern pike often act as a top-down predator and play an important role in structuring fish communities through predation (Paukert and Willis 2003). Our food habits results corroborate previous studies that found northern pike to be highly piscivorous (but see Chapman et al. 1989 for an exception) and will take advantage of almost any available prey fish in lake and river environments (Scott and Crossman 1973), including suckers (Diana 1979; Stephenson and Momot 1991), common carp *Cyprinus carpio* (Sammons et al. 1994), largemouth bass (Soupir et al. 2000; Paukert and Willis 2003), crappies *Pomoxis* spp. (Stephenson and Momot 1991), minnows, and juvenile salmonids (Rich 1992; Schmetterling 2001, 2003).

Consumption of native juvenile salmonids by introduced northern pike has been observed in other systems in the northwestern United States (Rich 1992; McMahon and Bennett 1996; Schmetterling 2001). Rich (1992) reported that migratory westslope cutthroat trout comprised up to 45% of the biomass of dietary items of northern pike in the Coeur d' Alene Lake system, Idaho. During some seasons, our estimates of dietary abundance were similar to those studies. Further, westslope cutthroat trout was the most commonly consumed salmonid, whereas bull trout were found only in large northern pike in seasons other than summer. These combined studies show that introduced northern pike often negatively affect native salmonid populations where they overlap each other in time and space and thus may pose a threat to the growth and persistence of species and populations that require interconnected habitats to complete their life history.

We believe that prey availability largely affected the consumption rates observed in our study. Although our population consumption rates suggest high consumption of juvenile westslope cutthroat trout (13,379) and lower consumption of bull trout (~3,500), we believe that northern pike may be selecting them as prey items, especially during the spring. Muhlfeld et al. (2000) found that native salmonids comprised 1.7% of the annual community composition of prey fish in the Flathead River sloughs in 1997, whereas the current study found that native salmonids accounted for nearly 5% of the total fish consumption of northern pike, suggesting possible selection. The disproportionate occurrence of salmonids in northern pike diets may also be explained by the preference for soft-rayed fishes over spiny-rayed fishes (Beyerle and Williams 1968; Wahl and Stein 1988) and the adfluvial habits of both subadult westslope cutthroat trout and bull trout (Shepard et al. 1984; Muhlfeld and Marotz 2005), which makes them highly vulnerable to an ambush predators like the northern pike.

The high degree of spatial and temporal habitat overlap between salmonids and northern pike probably accounts for the westslope cutthroat trout and bull trout consumption (Shepard et al. 1984; Muhlfeld et al. 2000; Muhlfeld and Marotz 2005). Northern pike are known to flourish in flooded areas with submerged vegetation, deep thermal (coolwater) refuge habitats, and waters that contain large-sized prey (Scott and Crossman 1973). The lake-influenced portion of the Flathead River appears to provide highly suitable pike habitat that supports a wide diversity and abundance of prey fish, the availability of which is enhanced by drawdown in the fall and winter. Muhlfeld et al. (2000) found that radio-tagged northern pike inhabited the study area (main-stem river and connected sloughs) throughout the year, which are the same areas found to be critical rearing and overwintering habitats for migratory bull trout (Fraley and Shepard 1989; Muhlfeld and Marotz 2005; Muhlfeld et al. 2005) and westslope cutthroat trout populations (Shepard et al. 1984; Muhlfeld et al. 2000). Indeed, Muhlfeld and Marotz (2005) reported that subadult bull trout made downriver movements to lower portions of the Flathead River system and to Flathead Lake during high spring flows and as temperatures declined in the fall and winter, and used the deep lake-influenced areas and connected sloughs of the lower river system for extended periods of time along their migration pathway to Flathead Lake. Thus, both temporal and spatial habitat overlaps, especially in the winter and spring, probably explain the presence of salmonids in the diet at those times.

Populations of bull trout and westslope cutthroat trout have declined throughout much of their native range, including the Flathead River and Flathead Lake system, which is a recognized regional stronghold for these species (Rieman et al. 1997; Shepard et al. 2005). Declines are attributed, in part, to interactions with nonnative fishes and aquatic organisms. Maintaining natural connections of suitable conditions for growth and survival is probably key to the persistence of migratory salmonid populations, including the threatened bull trout (Rieman and Allendorf 2001). In the Flathead River system, subadult bull trout and westslope cutthroat trout must travel through the lower river to reach Flathead Lake, where they grow to maturity, and the major nonnative predators along their migration pathway are northern pike (in the river and sloughs) and lake trout (in the lake and river) (Deleray et al. 1999; Muhlfeld et al. 2000). The other potential native predator in the lower river is the northern pikeminnow, which has been shown to consume juvenile salmonids (Vigg et al. 1991); however, the available data do not indicate significant occurrence (<0.2%) of salmonids in their diets in the upper Flathead River system (Zollweg 1998).

A number of assumptions are inherent in estimating prey consumption with bioenergetics models. However, we believe the input data into the bioenergetics model provide estimates that are representative of northern pike consumption of native salmonid fishes in the upper Flathead River system. In our study, tag reporting by anglers may have inflated the tag-derived population estimates (Miranda et al. 2002). However, angler nonreporting rates were probably low because we used reward tags (Rieman 1987), and intensive creel surveys during the study period corroborated the return rates; overall, 36% of the northern pike tags were removed by anglers and returned to us for cash, which is a high proportion and represents almost 450 fish annually. Another potential source of uncertainty was applying dietary information to two northern pike cohorts (ages 1–3 and ages 4–7). Ideally, but not realistically, diet information for each cohort would provide the best estimate of consumption, yet sample sizes were sufficient to assess seasonal and size-specific (small and large fish) consumption by northern pike. Additionally, smaller northern pike could have consumed bull trout of the sizes observed (263–308 mm), but we did not detect them in the diets. Thus, the estimated consumption of bull trout may be a significant underestimate as the maximum sizes of age-1 (436 mm) and age-2 pike (541 mm) were probably sufficiently large to consume bull trout of the lengths observed in the stomach contents; the optimum prey size consumed by northern pike ranges from one-third to one-half of the pike's body length (Scott and Crossman 1973; Rich 1992). Finally, we found a negative although nonsignificant relationship between salmonid prey length and length of northern pike, which was probably a result of a small sample size and a small range in lengths of northern pike that consumed salmonids.

Our data suggest that the northern pike population in the upper Flathead River system is self-sustaining and abundant and that this illegally introduced predator is having an effect on native salmonid populations. Beauchamp et al. (2006) recently developed a bioenergetics model for Flathead Lake, located immediately downriver from our study area, to estimate food consumption by certain fishes, including nonnative lake trout that are known to eat bull and cutthroat trout (Deleray et al. 1999; Vidergar 2000). The authors reported that lake trout consumed approximately 13 mt of westslope cutthroat trout and 2 mt of bull trout in the lake. Thus, the combined estimated consumption by two nonnative predator fishes in the Flathead River and Flathead Lake system were nearly 13.7 mt of westslope cutthroat trout and 2.8 mt of bull trout. These combined results call for concern because juvenile salmonids are probably experiencing an additive source of mortality owing to predation by nonnative northern pike and lake trout in the system.

Our data confirm that we should be very cautious about introducing northern pike into systems with native salmonid fishes, as McMahon and Bennett (1996) have advocated. As populations of many native salmonid fishes decline, concern over intentional and unintentional introductions must increase. We believe a possible benefit might accrue to native salmonids by reducing predatory interactions with introduced northern pike in areas currently managed for native species and populations.

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