

Ranking Predatory Threats by Nonnative Fishes in the Yampa River, Colorado, via Bioenergetics Modeling

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Abstract.—Because of its relatively natural hydrograph, the Yampa River, Colorado, is considered the crown jewel of native fish habitat in the upper basin of the Colorado River and has supported a relatively intact native fish assemblage. Nonnative fishes are thought to pose the greatest threat to native fishes in this system. Removal programs for nonnative northern pike *Esox lucius* and channel catfish *Ictalurus punctatus* have highlighted managers' perception of the threat posed by each species. Recent expansion of nonnative smallmouth bass *Micropterus dolomieu* in the Yampa River attracted an avid angling clientele but also coincided with a precipitous decline in native fishes, necessitating a rigorous assessment of the relative impact of all three nonnative predators on the native fishes. We used abundance, growth, and diet estimates for each predator species to quantify consumptive demand using bioenergetics models. Despite a low abundance of small-bodied fishes and thus a low number of fish in the smallmouth bass diet, total fish consumption by smallmouth bass (mean = 15.2 kg·km⁻¹·year⁻¹; 95% confidence interval [CI] = 13.3–17.1 kg·km⁻¹·year⁻¹) was similar to that estimated for northern pike (mean = 13.7 kg·km⁻¹·year⁻¹, 95% CI = 11.4–16.0 kg·km⁻¹·year⁻¹) and was about 65 times higher than the estimate for channel catfish (mean = 0.22 kg·km⁻¹·year⁻¹; 95% CI = 0.05–0.40 kg·km⁻¹·year⁻¹). Diet data from the upper Colorado River, where small-bodied fish were plentiful, suggested that piscivory by smallmouth bass in the Yampa River could be 10 times the piscivory by northern pike and channel catfish, or about 168.5 kg·km⁻¹·year⁻¹ (95% CI = 147.0–189.9 kg·km⁻¹·year⁻¹), if prey fish were more available. This level of piscivory suggested that smallmouth bass presented the greatest predatory threat to native fishes of the Yampa River. As environmental conditions change, use of field monitoring together with bioenergetics modeling will be an effective framework to assist managers in adapting their nonnative fish control efforts to maximize the likelihood of native fish recovery.

Native fishes are declining at alarming rates (Leidy and Moyle 1998), and imperilment is most severe in the arid southwestern United States (Warren and Burr 1994), where persistence of more than 60% of the native fishes of Nevada and Arizona is at risk (Master et al. 1998). The upper Colorado River basin (above Glen Canyon Dam) is inhabited by only 14 native fish species, including several endemics and four species that are federally listed as endangered (bonytail *Gila elegans*, Colorado pikeminnow *Ptychocheilus lucius*, humpback chub *G. cypha*, and razorback sucker *Xyrauchen texanus*). The roundtail chub *G. robusta* is listed as endangered, threatened, or a species of special concern by five of the seven states within the Colorado

River basin, and the species is under review for listing at the federal level (Bezzzerides and Bestgen 2002; Brouder 2005). Habitat degradation, primarily hydrographic alteration (Richter et al. 1997), is an important factor in the declines of native fish in the Colorado River (USFWS 2004). Water depletions for human use, streamflow regulation, and associated instream barriers to migration continue to disrupt natural riverine processes (Poff et al. 1997) to the detriment of the fishes that have evolved over millions of years in the warm, turbid water and extreme flow variations.

The introduction or invasion of nonnative fishes is also a major contributing factor in the decline of native fish faunas (Courtenay 1995; Rahel 2002; Eby et al. 2006), including that of the Colorado River (Tyus and Saunders 2000; Olden et al. 2006). Over the past century, more than 60 nonnative fish species have become established in the Colorado River basin (Rinne

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and Minckley 1991; Olden et al. 2006), and over 40 of these are established in the upper basin alone. Preventing introductions has proven to be very difficult, and it is now recognized that coping with invasions will require the ability to predict range expansions and the intensity of effects based on life histories of native and invasive species and characteristics of recipient systems (Moyle and Light 1996; Ricciardi and Rasmussen 1998; Kolar and Lodge 2001; Iguchi et al. 2004; Vander Zanden et al. 2004; Bestgen et al. 2006). Case studies of the relative effects of invasions by multiple species can provide valuable insights that will assist managers in anticipating and controlling new invaders.

Debate continues regarding the relative importance of habitat loss versus nonnative fishes in rivers of the region, but the two factors usually operate concurrently and even synergistically and are thus confounded. The Yampa River is unique in that it allows for an assessment of the magnitude of nonnative fish effects, as it has the most natural hydrograph of any river of its size in the upper Colorado River basin (Roehm 2004). The lack of main-stem dams below the headwaters and the absence of large diversions have maintained the natural spring peak in discharge, although summer flow has been reduced by agricultural withdrawals (Stewart et al. 2005). Despite the availability of relatively high-quality habitat, populations of small-bodied native fishes and juvenile life stages of larger species have declined precipitously during the past decade. Native speckled dace *Rhinichthys osculus*, mottled sculpin *Cottus bairdii*, bluehead suckers *Catostomus discobolus*, and flannelmouth suckers *Catostomus latipinnis* were strikingly lower in abundance or were extirpated in some reaches of the Yampa River, and nonnative fish abundance was higher in 2002–2003 than in 1998–1999 (Anderson 2005). Predation by nonnative fishes has been implicated in the decline of small-bodied fishes and may also be responsible for local declines in large-bodied species, such as Colorado pikeminnow (Bestgen et al. 2007). However, information on the relative predatory impact of various introduced species was lacking, and control of myriad species would be impractical. Further, some of these species are popular sport fish, so their control would require explanation and justification to the public.

One widely held opinion was that northern pike *Esox lucius* posed the gravest threat to native fishes of the Yampa River. This assumption presumably arose because northern pike are notoriously piscivorous, large, and able to prey on a wide range of fish sizes (Scott and Crossman 1998). Diet studies in the system confirmed that northern pike preyed upon native fishes

(Tyus and Beard 1990). Channel catfish *Ictalurus punctatus* were also considered a threat, both as predators and as competitors (Tyus and Nikirk 1990; Tyus and Saunders 2000). Removal programs for both species were implemented in 1998 (Hawkins et al. 2005; Mueller 2005). The potential impact of small-mouth bass *Micropterus dolomieu* on native fishes may have been discounted, because historically they were very rare. Additionally, many sources (Carlander 1977; Scott and Crossman 1998; Tomelleri and Eberle 1990; Sigler and Sigler 1996) have noted the predominance of crayfishes in the diet of smallmouth bass; this notion is well entrenched in sportfishing lore. An unprecedented increase in the abundance of smallmouth bass in parts of the Yampa River during the past decade prompted interest in determining their diet and the predation pressure they exerted on native fishes in the system relative to predation by channel catfish and northern pike. A predominately local but avid angling clientele developed as abundance of smallmouth bass increased, necessitating objective information and a thorough analysis of the effects of this nonnative predator before management actions aimed at reducing its abundance could be considered.

Assessing the potential predatory impacts on native species by channel catfish, northern pike, and small-mouth bass requires information on the diets of each predator species. However, to determine the relative intensity of piscivory on prey populations, information on consumption rates and demographics of each population are also required. Further, in some situations, predation may have already depleted prey species of concern and predators will have switched to alternate prey; in those cases, contemporary diet information gives a misleading impression of predators' potential impacts on species of concern. Bioenergetics models can integrate ecological, physiological, and demographic information to compute consumptive demand of predator populations, a relevant metric when assessing relative impacts. A great strength of simulation modeling is that alternative scenarios can be evaluated to ask questions such as, "What if native prey fish populations rebound and predators begin feeding on them again?" or "How many of those prey could the predators consume?"

In this study, our objectives were to (1) assemble available data on diets and demographics of three nonnative predators from the Yampa River and diet information from a reference system and (2) employ bioenergetics models to quantify the relative predatory threat of each species. The information was then provided to managers so that predatory fish control efforts could be prioritized and applied in an ecologically and fiscally efficient manner and so that

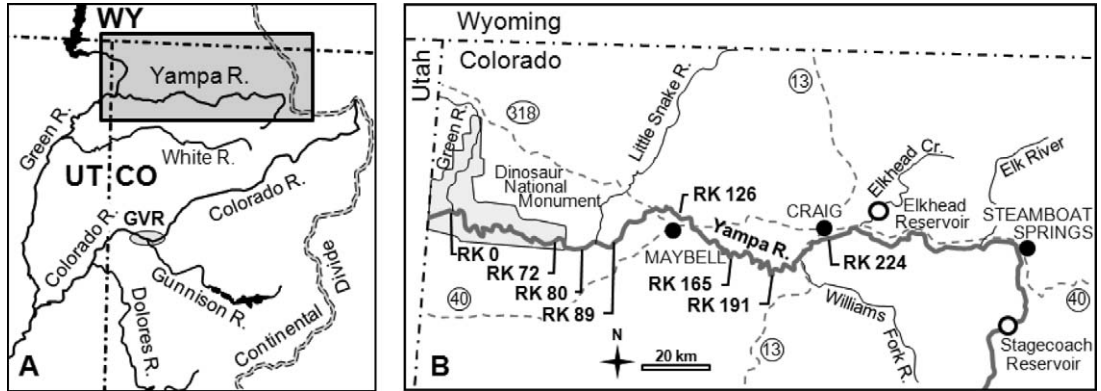


FIGURE 1.—Maps of (A) the upper Colorado River and some of its tributaries in eastern Utah, southwest Wyoming, and northwest Colorado (shaded rectangle = portion of the Yampa River shown in B; shaded oval = Grand Valley reach [GVR]) and (B) the Yampa River, showing river kilometer (RK; RK 0 = confluence with the Green River) designations for locations mentioned in the text. The lower bound of the study area was at approximately RK 80, but sampling was concentrated between RK 165 and 191. Upstream boundaries of endangered species critical habitat for endangered fishes were at RK 72 for bonytails and humpback chub, RK 89 for razorback suckers, and RK 224 for Colorado pikeminnow (Roehm 2004).

these actions could be explained and justified to the public.

Study Area

The Yampa River, located in northwest Colorado (Figure 1), is bounded by the Continental Divide to the east (elevation = 3,712 m above sea level [ASL]) and terminates at its confluence with the Green River in Dinosaur National Monument (1,548 m ASL). Climatic conditions vary with elevation, but the area is characterized by relatively cool, dry summers (July mean air temperature = 19.5°C at river kilometer [RKM] 126 and 224) and cold winters. Average summer water temperature at RKM 126 during May–August 1996–2002 was 17.5°C, and the mean peak water temperature was 22.0°C (July) during that period (USGS 2006a). The Yampa River displays a snowmelt hydrograph (Van Steeter and Pitlick 1998) typical of the region (Poff and Ward 1989); peak flows occur during spring (median $\approx 280 \text{ m}^3/\text{s}$; USGS 2006b), and mean annual flow is approximately $42 \text{ m}^3/\text{s}$ (USGS 2006a).

The fish assemblage was historically limited to 12 species (Table 1). Today, four of the species are federally listed as endangered and another two are listed as species of special concern by the state of Colorado. The lower 80-km reach of the Yampa River is designated as critical habitat for all four of the endangered fishes, and Colorado pikeminnow critical habitat extends upstream to RKM 224 (Figure 1). Intentional and unintentional nonnative fish stocking and immigration are common, and the assemblage is currently dominated by species in a variety of trophic

and thermal guilds. Several nonnative game fishes provide popular recreational fisheries. Channel catfish were introduced into the basin in 1892 and have been abundant in the Yampa River for decades (Holden and Stalnaker 1975; Tyus and Nikirk 1990). Northern pike were first stocked in the Yampa River basin in 1977 (Hawkins et al. 2005) and became abundant in the main-stem Yampa River beginning in the mid-1980s (Tyus and Beard 1990). Smallmouth bass were introduced into the basin in the late 1970s, when they were stocked into Elkhead Reservoir (on Elkhead Creek, a Yampa River tributary; P.J.M., unpublished data). Smallmouth bass were rarely found in the Yampa River until the early 1990s (Tyus et al. 1982; Nesler 1995), when a rapid drawdown of Elkhead Reservoir in the winter of 1991–1992 introduced many into the river (Martinez 2003). Several subsequent years of low river flows, which were probably favorable for recruitment, were thought to have increased the primarily downstream distribution and abundance of smallmouth bass (Martinez 2005).

Methods

Sampling locations were designated according to their distance upstream (km) from the Yampa River's confluence with the Green River (RKM 0; Figure 1b). Most of our work focused on a 26-km reach of the Yampa River from the Duffy Mountain boat ramp (RKM 165) to just above Milk Creek (RKM 191); this reach is considered to be the epicenter of the smallmouth bass population's recent rapid expansion. Channel catfish, northern pike, and smallmouth bass were collected for population estimates by boat

TABLE 1.—List and status of fish species occurring in the Yampa River, Colorado (E = federally endangered; SE = state endangered; ST = state threatened; SC = state species of special concern; CS = conservation species as designated by the 2004 Rangewide Conservation Agreement (UDWR 2004) among Arizona, Colorado, Nevada, New Mexico, Utah, and Wyoming; * = intermittent inhabitants [all are salmonids]; † = extirpated species).

Species	Status
Native	
Bluehead sucker <i>Catostomus discobolus</i>	CS
Bonytail <i>Gila elegans</i> †	E, SE
Colorado River cutthroat trout <i>Oncorhynchus clarkii pleuriticus</i> *	SC
Colorado pikeminnow <i>Ptychocheilus lucius</i>	E, ST
Flannelmouth sucker <i>Catostomus latipinnis</i>	CS
Humpback chub <i>Gila cypha</i>	E, ST
Mottled sculpin <i>Cottus bairdii</i>	
Mountain sucker <i>Catostomus platyrhynchus</i>	
Mountain whitefish <i>Prosopium williamsoni</i> *	
Razorback sucker <i>Xyrauchen texanus</i>	E, SE
Roundtail chub <i>Gila robusta</i>	SC, CS
Speckled dace <i>Rhinichthys osculus</i>	
Nonnative	
Black bullhead <i>Ameiurus melas</i>	
Black crappie <i>Pomoxis nigromaculatus</i>	
Bluegill <i>Lepomis macrochirus</i>	
Brook stickleback <i>Culaea inconstans</i>	
Brook trout <i>Salvelinus fontinalis</i> *	
Brown trout <i>Salmo trutta</i> *	
Channel catfish <i>Ictalurus punctatus</i>	
Common carp <i>Cyprinus carpio</i>	
Creek chub <i>Semotilus atromaculatus</i>	
Fathead minnow <i>Pimephales promelas</i>	
Green sunfish <i>Lepomis cyanellus</i>	
Iowa darter <i>Etheostoma exile</i>	
Northern pike <i>Esox lucius</i>	
Northern plains killifish <i>Fundulus kansae</i>	
Rainbow trout <i>Oncorhynchus mykiss</i> *	
Red shiner <i>Cyprinella lutrensis</i>	
Redside shiner <i>Richardsonius balteatus</i>	
Sand shiner <i>Notropis stramineus</i>	
Smallmouth bass <i>Micropterus dolomieu</i>	
White sucker <i>Catostomus commersonii</i>	

electrofishing during 10 May–3 July 2003. Each fish was measured (total length [TL], mm); most were weighed (wet weight, g). Individuals exceeding a minimum size (channel catfish: 275 mm TL; northern pike: 260 mm TL; smallmouth bass: 150 mm TL) were marked with a numbered Floy tag that was inserted below the dorsal fin. Smallmouth bass were sampled on five capture occasions (average electrofishing time = 14 h/occasion); channel catfish and northern pike were sampled on three capture occasions (55 h/occasion). Because of their lower relative densities, channel catfish and northern pike were marked and recaptured over a much larger reach, which extended to just below the Little Snake River (~RKM 80). Abundance estimates were computed using CAPTURE (White et al. 1982), and uncertainty was expressed as 95% confidence intervals (CIs) based on profile

likelihood intervals (Evans et al. 1996). To normalize abundance of each species, abundance was divided by the river segment length over which abundance was estimated. We computed areal fish densities from a mean channel width (62 m) measured at RKM 84, 103, and 175 at a flow of 17 m³/s (Stewart et al. 2005).

For predators that were not weighed, estimated weights (*W*) were computed from weight–length relationships derived from field measurements ($W = a \times TL^b$, where $a = 2.0 \times 10^{-7}$ and $b = 3.671$ for channel catfish [$n = 365$]; $a = 1.0 \times 10^{-5}$ and $b = 2.929$ for northern pike [$n = 297$]; and $a = 7.0 \times 10^{-7}$ and $b = 3.538$ for smallmouth bass [$n = 1,135$]). Body condition was expressed as relative weight (W_r ; Anderson and Neumann 1996). Channel catfish, northern pike, and smallmouth bass used for diet analysis were collected from the Yampa River between RKM 165 and 191. Channel catfish and northern pike were collected during June–November 2005, and smallmouth bass were collected during June–October 2003, June 2004, and May–September 2005. A sample of smallmouth bass was also collected for diet analysis from the Grand Valley reach (GVR; Figure 1), a 55-km section of the upper Colorado River, during April–August 2004. Although crayfish were not as abundant as in the Yampa River (P.J.M., personal observation), small-bodied fishes were abundant and well studied in the GVR (McAda et al. 1994; McAda and Ryel 1999; Bundy and Bestgen 2001); thus, it served as a useful reference system, representing fish prey resource availability in the Yampa River prior to the population crashes of small-bodied fishes. Fish were measured (TL, mm) and weighed (wet weight, g). Whole fish or their stomachs were then fixed in 10% formalin for diet analysis. Otoliths were collected from smallmouth bass, and we used thin sections to determine their ages (Martinez 2004). Northern pike ages were determined from scales by Martinez (1995) and Nesler (1995). We obtained information on size at age of channel catfish from Tyus and Nikirk (1990). Growth rates were determined by fitting von Bertalanffy growth functions (Isely and Grabowski 2007) to size at age.

We dissected predator stomachs and removed all food items from the esophagus to the pyloric sphincter. Prey items were identified to the lowest practical taxonomic level. Partially digested fish were identified from endoskeletal remains (Eddy and Underhill 1978; Hansel et al. 1988). Pharyngeal teeth and cleithra were also compared to those from reference fish to confirm identifications. Prey items were measured under a stereomicroscope, and head capsule widths (Smock 1980) of insects, carapace lengths of crayfish (Roell and Orth 1992), and vertebral column lengths of fish (Clothier 1950) were recorded. Insect measurements

were converted to wet mass using family- or order-specific functions derived from the literature (Smock 1980; Burgherr and Meyer 1997; Benke et al. 1999). Crayfish carapace lengths were also converted to wet mass (Roell and Orth 1992). Species-specific functions were used to convert fish vertebral column length to wet mass (B.M.J., unpublished data), which allowed us to compute diet composition on a wet-mass basis.

We estimated predator consumptive demand by performing simulations with Fish Bioenergetics software (Hanson et al. 1997). A revised parameter set for smallmouth bass was derived from Whitley et al. (2003). Parameters for channel catfish simulations were obtained by adjusting temperature-dependent physiological inputs reported for flathead catfish *Pylodictus olivaris* (Roell and Orth 1993) to approximate the thermal preferences of channel catfish (Becker 1983), as described by Hanson et al. (1997). Northern pike parameters were not changed from Fish Bioenergetics defaults. Per-capita consumption was simulated for the average adult of each population and was computed from the annual growth increment, predator diet, river temperature, predator energy density, and prey energy density. Growth increment used in simulations was calculated from the geometric mean weight of the fish collected in the mark-recapture samples and the von Bertalanffy growth function fitted to weight at age.

Each simulation encompassed 1 year. The thermal experience of each species was estimated from mean temperatures of the Yampa River recorded at the Maybell gauge station (U.S. Geological Survey, Station 09251000; RKM 126) during 1996–2002. Energy density was set at 3.6 kJ/g of wet weight for northern pike and at 4.2 kJ/g for smallmouth bass and channel catfish (Hanson et al. 1997). Energy lost to spawning (smallmouth bass: 7% loss on 20 May; northern pike: 10% on 15 March; channel catfish: 7% on 1 July) was incorporated into the simulations. Literature-based estimates of energy density (wet-mass basis) were obtained for aquatic insects (4.3 kJ/g; Cummins and Wuycheck 1971), fish prey (4.2 kJ/g; Hanson et al. 1997), and crayfish (3.8 kJ/g; Roell and Orth 1993).

We performed simulations using two diet scenarios. The nominal run (realized piscivory) used the diet information we collected from smallmouth bass, northern pike, and channel catfish in the Yampa River during 2003–2005, when the availability of small-bodied fish prey was low. The second set of simulations represented potential consumptive demand before the observed decline of small-bodied fishes (potential piscivory scenario). For these simulations, we used northern pike diet information (90% fish, 10% invertebrates) reported by Nesler (1995). Diet infor-

mation was not available for smallmouth bass before 2003; diet composition for smallmouth bass collected from GVR was used to represent the Yampa River diet as if small-bodied fishes had not already been depleted. We assumed that this set of simulations represented the latent piscivory within the piscivore populations and was an indicator of their potential to prevent the recovery of small-bodied fishes via predation. Potential consumption by channel catfish was not computed, because the incidence of fish in the diet was low during the late 1980s (Tyus and Nikirk 1990).

Annual per-capita consumption (c) by each predator species (i) was scaled up to consumption by the entire population (B) based on the mark-recapture abundance estimate (\hat{N}_i) and its confidence limits:

$$B_i = (c_i \times \hat{N}_i) \pm (t_{0.05} \times c_i \times SE_{N_i}).$$

We apportioned the estimated biomass of fish consumed by smallmouth bass and northern pike into small-bodied fish equivalents (SBFs) to evaluate the intensity of predation on native fish populations on a numerical basis. The SBFs were computed for eight native prey fishes: the bluehead sucker, flannelmouth sucker, razorback sucker, humpback chub, Colorado pikeminnow, roundtail chub, mottled sculpin, and speckled dace. The number of prey of each species consumed was computed from prey mean weight at a specified size and the total biomass consumed per predator population:

$$SBF_{ij} = B_i / [a_j \times (\bar{P}_i \times \bar{p}_i)^{b_j}],$$

where i is the predator species, j is the prey species, B is fish biomass consumed per year, \bar{P} is predator size (mean TL, mm), \bar{p} is the median prey : predator size ratio observed in predator guts, and a and b are coefficients of prey length-weight regressions (Carlander 1969; Didenko and Bonar 2004). The 5th and 95th percentiles of the prey : predator size ratio (p_5 and p_{95}) were used to compute a range of small-bodied fish that could reasonably occur with changes in the size structure of the extant prey assemblage. The number of age-1 fish consumed was computed by dividing consumption by prey weight at age (Bailey 1952; Vanicek and Kramer 1969; Minckley 1983; McAda and Wydoski 1985; Osmundson et al. 1997; Robinson and Childs 2001:). The maximum age of each prey species that was vulnerable to the smallmouth bass and northern pike populations was computed from prey length at age and predator gape limits (60% of predator length for smallmouth bass: Katano and Aonuma 2001; 50% for northern pike: Mittelbach and Persson 1998).

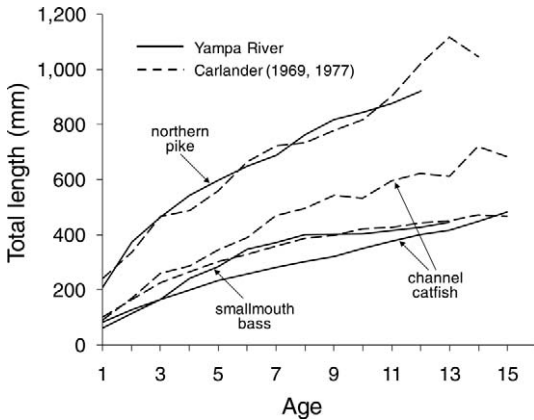


FIGURE 2.—Observed growth of channel catfish (1979–1988; Tyus and Nikirk 1990), northern pike (1987–1991; Martinez 1995; Nesler 1995), and smallmouth bass (2003; Martinez 2004) in the Yampa River, Colorado. “Typical” growth trajectories across the species’ ranges (Carlander 1969, 1977) are shown for comparison.

Results

For channel catfish marked for the population estimate ($n = 364$ fish), the arithmetic mean TL was 472 mm (SE = 4.7) and the geometric mean weight was 1,101 g; this body size corresponded to an age of 14 years. For northern pike ($n = 295$ fish), mean TL was 560 mm (SE = 9.0) and geometric mean weight was 990 g, corresponding to an age of 4 years. For smallmouth bass ($n = 1,400$ fish), mean TL was 241 mm (SE = 2.2) and geometric mean weight was 290 g, corresponding to an age of 4 years. Smallmouth bass were substantially more numerous ($\hat{N} = 267$ fish/km; 95% CI = 234–304 fish/km) than northern pike (5 fish/km; 95% CI = 4.3–6.1 fish/km) or channel catfish (68 fish/km; 95% CI = 34–166 fish/km). Channel catfish from the Yampa River grew considerably more slowly than the national average (Carlander 1969), and this disparity increased with age (Figure 2). By age 8, channel catfish were approximately 200 mm smaller than the length at age reported for channel catfish elsewhere. The growth of northern pike as reported by Nesler (1995) was similar to the national average (Carlander 1969), as was the growth of smallmouth bass (Carlander 1977). In 2003 and 2004, mean W_r was 118 for channel catfish, 93 for northern pike, and 102 for smallmouth bass.

The channel catfish diet ($n = 32$ stomachs examined; 30 were nonempty) included very few fish (0.2% by mass); only 6.6% of stomachs with food contained any fish remains. Most of the diet consisted of virile crayfish *Orconectes virilis* (53.7%) and plant matter (36.0%); insects (primarily Ephemeroptera, Trichoptera, and Plecoptera) made up the remainder of the diet

(10.1%). Northern pike ($n = 45$ stomachs; 33 were nonempty) were primarily piscivorous; fish constituted 72.2% of the diet (by mass). Northern pike also ate crayfish (24.5%) and a few insects (3.3%). Northern pike preyed nearly equally on catostomids, centrarchids, cyprinids, and salmonids. Smallmouth bass ($n = 178$ stomachs; 149 were nonempty) consumed mainly crayfish (51.5% by mass). Aquatic insects, including Ephemeroptera (80% by number), Plecoptera (15%), Hemiptera (Corixidae and Notonectidae: 3%), and Trichoptera (<1%), made up 42.8% of the diet. Only 5.7% of the diet consisted of fish; because of the advanced state of digestion in the samples, most fish remains could not be definitively identified below the family level. Small cyprinids and smallmouth bass each constituted 40% of the fish prey, and suckers and sunfish made up the remainder. In contrast, fish (minnows and suckers) were the primary prey (67.7%) of smallmouth bass collected from the upper Colorado River ($n = 325$ stomachs), while crayfish (12.9%) and insects (19.4%) made up much smaller proportions of the diet than was observed in the Yampa River. Northern pike and smallmouth bass consumed fish that were similar in size relative to predator size. The median prey : predator size ratio (TL) of fish in stomachs was 0.22 for northern pike and 0.21 for smallmouth bass. Northern pike consumed proportionately larger prey ($p_{95} = 0.50$) than smallmouth bass ($p_{95} = 0.39$), but the minimum prey size consumed was similar between the two species ($p_5 = 0.12$ for northern pike and 0.11 for smallmouth bass).

Per-capita consumption of fish was highest for northern pike (2.7 kg/year; Table 2). Fish constituted a small fraction of the diet in channel catfish simulations; thus, consumption of fish by the average channel catfish was predicted to be only 3.3 g/year. Per-capita consumption of fish by smallmouth bass was estimated at 0.06 kg/year. At the population level, realized fish consumption by smallmouth bass (mean = 15.2 kg·km⁻¹·year⁻¹; 95% CI = 13.3–17.1 kg·km⁻¹·year⁻¹) was similar to fish consumption by northern pike (mean = 13.7 kg·km⁻¹·year⁻¹; 95% CI = 11.4–16.0 kg·km⁻¹·year⁻¹) and was about 65 times higher than fish consumption by channel catfish (mean = 0.22 kg·km⁻¹·year⁻¹; 95% CI = 0.05–0.40 kg·km⁻¹·year⁻¹).

Potential piscivory by channel catfish was not different from realized consumption, because we assumed that no diet shift would occur. Potential piscivory by the smallmouth bass population was 168.5 kg·km⁻¹·year⁻¹ (95% CI = 147.0–189.9 kg·km⁻¹·year⁻¹), or about 10 times higher than that by the northern pike population (17.2 kg·km⁻¹·year⁻¹; 95% CI = 14.2–20.1 kg·km⁻¹·year⁻¹). Combined

TABLE 2.—River temperature ($^{\circ}\text{C}$) and per-capita consumption (g) by smallmouth bass, northern pike, and channel catfish in the Yampa River, Colorado, over four seasonal time periods. Two simulations were performed: (1) realized piscivory (RP) based on diet data from 2003–2005 and (2) potential piscivory (PP) based on diet observations when small-bodied fishes were abundant (see Methods). The PP scenario for channel catfish is not presented, because diet did not differ from that measured during the late 1980s (Tyus and Nikirk 1990).

Time period	Mean temperature	Smallmouth bass			Northern pike			Channel catfish		
		Crayfish, insects (RP)	Fish (RP)	Fish (PP)	Crayfish, insects (RP)	Fish (RP)	Fish (PP)	Crayfish, insects (RP)	Plant matter (RP)	Fish (RP)
Jan–Mar	0.8	18.0	1.2	12.8	63.0	163.7	205.3	23.0	13.0	0.1
Apr–Jun	11.9	259.6	16.6	183.8	288.3	748.8	939.5	354.0	199.7	1.1
Jul–Sep	19.8	578.8	36.9	409.7	577.0	1,498.5	1,880.3	653.2	368.6	2.0
Oct–Dec	3.9	35.9	2.3	25.4	115.8	300.8	377.4	37.4	21.1	0.1
Annual	9.2	892.4	57.0	631.7	1,044.1	2,711.7	3,402.5	1,067.6	602.4	3.3

potential piscivory by the smallmouth bass and northern pike populations was about 186 $\text{kg}\cdot\text{km}^{-1}\cdot\text{year}^{-1}$, and total consumptive demand (of all food types) by these two populations was 269 $\text{kg}\cdot\text{km}^{-1}\cdot\text{year}^{-1}$. The majority (55–67%) of each predator's annual consumption occurred during July–September (Table 2), when water temperatures were closest to the thermal optima of these species.

The potential number of age-1 prey (i.e., SBFs) consumed by smallmouth bass ranged from 23,500 to 470,000 $\text{fish}\cdot\text{km}^{-1}\cdot\text{year}^{-1}$ (3,800–75,800 $\text{fish}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), depending on prey species. This amount was approximately an order of magnitude higher than SBF consumption by northern pike (Table 3) and was proportional to the difference in biomass consumed by the two species. Because of their relatively small weights at age 1, the potential number of roundtail chub, speckled dace, and mottled sculpin consumed was about 2–20 times higher than that of the remaining five species (Table 3). If smallmouth bass consumed fish of a size equal to the median prey : predator length ratio calculated from gut analyses, then the number consumed would range from 93,600 bluehead

suckers $\cdot\text{km}^{-1}\cdot\text{year}^{-1}$ (15,100 $\text{fish}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) to 301,000 speckled dace $\cdot\text{km}^{-1}\cdot\text{year}^{-1}$ (48,500 $\text{fish}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). Alternatively, if smallmouth bass consumed the same biomass of fish but at sizes near the p_5 of the prey : predator length ratio, then the number of fish consumed would be about sevenfold higher. Northern pike chose to consume much larger individuals and thus a lower number of prey (700–1,300 $\text{fish}\cdot\text{km}^{-1}\cdot\text{year}^{-1}$ or 113–210 $\text{fish}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). Growth trajectories of prey indicated that speckled dace and mottled sculpin do not ultimately grow large enough to exceed the smallmouth bass gape limit, but the other six species outgrow that size at some point between ages 1 and 2. Only Colorado pikeminnow and flannelmouth suckers reach a body size greater than the gape limit of the average northern pike; this occurs at a point between ages 3 and 4.

Discussion

Bioenergetics model simulations allowed us to (1) provide quantitative evidence that nonnative fish predation was probably having a significant impact on native fish populations of the Yampa River and (2)

TABLE 3.—Potential annual consumption of small-bodied native fishes by smallmouth bass and northern pike populations in the Yampa River, Colorado, 2003–2005. Small-bodied fish equivalents (SBFs) were computed from annual biomass consumed by each predator population and (1) the mean weight of each prey species at age 1 (see Methods) or (2) the median (and 5th and 95th percentiles) of the prey : predator size ratio (total length [TL], mm) estimated from predator stomach contents. Blank cells indicate that the size computed from the prey : predator ratio was not attained by that prey species.

Prey species	Prey size at age 1		Smallmouth bass SBFs (10^3 prey/km)		Northern pike SBFs (10^3 prey/km)	
	TL (mm)	Weight (g)	Age 1	Size thresholds	Age 1	Size thresholds
Bluehead sucker	81	7.2	23.5	93.6 (15.2–626)	2.4	0.7 (0.1–4.1)
Colorado pikeminnow	71	2.3	72.0	207 (29.9–1,566)	7.3	1.3 (0.1–8.7)
Flannelmouth sucker	73	2.8	59.2	183 (26.4–1,384)	6.0	1.2 (0.1–7.7)
Humpback chub	76	3.5	47.8	168 (24.8–1,246)	4.9	1.1 (0.1–7.1)
Razorback sucker	78	5.8	29.0	106 (16.7–731)	3.0	0.8 (0.1–4.6)
Roundtail chub	55	1.3	127	164 (24.2–1,203)	12.9	1.1 (0.1–6.9)
Speckled dace	69	1.4	117	301 (45.7–2,160)	11.9	(12.9)
Mottled sculpin	32	0.4	470	110 (5.6–852)	47.9	(4.6)

objectively rank the threat posed by the three nonnative predators based on relative consumptive demands. Determining the predatory threat posed by a fish population cannot be gauged simply by its abundance, size structure, or characteristic dietary preferences. Rather, we have shown how a number of factors interact to determine a given species' capacity to harm native fish populations; these factors include prey choice, population size structure, abundance, and physiological attributes and environmental suitability. Bioenergetics models integrated all of these factors to provide direct impact estimates in the form of the consumptive demand for native fishes by each predator population. These consumption estimates quantified the current relative predatory threat posed by each nonnative species, providing managers with hard evidence with which to prioritize control efforts.

Despite their moderately high abundance, channel catfish in the Yampa River contributed only about 1% of total piscivory because their diet contained few fish. Channel catfish were the most gape limited of the three piscivores in our study; the gape width of a 400-mm channel catfish was only about 77% of the gape width of a 400-mm smallmouth bass (B.M.J., unpublished data). Low piscivory is consistent with findings of Tyus and Nikirk (1990), who reported that channel catfish in the Yampa River rarely ate fish, even when small-bodied fishes were abundant. In that study, only large channel catfish (mean TL = 392 mm) were found to have consumed any fish. Brooks et al. (2000) found that piscivory by channel catfish was also low in the San Juan River, Colorado–New Mexico–Utah, where the prey assemblage was similar to that of the Yampa River. Crayfish and insects were the predominant food source of channel catfish in the Yampa River. Competition for food between channel catfish and native fishes has been put forward as a rationale for channel catfish control efforts. Based on comparisons of our channel catfish diet data with diet studies of native fishes elsewhere (Vanicek and Kramer 1969; Karp and Tyus 1990; Quist et al. 2006), considerable diet overlap between channel catfish and native species probably exists in the Yampa River. However, biomass and production of invertebrate prey organisms in the Yampa River are unknown; hence, resource limitation and competition for food among native and nonnative fishes cannot be inferred.

On a per-capita basis, northern pike consumed more fish than the other predators in both the realized and potential piscivory scenarios; this result is attributable to the large body size of northern pike, their preference for piscine prey, and the suitability of environmental temperatures. However, because northern pike abundance was relatively low, population-scale consump-

tion of fish by northern pike was similar to that by smallmouth bass even though the smallmouth bass diet contained a much smaller percentage of fish. Because they were far less gape limited than smallmouth bass, northern pike were able to maintain a relatively high fraction of fish in their diets after small-bodied fishes declined; thus, northern pike were able to prey on older, larger individuals that were still relatively common in the system (Anderson 2005). Northern pike are potent piscivores, capable of ingesting adults of even large-bodied native species; therefore, continuing efforts to reduce northern pike numbers in riverine habitats where they prey on native species are warranted.

We believe that the small contribution of fish to the smallmouth bass diet and the incidence of cannibalism in our data suggest that piscivory in the Yampa River was limited by low availability of fish prey within the gape limit of smallmouth bass. Spatial overlap between small-bodied fishes and smallmouth bass (and northern pike) is high all year long, and there are no microhabitats that serve as refuges for native fishes. Total piscivory by the smallmouth bass population was similar to that by northern pike simply because smallmouth bass were more abundant than northern pike. Smallmouth bass were highly piscivorous in the GVR, where the invasion was more recent and where small-bodied fishes were common (Bundy and Bestgen 2001). Based on potential piscivory scenarios, if suitably sized fish prey were available in the Yampa River, then smallmouth bass predation could have been 10-fold higher than that of the other two predators combined. Thus, the Yampa River smallmouth bass population possessed a considerable level of latent piscivory. Our analysis indicates that smallmouth bass and northern pike each pose a serious threat to native fishes but that smallmouth bass have the greatest capacity to hamper native fish recovery in the Yampa River by virtue of their high abundance. The synergistic effects of the two predators may be particularly devastating, because prey fish that manage to outgrow the gape of smallmouth bass will remain vulnerable to northern pike for years or a lifetime, depending on the species.

Historic data on the fish assemblage in the Yampa River before either northern pike or smallmouth bass were abundant suggest that small-bodied fish density was similar to present-day density in the GVR. Wick et al. (1985) performed seining in shoreline and backwater habitats ($n = 1,828$ seine hauls) in the Yampa River during 1981 and 1982. Mean density of mostly native, small-bodied fishes for the 2 years combined was 34,000 fish/ha at RKM 165–191 and 45,000 fish/ha over our entire study area (RKM 80–191). In the GVR,

estimates of small-bodied fish density bracketed those of Wick et al. (1985); Bundy and Bestgen (2001) reported a density of 30,000 fish/ha in 46 backwaters of the GVR, and Osmundson et al. (1998) reported an average density of 45,000 fish/ha. If such densities of age-1, small-bodied fish were to occur in the Yampa River again and if potential smallmouth bass predation were to become focused on a single species, such predation could eliminate all yearling mottled sculpin ($69,000 \text{ fish} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$), half of the age-1 speckled dace or roundtail chub ($18,000 \text{ fish} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$), or about a quarter of age-1 flannelmouth suckers ($9,600 \text{ fish} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) across large sections of river. Obviously, if smallmouth bass prey on younger native fish with low accumulated body mass, a given level of consumptive demand will deplete a much greater number of prey individuals. Northern pike predation may affect prey populations differently because they feed on larger, older individuals. Some of the native fishes found in the Yampa River have a life span exceeding 40 years and reproduce intermittently (Minckley and Deacon 1991). Populations with this life history type become vulnerable to collapse as mortality of older life stages increases due to such factors as predation by introduced species (Winemiller and Rose 1992; Musick 1999).

Clearly, nonnative fish consumptive demand was sufficient to cause notable mortality in native fish populations, and our analysis provides managers with the information to prioritize predatory fish control programs. The next obvious question is one posed by Mueller (2005): "Is mechanical predator control feasible?" Political resistance to sport fish removal is a significant impediment in spite of continued imperilment of species protected by listing under the Endangered Species Act (see Clarkson et al. 2005). In principle, the Yampa River system is unique enough to warrant freshwater protected area status (Suski and Cooke 2007), a designation that could build societal support for more-aggressive predator removals (Martinez 2005). From a biological standpoint, we believe that the likelihood of achieving a predator population suppression target is directly linked to the population's recruitment patterns. The potential number of nonnative fish that could be produced in such a large system could easily overwhelm removal crews. Fortunately, northern pike recruitment may be constrained somewhat, because their abundance appears to depend on immigration from upstream impoundments and off-channel habitats. Concerted efforts to (1) reduce immigration to the Yampa River from these sources and (2) remove adults from the river offer a practical strategy to reduce piscivory there.

Smallmouth bass recruitment in the Yampa River

appears to be dependent upon below-normal flows; their recruitment in streams is sensitive to high spring and summer flows, which disrupt nesting and reduce survival of young (Simonson and Swenson 1990; Peterson and Kwak 1999; Smith et al. 2005). Several successive normal to wet years could allow managers to deplete the adult stock of smallmouth bass before new recruits can replenish it. Intense removal efforts would be required to avoid the compensatory increases in reproduction (Dong and DeAngelis 1998; Peterson and Kwak 1999; Weidel et al. 2007) that can occur when physical conditions became favorable. If smallmouth bass cannot be suppressed in the Yampa River, then managers should at least make all possible attempts to contain the spread of the species. The present study and many others suggest that the recent expansion of smallmouth bass in the Yampa River and elsewhere in the upper Colorado River basin (Anderson 2005; Martinez 2005) poses a significant threat to small-bodied fishes throughout the system. The literature is replete with cases where smallmouth bass entering new systems have reduced or eliminated small-bodied fishes. Deleterious effects of smallmouth bass on native species have occurred in locations adjacent to the native range of smallmouth bass (MacRae and Jackson 2001; Vander Zanden et al. 2004), in the northeastern United States (Whittier and Kincaid 1999), the Adirondacks (Findlay et al. 2000; Weidel et al. 2007), the western United States (Gard 2004; Fritts and Pearson 2006), and on other continents (Gore et al. 1991; Iguchi et al. 2004). These cases and the present study draw attention to the potential detrimental effects of smallmouth bass, highlight the need to prevent this species' transfer to other waters, and should assist managers in striving to protect and recover native fish assemblages.

Climate forecasts and human population trends suggest that physical conditions in the Yampa River will become more favorable for nonnative fishes in the future and add urgency to predator fish control plans. Present-day water temperatures are cooler than optimum for all three nonnative predator species; consumptive demand by the three species will increase if the river becomes warmer, thus exacerbating deleterious trophic interactions among native and nonnative fishes. Warming of the Yampa River should be expected in response to (1) regional climate change (Balling and Goodrich 2007) and (2) reductions in streamflow from withdrawals to satisfy growing human demand for water (Stewart et al. 2005; USFWS 2005). Warmer water may make reproductive conditions more favorable for smallmouth bass (Shuter et al. 1980; Serns 1982; Casselman 2002) and northern pike (Casselman and Lewis 1996). Simultaneously, native

fishes may fall into greater peril as disruption of the natural hydrograph compounds the direct effects of nonnative predators. The natural flow regime that is characteristic of streams in the southwestern United States can favor recruitment of native fishes and can be detrimental to nonnative species (Minckley and Meffe 1987; Marchetti and Moyle 2001; Propst and Gido 2004). Thus, protecting the Yampa River's relatively natural hydrograph should be part of a native fish management strategy, providing direct and indirect benefits to native fishes.

Continued monitoring of the diet and demographics of all nonnative piscivores and a reassessment of the relative predatory threats to small-bodied fishes could alert agencies to native and nonnative fish abundance changes that may arise from altered riverine conditions. As hydrologic and thermal conditions change, the coupling of rigorous field monitoring and bioenergetics modeling will be a valuable framework for assisting managers in adapting nonnative fish control efforts to maximize the likelihood of native fish recovery.

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