DIET AND CONSUMPTION RATES OF NATIVE FISHES BY NONNATIVE FISHES IN THE VERDE RIVER, ARIZONA

by

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Abstract

Predation by nonnative fishes is thought to contribute to the decline of native fishes in southwestern rivers. We conducted field investigations from March 2002 through January 2003 on the Verde River, Arizona to estimate the impact of predation by of nonnative fishes on the abundance and distribution of native fishes. We identified the percentage of fish, including native fish, in the diet of nonnative fishes and used Wisconsin bioenergetics model to estimate consumption rates of fish by nonnative fishes. Largemouth bass *Micropterus salmoides* had the highest percentage of fish and native fish in their diet and the highest consumption rates of fish, including native fish. Rainbow trout *Oncorhynchus mykiss* had the second highest consumption rate of fish. The daily ration of prey fish for smallmouth bass *M. dolomieui*, channel catfish *Ictalurus punctatus*, flathead catfish *Pylodictis olivaris*, rainbow trout, and yellow bullhead *Ameiurus natalis* was less than half of that for largemouth bass and rainbow trout. Predation on fish, including native fish was highest during the spring and summer, which overlaps with spawning of native fishes. We also primarily found predation on native fishes occurring below Bartlett Dam, which coincides with the highest density of native fishes. Data on consumption rates of native fishes suggests that the abundance and distribution of native fishes in the Verde River might be increased if focusing future management efforts reduce the abundance of all age classes of largemouth bass and rainbow trout during the spring and summer seasons across the Verde River. Continued research is needed to test the effect of removing the primary piscivores from the Verde River on the abundance and distribution of native fishes.

Introduction

Native fishes have been rapidly declining across the desert Southwest over the last century (Minckley and Deacon 1991). The desert aquatic environments in which they have evolved have been altered by various chemical, physical, and biological impacts, mostly human caused (Minckley and Deacon 1991; Rinne 1994; Johnson and Hinnes 1999). As a result, many native desert fishes have been listed as threatened or endangered under the Endangered Species Act of 1973 (Minckley and Deacon 1991).

Within Arizona, populations of native fishes have been reduced by construction of dams, alterations in flow regimes, loss of surface water, degradation of riparian vegetation, and the introduction of various nonnative species (Rinne et al. 1998). Over 60 species of fish were introduced into Arizona rivers and streams betweens 1900 and 1970 (Rinne 1992). These fishes have had detrimental effects on native fishes through competition, hybridization, alteration of habitat, disease transfer, and predation (Rinne and Minckley 1991; Lassuy 1995; Marsh and Douglas 1997).

Predation on native fishes by nonnative fishes in Arizona streams is well documented (Blinn et al. 1993; Marsh and Douglas 1997; Brouder et al. 2000). However, there is little information that identifies which piscivorous nonnative species and size classes are having the largest impact on native fishes or that characterizes the spatial and temporal patterns of this predation. This information would help managers to protect native fishes while maintaining valuable sport fisheries at some locations. Managers would be able to focus removal or management efforts on specific environments and on the most threatening nonnative fishes.

This thesis is organized into two papers that will be submitted to journals for publication. The first paper (Appendix A) identifies species of nonnative fishes with the highest percentage of fish in their diets, and characterizes changes in the percentage of fish in their diets across the Verde River, by season and environment (i.e., pools, riffles, and runs). The second paper (Appendix B), quantifies consumption rates of native fishes by nonnative piscivores to identify (1) which species and age classes of nonnative fishes exhibit the highest daily consumption rates (2) the season when consumption rates of native fishes were the highest and (3) the geographic region in which consumption is primarily occurring.

This study will be combined with work by Cristina Velez (2003) to determine the impact of predation by nonnative fishes on the abundance and distribution of native fishes in the Verde River.

Present Study

The methods, results, and conclusions of this study are presented in the papers appended to this thesis. The following is a summary of the most important findings in these papers.

The importance of native fishes as prey for nonnative fishes (Appendix A) was estimated by environment type, season, and river section across the entire 300 km of the Verde River, Arizona, from March 2002 to January 2003. Tilapia *Tilapia spp.*, common carp *Cyprinus carpio*, red shiners *Cyprinella lutrensis*, mosquito fish *Gambusia affinis*, and threadfin shad *Dorosoma petenense* were primarily herbivores and insectivores. Bluegill *Lepomis macrochirus*, rainbow trout *Oncorhynchus mykiss,* and green sunfish *L. cyanellus*, were primarily insectivores and their diets consisted of less than four percent of fish. Largemouth bass *Micropterus salmoides*, flathead catfish *Pylodictis olivaris*, channel catfish *Ictalurus punctatus*, smallmouth bass *M. dolomieui*, and yellow bullhead *Ameriurus natalis* contained the highest percentage of fish in their diets. Native fish were found in the diets of largemouth bass, flathead catfish, channel catfish and yellow bullhead only below Bartlett Dam and in the diet of smallmouth bass in the headwaters of the Verde River. The percentage of native fish in the diets of piscivores was highest in spring and summer in pools and riffles. Sonora and desert suckers primarily occurred in the diet of primary piscivores in pools, and longfin dace occurred in their diets in riffles. Overall, largemouth bass had the highest percentage of fish and native fish in their diet (16.7%, and 8.3% respectively), four times that of any other piscivore in the Verde River.

The Wisconsin bioenergetics model (Hanson et al. 1997) was used to quantify variation in daily ration of fish, including native fish consumed by largemouth bass, smallmouth bass, channel catfish, flathead catfish, yellow bullhead, and rainbow trout (Appendix B). Largemouth bass had the highest overall daily ration of fish and native fish, more than twice that of any other species. The daily ration of fish consumed by largemouth bass was highest below Bartlett Dam where native fish densities were the highest and when native fishes were spawning (spring and summer). Finally, daily ration of juvenile largemouth bass (< age 1) was higher than other juvenile nonnative fishes, which corresponds with overlap in use of habitat with age 0 native fishes. Although fish were a small percentage of the diet of rainbow trout, they had the second highest daily ration of fish (exclusively nonnative), while all other species had similar lower daily rations of fish and native fish. Largemouth bass and rainbow trout had the highest consumption rate of fish in the Verde River; by decreasing the abundance and distribution of these species, managers may be able to increase the abundance and distribution of native fishes. Future research is needed to determine what methods will be most effective in reducing densities of largemouth bass and to determine stocking locations and densities for rainbow trout to reduce the potential predation impacts on native fishes.

APPENDIX A

Diet of Nonnative Fishes in the Verde River, Arizona

Diet of Nonnative Fishes in the Verde River, Arizona

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Key Words: Tilapia, carp, red shiner, mosquito fish, threadfin, bluegill sunfish, rainbow trout, green sunfish, largemouth bass, channel catfish, flathead catfish, smallmouth bass, yellow bullhead catfish, desert fishes, predation

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Abstract

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Within Arizona, populations of native fishes have been reduced by construction of dams, alterations in flow regimes, loss of surface water, degradation of riparian vegetation, and the introduction of various nonnative species (Rinne et al. 1998). Over 60 species of fish were introduced into Arizona rivers and streams betweens 1900 and 1970 (Rinne 1992). These fishes have had detrimental effects on native fishes through competition, hybridization, alteration of habitat, disease transfer, and predation (Rinne and Minckley 1991; Lassuy 1995; Marsh and Douglas 1997).

Predation on native fishes by nonnative fishes in Arizona streams is well documented (Blinn et al. 1993; Marsh and Douglas 1997; Brouder et al. 2000). However, there is little information that identifies which piscivorous nonnative species and size classes are having the largest impact on native fishes or that characterizes the spatial and temporal patterns of this predation. This information would help managers to protect native fishes while maintaining valuable sport fisheries at some locations. Managers would be able to focus removal or management efforts on specific environments and on the most threatening nonnative fishes. Our goals were to identify which species of nonnative fishes had the highest percentage of fish in their diets, and characterize changes in the percentage of fish in their diets across the Verde River, by season and environment (i.e., pools, riffles, and runs).

Study Area

The Verde River, located within the Gila River basin, is one of the last perennial rivers in Arizona. The Verde River flows approximately 300 km from Sullivan Lake to its confluence with the Salt River. The Verde River watershed drains 17,212 km^2 from its origin at an elevation of 1,325 m in the forested mountains of northern Arizona to the Sonoran desert scrub communities at its confluence at an elevation of 402 m. The first 200 km of the Verde River are free flowing, and Horseshoe and Bartlett Dams control the flow in the lower 100 km of river. Considerable groundwater pumping occurs within the Verde River basin to support 20 communities and many nearby agriculture activities (Averitt et al. 1994).

The Verde River system contains a variety of native and nonnative fish species, (Table 1; Rinne et al. 1998; Bryan et al. 2000). Historically, the Verde River was home to 10 native fish species. Five of these species are federally listed as threatened or endangered: razorback sucker *Xyrauchen texanus*, Colorado pikeminnow *Ptychocheilus lucius*, loach minnow *Tiaroga cobitis*, spikedace *Meda fulgida*, and Gila topminnow *Poeciliopsis occidentalis occidentalis* (Minckley and Deacon 1991; Rinne et al. 1998; Bryan et al. 2000). We encountered only six native fishes in the Verde River including the Sonora sucker *Catastomus insignis*, desert sucker *C. clarki*, longfin dace *Agosia chrysogaster*, roundtail chub *Gila robusta*, razorback sucker, and Colorado pikeminnow.

Methods

We divided the Verde River into four sections based on the degree and type of anthropogenic impact (Figure 1; Rinne et al. 1998). The first section (Section I), which flowed approximately 69 km from Sullivan Dam to Clarksdale, was largely free of anthropogenic impacts. The second section (Section II), which flowed 49 km from Clarksdale to Beasley Flats, was the most developed section of the river, characterized by many irrigation diversions, sites of ground water pumping and considerably altered riparian vegetation. The third section (Section III), federally designated as “Wild and Scenic” in 1984 under the Wild and Scenic Rivers Act, flowed 90 km from Beasley Flats to Horseshoe Dam. The fourth section (Section IV), flowed 41 km from below Bartlett Dam to the Salt River, had regulated flows and a larger volume of water than all the other sections. We did not sample the area between Horseshoe and Bartlett Dams because this is an isolated section that is not representative of the reset of the Verde River.

Site Selection

We randomly chose three sample sites from available access points within each of the four sections for a total of 12 sites across the river. A randomly chosen pool, riffle, and run were sampled at each site. We used definitions from Arend (1999) to define pools, riffles and runs. Surface area of each sampled pool, riffle, and run was estimated from measures of length and width of each site to allow for across-site comparisons.

Collection of Fish

We sampled fish monthly at each site from March 2002 through January 2003. Block nets measuring 48.8 x 1.8 m with bar mesh size of 3.8 cm were set at each sample site to isolate each pool, riffle, and run. Block nets had float and lead lines; additional weights were added to lead lines when necessary to insure attachment to the stream bed.

We used a combination of raft-mounted and backpack electrofishing to capture fish in each enclosed section. We used a raft-mounted electrofishing unit, equipped with a VVP-15 Coffelt unit, to collect fish from deeper pools and runs. The raft had two anodes, each consisting of a Wisconsin ring and eight cable droppers. Two dropper cable cathode arrays were hung from each side of the raft. We used Smith-Root Model 12 and 15 backpack electrofishing units to collect fish along shallow shorelines where the raft was not able to reach and in riffles and shallow pools and runs. An average setting of 7 amps, 40 Hz, and 60 pulses per second was used to capture fish.

Electrofishing started at approximately 0800 and concluded when each pool, riffle and run had been sufficiently sampled. At least three passes were made in each pool, riffle, and run and the entire area was sampled in each pass. Experimental gill nets, 47.5 m long with six, 7.6 m panels of 1.3 cm, 1.9 cm, 2.5 cm, 3.2 cm, 3.8 cm, and 5.1 cm mesh, were set on two occasions in deep pools to test the capture efficiency of the raft electrofishing unit. Gill nets were set after depletion sampling was complete and we electrofished toward the nets on all sides to herd any remaining fish into the nets.

Seasons

Three seasons were delineated based on observed growth rates of nonnative fishes and fluctuations in water temperature. March through May was designated as spring, June through September as summer, and October through January as winter.

Diet Analysis

Nonnative fishes were collected for diet analysis from each pool, riffle and run. We anesthetized fish, weighed them to the nearest 0.1 g, and measured their total length to the nearest 1 mm. We used the gastric lavage technique (Seaburg 1957), to collect stomach samples from all sizes of fish. We used an agricultural sprayer and various sizes of copper tubing attachments to collect samples from fish with true stomachs. We used forceps to remove prey items, such as crayfish, that could not be flushed from the stomach. These fish were then released back into the river. For fish without true stomachs, (carp *Cyprinus carpio*, mosquito fish *Gambusia affinis*, red shiners *Cyprinella lutrensis*, threadfin shad *Dorosoma petenense,* and tilapia *Tilapia* spp.), we removed the foregut from 10-15 randomly selected individuals from each pool, riffle and run. We did not sample more individuals because we wanted to minimize the effect of sampling mortality on the populations. All stomach contents were preserved in 90% ethanol and transported to the laboratory.

In the laboratory, we examined the contents of each diet sample under a dissecting microscope to separate items into the following categories: fish (by species and developmental stage), insects (by order), plants, crayfish, amphibians, tapeworms, and other nonfood or unidentifiable items. We used the dentary, cleithrum, pharyngeal arch and opercle diagnostic bones (Hansel et al. 1988) to identify fish prey to species. We used methods outlined by Snyder (1979) and Snyder and Muth (1990) to identify larvae and fish eggs. Field guides (Phillips and Comus 1999) were used to attempt to identify amphibians. The U.S. Fish and Wildlife Service (USFWS) Pinetop Fish Health Unit identified parasites found in samples. After identification, all prey items were blotted dry with a paper towel and weighed to the nearest 0.01 g. Parasites and nonfood items were excluded from the diet analysis.

Data Analysis

Diet proportions of each nonnative fish species were averaged across all sites and dates. The top five piscivores were identified based on percentage of fish (native, nonnative, and unknown prey fish) in their diet and the relative abundance of each species (Velez et al. *in prep.*, this issue). For the five top piscivores, we used one-way analysis of variance (ANOVA) and linear combinations to estimate variation in the percent fish (by wet weight) and percent native fish in their diet by section of river, environment, and season. We did not test for interactions between section of river, environment, and season because we did not capture fish in each environment and season within each section. The proportion of fish and native fish consumed was transformed (logit) to account for lack of homogeneity of variance. Untransformed mean proportions were converted to percents for ease of interpretation.

Results

Largemouth bass, flathead catfish, channel catfish, smallmouth bass, and yellow bullhead catfish were the primary piscivores (Table 2). Tilapia, common carp, red shiners, mosquito fish, and threadfin shad primarily fed upon insects and plant material (Table 2). Less than 1% (wet weight) of their diets consisted of fish, all of which were nonnative fishes. Bluegill, green sunfish, and rainbow trout fed primarily on insects; the diets of these fishes consisted of a small percentage (< 5%) of both native and nonnative fishes (Table 2).

Largemouth bass

Largemouth bass ate primarily insects (Tricoptera, Ephemeroptera, and Odonata; Table 2). Of all nonnative fishes, largemouth bass contained the highest percentage of fish in their diet (16.8%, SE = 1.05). Their diet also contained the highest percentage of native fish (8.3%, SE = 0.80), which consisted of longfin dace, desert sucker, and Sonora sucker.

Largemouth bass ate the highest percentage of fish in Section IV (Figure 2); exactly 18.68% (SE = 2.16) higher than in both Sections II and III (Table 3; linear combinations, $F_{1,1106} = 74.45$, $P < 0.01$). We never found largemouth bass in Section I. Fish composed the highest percentage of their diet in spring and summer (Figure 3); 6.6% (SE = 2.47) higher than in winter (Table 3; linear combinations, $F_{1,1106} = 7.24$, $P = 0.01$). The percentage of fish in their diet was also highest in pools (Figure 4); 5.3% (SE = 2.44) higher than in riffles and runs (Table 3; linear combinations, $F_{1,1106} = 4.80$, $P = 0.03$).

Native fish were only observed in the diet of largemouth bass in Section IV (Figure 2) and they composed the highest percentage of the diet in pools (Figure 4); 5.3% (SE = 1.84) higher than in riffles and runs (Table 3; linear combinations, $F_{1,1106} = 8.22$, $P < 0.01$).

Longfin dace were only found in the diet of largemouth bass in riffles. Sonora suckers and unidentified suckers were primarily found in the diet of largemouth bass in pools (Table 4). Desert suckers were primarily found in the diet of largemouth bass in riffles.

Flathead catfish

The diet of flathead catfish consisted primarily of insects (Ephemeroptera and Trichoptera; Table 2). Fish composed 6.8% of the diet, less than half of which were native fish, desert and Sonora suckers. The highest percentage of fish in the diet occurred in Section IV (Table 3; linear combinations, $F_{1,150} = 4.75$, $P = 0.03$). Native fish were only found in the diet of flathead catfish in runs in Section IV during the spring and summer (Figure 2, 3 and 4).

Channel Catfish

The diet of channel catfish consisted primarily of plant material and insects (Trichoptera, Ephemeroptera, and Diptera; Table 2). Fish composed less than 5% of the diet, over half of which were native fish (Sonora sucker and desert sucker).

Fish and native fish composed the highest percentage of the diet during the spring (Figure 3); 7.37% (SE = 2.52) and 5.10% (SE = 2.01) higher, respectively, than in summer and winter (Table 3; linear combinations, $F_{1,245} = 8.54$, $P < 0.01$; $F_{1,245} = 6.42$, $P = 0.01$, respectively). Native fish were observed only in the diet of channel catfish in pools in Section IV (Figure 2 and 4).

Smallmouth bass

The diet of smallmouth bass consisted primarily of insects (Trichoptera, Coleoptera, Diptera, and Hemiptera; Table 2). Native fish composed less than 0.1% of the fish consumed (Table 2).

Smallmouth bass had the highest percentage of fish in their diet during the summer (Figure 2); 2.17% (SE = 0.89) higher than in the spring and winter combined (Table 3; linear combinations, $F_{1,1438} = 5.99$, $P = 0.01$). Native fish (Sonora sucker) were only observed in the diet in Section I during the spring and summer in runs and riffles (Table 4). Smallmouth bass were also never captured in Section IV.

Yellow bullhead

The diet of yellow bullhead consisted primarily of plant material, insects (Ephemeroptera, Diptera, and Coleoptera) and crayfish. Native fish (Sonora sucker and unidentified sucker*)* composed less than 1% of the fish consumed (Table 2).

The percentage of fish in the diet was not significantly different by section of river, season or environment (Table 3; Figure 2). Native fish (longfin dace, desert sucker, and Sonora sucker*)* were found in the diet only in Section IV (Figure 2).

Discussion

Largemouth bass, smallmouth bass, channel catfish, flathead catfish, and yellow bullhead are the primary piscivores in the Verde River. Tilapia, common carp, red shiners, mosquito fish, and threadfin shad were primarily herbivores and insectivores and probably are not having a predatory impact on the abundance and distribution of native fishes. Green sunfish, bluegill, and rainbow trout were primarily insectivores with a small percentage of fish (< 5%) in their diet; the impact of predation by these species on native fishes would only be significant if their consumption rates or population numbers were high.

These results are consistent with dietary studies on these species (Odum 1971; Marsden 1996; Garcia-Berthou 2001). Marsden (1996) and Garcia-Berthou (2001) found carp to be primarily herbivores and insectivores however they did find evidence of carp consuming a small percentage of fish eggs; we found no evidence of fish eggs in the diet of carp. Ruppert et al. (1993) found fish larvae in the diet of red shiners in Colorado; however we found no evidence of larval fish or fish eggs in the diet of red shiners. We believe eggs and larvae would have been detected if they were in the diets of these species because we were able to detect eggs and larvae in the diets of other species. Eggs of native fish in the Verde River may not be easily accessible to carp and red shiners (Marsden 1996), or there may be higher concentrations of their preferred prey items (aquatic plants and insects) in the Verde River than there were in areas studied by Marsden (1996) and Garcia-Berthou (2001), for carp and red shiners to consume.

Only a small percentage of fish, including native fish (Sonora sucker and unidentified sucker), were found in the diets of green sunfish, bluegill, and rainbow trout. Other studies indicate that bluegill and green sunfish may cause decreased recruitment of razorback suckers in Lake Mohave by preying upon eggs and larvae (Minckley and Deacon 1991). Predation by and competition with green sunfish are also believed to be the reason for the decline in Gila chub *Gila intermedia,* in Sabino Canyon, Arizona (Dudley and Matter 2000). In the Verde River, abundance of green sunfish is low (Velez et al. *in prep.*), and the percentage of their diet consisting of fish is low so they probably are not having a significant impact on the abundance and distribution of native fishes.

Rainbow trout occurred in our sampling areas in very low numbers; however, they are stocked into the Verde River each year. In 2002, approximately 60,000 trout were stocked in the Camp Verde area (Section II) and 4,500 were stocked below Bartlett Dam (Section IV) to provide angling opportunities and to supplement the diet of bald eagles, *Haliaeetus leucocephalus*, on Native American reservation lands (Scott Bryan, personal communication). The percentage of fish consumed by rainbow trout could be as high as 9.3% (upper 95% C.I.). With high stocking densities, this species has the potential to impact native fish populations though predation, especially with spring stockings that coincide with the spawning time of many native fishes (Sublett et al. 1990).

Largemouth bass

Of all nonnative fishes, largemouth bass contained the highest percentage of fish and native fish in their diet, four times the amount of any other piscivore in the Verde River. These results are not surprising given that largemouth bass are primary piscivores (Keast 1985) and become piscivorous when they reach 51 mm (Becker 1983).

The percentage of fish (native and nonnative) in the diet was the highest below Bartlett Dam. The area below Bartlett Dam also contained the highest density of native fishes, especially young of the year Sonora and desert suckers (Velez et al. *in prep.*). The high percentage of native fish in the diet in the spring coincides with spring spawning of Sonora and desert suckers, and reflects the sites where bass were most frequently caught.

Roundtail chub were never observed in the diet of any nonnative fishes. Longfin dace were observed in the diets of largemouth bass only in riffles, which reflects the primary habitat of longfin dace (Sublette et al. 1990). The pharyngeal arch of longfin dace was indistinguishable from that of red shiners, so it is possible that the percent of longfin dace in the diet was underestimated. Only four longfin dace were identified in stomach samples, all of which were in early stages of digestion and could be easily identified.

Flathead catfish

Predation by flathead catfish is thought to be the primary reason for decline of many native fishes in the Lower Colorado River and the Salt River (Marsh and Brooks 1989; Arizona Game and Fish Department 1995). The differences in size structure between flathead catfish in the Verde and Salt Rivers may be the primary reason for this discrepancy. The average size of flathead catfish we collected was 142 mm TL and 85% were less than 250 mm. Flathead catfish are secondary piscivores, becoming piscivorous later in life (Keast 1985), when they reach 250 mm (Sublette et al. 1990). We also set gill nets in pools after completing our depletion sampling to test the effectiveness of our sampling methods; we never captured any fish in the gills nets.

Channel catfish

A small percentage of the diet of channel catfish consisted of desert sucker and Sonora suckers. Fish (native and nonnative) were most common in the diet of fish below Bartlett Dam, especially in pools. The majority of channel catfish were captured below Bartlett Dam, and these fish were significantly larger than those above Bartlett Dam. This difference in size structure between sections and the abundance of sucker below the dam may account for the commonness of fish in the diet of catfish below Bartlett Dam.

Marsh and Brooks (1989) found recently stocked razorback suckers in high densities in the diet of channel and flathead catfish in the Gila River, Arizona. Channel catfish have the potential to have a predation impact on the abundance and distribution of native fishes; they are opportunists and are also secondary piscivores (Keast 1985).

Smallmouth bass

Fish were most common in the diet of smallmouth bass in the relatively pristine headwaters of the Verde River (Section I) during spring and summer, however fish composed less that 5% of the diet. Previous studies have found native fish and fish in general to compose a higher percentage of the diet of smallmouth bass than we documented (Brouder et al. 2000; Robertson and Winemiller 2001). We observed native fish in very low densities in the upper Verde River and this may account for their rarity in the diets of smallmouth bass. However, fish of similar sizes, such as red shiners, were found in the diet in higher numbers. Smallmouth bass have the potential to have a predation impact on the abundance and distribution of native fish.

Yellow bullhead

The diet of yellow bullhead primarily consisted of insects, plants and crayfish. The percent of crayfish in the diet of yellow bullheads was greater than in other nonnative fishes; overall crayfish composed a small percentage of the diet of all nonnative fishes (< 14%). Fish composed less than 3% of the diet, one-third of which were native fish (longfin dace and unidentified sucker). Fish were most common in the diet of yellow bullhead below Bartlett Dam in riffles in spring and summer. Seaburg and Moyle (1964) also found bullheads to eat primarily crustaceans and only a few fish.

Even though yellow bullhead ate only a small percentage of fish, one-third were native fishes, so yellow bullhead have the potential to have an impact on the abundance and distribution of native fishes.

Conclusions

Based on diet alone, largemouth bass are the primary piscivore in the Verde River both for native and nonnative prey fishes. Native fish composed the highest percentage of the diet of all nonnative fishes below Bartlett Dam, which coincides with the highest abundances of native fishes. Fish, including native fish composed the highest percentage of the diet of all nonnative fishes during the spring and summer, which coincides with the spawning of native fishes. These trends suggest that these nonnative fishes, especially largemouth bass, could be negatively impacting the abundance and distribution of native fishes through predation. To determine if predation by nonnative fishes is significantly impacting native fish populations, the consumption rates and abundances of nonnative and native species are required.

Prey fish (native and nonnative) in the diet of nonnative fishes could be viewed as the highest percent of native fish these species could have in their diet. Piscivores are opportunistic (Hodgson and Kitchell 1987); they are not seeking out specific species of native fish to feed upon. If native fishes were in higher density above Bartlett Dam we might see the same predation patterns occurring. The low densities of native fish above Bartlett Dam may be caused by continual predation since the early 1900s, Velez et al. (*in prep.*) discusses this topic in more detail.

Arizona’s nonnative sport fishery is a major funding source for the Arizona Game and Fish Department and it generates more revenue for Arizona than any other recreational source. If native fish are going to be conserved, and a sport fishery maintained, the impact of predation by nonnative fishes needs to be considered. The three companion papers, which follow in this issue, further define the impact these nonnative fishes are having on native fishes in the Verde River.

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Table 1. - Native and nonnative fishes found during our study (March 2002-2003) and historically in the Verde River, Arizona.

Common Name	Scientific Name
Native Fishes	
Colorado Pikeminnow*+	*Ptychocheilus lucius*
Desert Sucker*	*Catastomus clarki*
Gila Topminnow+	*Poeciliopsis occidentalis*
Loach Minnow+	*Tiaroga cobitis*
Longfin Dace*	*Agosia chrysogaster*
Razorback Sucker*+	*Xyrauchen texanus*
Roundtail Chub*	*Gila robusta*
Sonora Sucker*	*Catastomus insignis*
Speckled Dace	*Rhinichthys osculus*
Spikedace+	*Meda fulgida*
Nonnative Fishes	
Black Crappie	*Pomoxis nigromaculatus*
Bluegill Sunfish*	*Lepomis macrochirus*
Channel Catfish*	*Ictalurus punctatus*
Common Carp*	*Cyprinus carpio*
Fathead Minnow	*Pimephales promelas*
Flathead Catfish*	*Pylodictis olivaris*
Green Sunfish*	*Lepomis cyanellus*
Largemouth Bass*	*Micropterus salmoides*
Mosquitofish*	*Gambusia affinis*
Rainbow Trout*	*Oncorhynchus mykiss*
Red Shiner*	*Cyprinella lutrensis*
Sailfin Molly	*Poecilia latipinna*
Shortfin Molly	*Poecilia mexicana*
Smallmouth Bass*	*Micropterus dolomieui*
Threadfin Shad*	*Dorosoma petenense*
Tilapia spp.*	*Tilapia spp.*
Yellow Bullhead Catfish*	*Ameriurus natalis*
Yellow Bass	*Morone mississippiensis*

* Fish species captured in this study

+ Fish species federally listed as threatened or endangered

Table 2.- Percent by weight and standard errors of prey consumed by nonnative fishes in the Verde River, Arizona (all sites and seasons combined), 2002-2003.

	Bluegill sunfish	Rainbow trout	Tilapia spp.	Green sunfish	Mosquito fish	Common carp	Red shiner
	N = 22	N = 32	N = 92	N = 754	N = 497	N = 316	N = 1557
	(19-190 mm)	(225-356 mm)	(22-317 mm)	(21-216 mm)	(13-56 mm)	(39-710 mm)	(6-89 mm)
Prey group	% (SE)	% (SE)	% (SE)	% (SE)	% (SE)	% (SE)	% (SE)
Total Fish	4.29 (4.25)	3.83 (2.71)	0	0.61 (0.24)	0.17 (0.17)	0.42 (0.30)	0.02 (0.84)
Native Fishes	4.29 (4.25)	0	0	0.48 (0.23)	0	0	0
Longfin dace	0	0	0	0.13 (0.13)	0	0	0
Desert sucker	0	0	0	0	0	0	0
Sonora sucker	0.04 (0.04)	0	0	0	0	0	0
Catastomus spp.	4.25 (4.25)	0	0	0.34 (0.71)	0	0	0
Nonnative Fishes	0	0	0	0.22 (0.14)	0	0.32 (0.32)	0
Yellow bullhead	0	0	0	0	0	0	0
Common carp	0	0	0	0	0	0	0
Red shiner	0	3.83 (2.71)	0	0.18 (0.14)	0	0.05 (0.05)	0
Mosquito fish	0	0	0	0	0.17 (0.17)	0	0
Channel catfish	0	0	0	0.04 (0.04)	0	0	0
Green sunfish	0	0	0	0	0	0.27 (0.27)	0
Micropterus spp.	0	0	0	0	0	0	0
Smallmouth bass	0	0	0	0	0	0	0
Largemouth bass	0	0	0	0	0	0	0
Tilapia spp.	0	0	0	0	0	0	0
Flathead catfish	0	0	0	0	0	0	0
Cypriniformes	0	0	0	0	0	0	0
Centrarchidae	0	0	0	0	0	0	0
Ictalurus spp.	0	0	0	0	0	0	0
Unknown Fishes	0	0	0	0.05 (0.04)	0	0.10 (0.10)	0.02 (0.84)
Invertebrates	75.98 (8.74)	63.98 (7.30)	14.26 (3.65)	78.85 (1.23)	93.50 (1.07)	20.82 (2.14)	96.65 (0.41)
Plants	19.72 (8.12)	32.15 (7.16)	84.67 (3.76)	13.03 (0.99)	6.23 (1.05)	76.39 (2.24)	3.26 (0.41)
Crayfish	0	0.04 (0.04)	1.07 (1.07)	7.09 (0.78)	0.10 (0.10)	2.37 (0.81)	0.06 (0.04)
Amphibians	0	0	0	0.41 (0.21)	0	0	0

Table 2 cont.- Percent by weight and standard errors of prey consumed by nonnative fishes in the Verde River, Arizona (all sites and seasons combined), 2002-2003.

Prey group	Threadfin shad N = 1 (51 mm) % (SE)	Largemouth bass N = 1109 (12-515 mm) % (SE)	Flathead catfish N = 154 (27-505 mm) % (SE)	Channel catfish N = 248 (21-573 mm) % (SE)	Smallmouth bass N = 1441 (10-340 mm) % (SE)	Yellow bullhead N = 271 (29-328 mm) % (SE)
Total Fish	0	16.76 (1.05)	6.84 (1.91)	4.11 (1.11)	3.43 (0.43)	2.71 (0.87)
Native Fishes	0	8.30 (0.80)	1.89 (1.05)	2.43 (0.88)	0.07 (0.06)	0.86 (0.53)
Longfin dace	0	0.34 (0.17)	0	0	0	0
Desert sucker	0	2.80 (0.47)	0.79 (0.62)	0.46 (0.36)	0	0
Sonora sucker	0	2.97 (0.49)	1.10 (0.76)	1.38 (0.62)	0.07 (0.06)	0.12 (0.12)
Catastomus spp.	0	2.20 (0.40)	0	0.60 (0.35)	0	0.74 (0.52)
Nonnative Fishes	0	6.17 (0.67)	4.96 (1.63)	0.94 (0.56)	2.79 (0.39)	0.89 (0.49)
Yellow bullhead	0	0	0	0	0.05 (0.03)	0.25 (0.25)
Common carp	0	0.30 (0.14)	0.18 (0.18)	0	0.11 (0.08)	0
Red shiner	0	2.23 (0.41)	3.83 (1.48)	0	1.65 (0.31)	0.34 (0.30)
Mosquito fish	0	1.44 (0.32)	0	0.62 (0.46)	0.57 (0.18)	0
Channel catfish	0	0.08 (0.08)	0	0	0	0
Green sunfish	0	0.20 (0.13)	0	0	0.06 (0.06)	0.29 (0.29)
Micropterus spp.	0	0.18 (0.13)	0	0	0.27 (0.13)	0
Smallmouth bass	0	0.18 (0.13)	0	0	0	0
Largemouth bass	0	0.33 (0.16)	0	0.32 (0.32)	0	0
Tilapia spp.	0	0.75 (0.25)	0	0	0	0
Flathead catfish	0	0.09 (0.09)	1.00 (0.72)	0	0	0
Cypriniformes	0	0	0	0	0.02 (0.02)	0
Centrarchidae	0	0.39 (0.16)	0	0	0.03 (0.03)	0
Ictalurus spp.	0	0	0	0	0.03 (0.03)	0
Unknown Fishes	0	1.97 (0.35)	0.005 (0.057)	0.73 (0.36)	0.66 (0.18)	0.95 (0.47)
Invertebrates	100	56.20 (1.36)	61.85 (3.61)	29.58 (2.74)	71.27 (1.06)	55.05 (2.64)
Plants	0	14.10 (0.92)	20.03 (3.02)	57.73 (2.89)	11.89 (0.81)	26.95 (2.30)
Crayfish	0	1.11 (0.87)	11.01 (2.23)	8.50 (1.66)	12.95 (0.81)	14.43 (1.95)
Amphibians	0	1.84 (0.37)	0	0.08 (0.07)	0.35 (0.14)	0.85 (0.52)

Table 3.- Results of one-way analysis of variance testing whether the mean percent of total fish and native fish in the diet of largemouth bass, flathead catfish, channel catfish, smallmouth bass, and yellow bullhead catfish varies by section of river, environment, and season. Separate analyses were done for each species.

	Largemouth bass			Flathead Catfish			Channel Catfish			Smallmouth bass			Yellow bullhead		
Variable	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
							Total Fish								
Section	53.01	2, 1106	<0.01	2.51	3, 150	0.06	1.15	3, 244	0.32	1.72	2, 1438	0.18	1.68	3, 267	0.17
Environment	3.36	2, 1106	0.02	0.82	2, 151	0.44	1.54	2, 245	0.22	0.14	2, 1438	0.87	1.32	2, 268	0.27
Season	3.97	2, 1106	0.02	1.22	3, 150	0.30	3.47	2, 245	0.03	4.15	2, 1438	0.02	1.25	2, 268	0.29
							Native Fish								
Section	72.11	2, 1106	<0.01	12.79	3, 150	<0.01	0.48	3, 244	0.70	0.44	2, 1438	0.64	2.13	3, 267	0.09
Environment	6.03	2, 1106	<0.01	0.81	2, 151	0.45	1.31	2, 245	0.27	0.75	2, 1438	0.47	0.94	2, 268	0.39
Season	1.06	2, 1106	0.35	0.48	2, 151	0.62	4.41	2, 245	0.01	0.23	2, 1438	0.79	0.72	2, 268	0.48

Table 4.- Percent by weight and standard errors of longfin dace, desert sucker, Sonora sucker, and unidentified suckers consumed by largemouth bass by season and environmental below Bartlett Dam (Section IV), Verde River, Arizona.

	Spring	**Summer**	**Winter**
	% (SE)	**% (SE)**	**% (SE)**
		Longfin Dace	
Pool	0	0	0
Riffle	6.18 (6.18)	0	2.11 (2.11)
Run	0	0	0
		Desert Sucker	
Pool	2.15 (1.49)	7.98 (5.01)	3.69 (3.69)
Riffle	16.66 (11.78)	0	0
Run	1.30 (1.29)	1.67 (1.67)	6.54 (4.61)
		Sonora Sucker	
Pool	18.07 (8.35)	9.17 (4.51)	0.73 (0.73)
Riffle	0.71 (0.71)	4.17 (4.17)	0
Run	0	4.09 (2.18)	3.53 (3.15)
		Catastomus spp.	
Pool	6.85 (3.45)	7.62 (3.07)	0
Riffle	4.79 (4.79)	0	0
Run	3.54 (2.43)	3.33 (2.25)	0.07 (0.07)

Figure 1.- Verde River location within Arizona and section and sample location on the Verde River, Arizona.

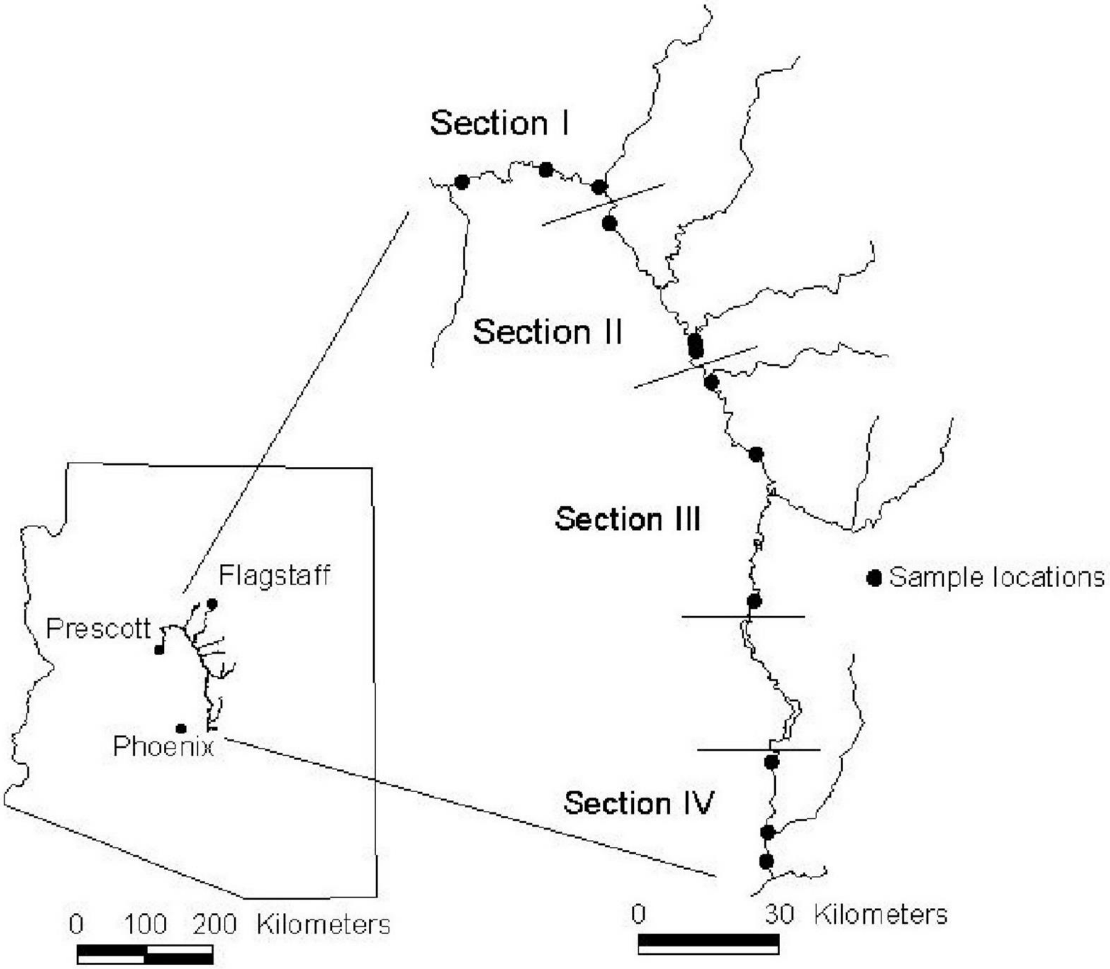


Figure 2.-Percent by weight of native and nonnative fish in the diet of largemouth bass (LMB), flathead catfish (FHC), channel catfish (CCF), smallmouth bass (SMB), and yellow bullhead (YBH) by section of river.

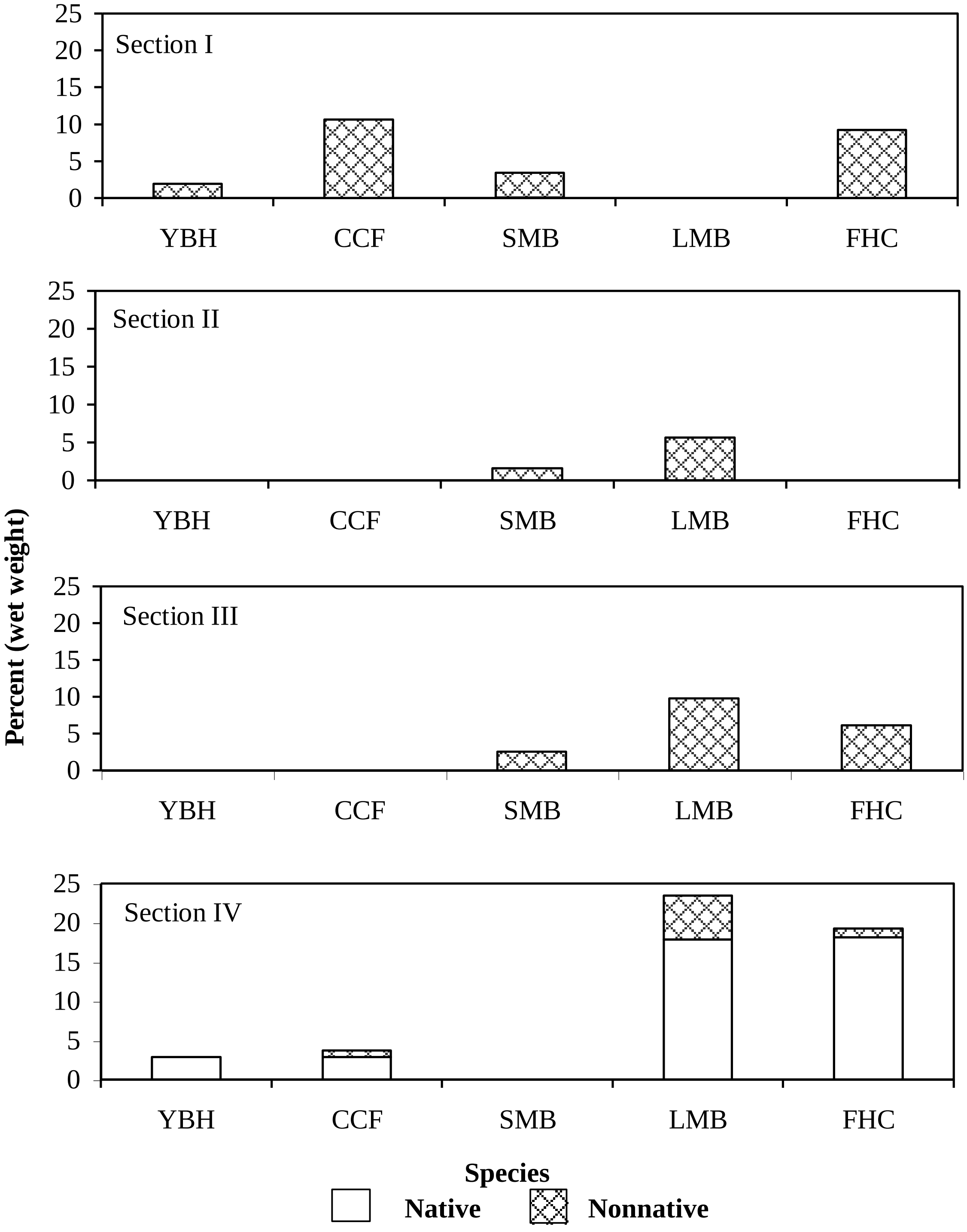


Figure 3.-Percent by weight of native and nonnative fish in the diet of largemouth bass (LMB), flathead catfish (FHC), channel catfish (CCF), smallmouth bass (SMB), and yellow bullhead (YBH) by season.

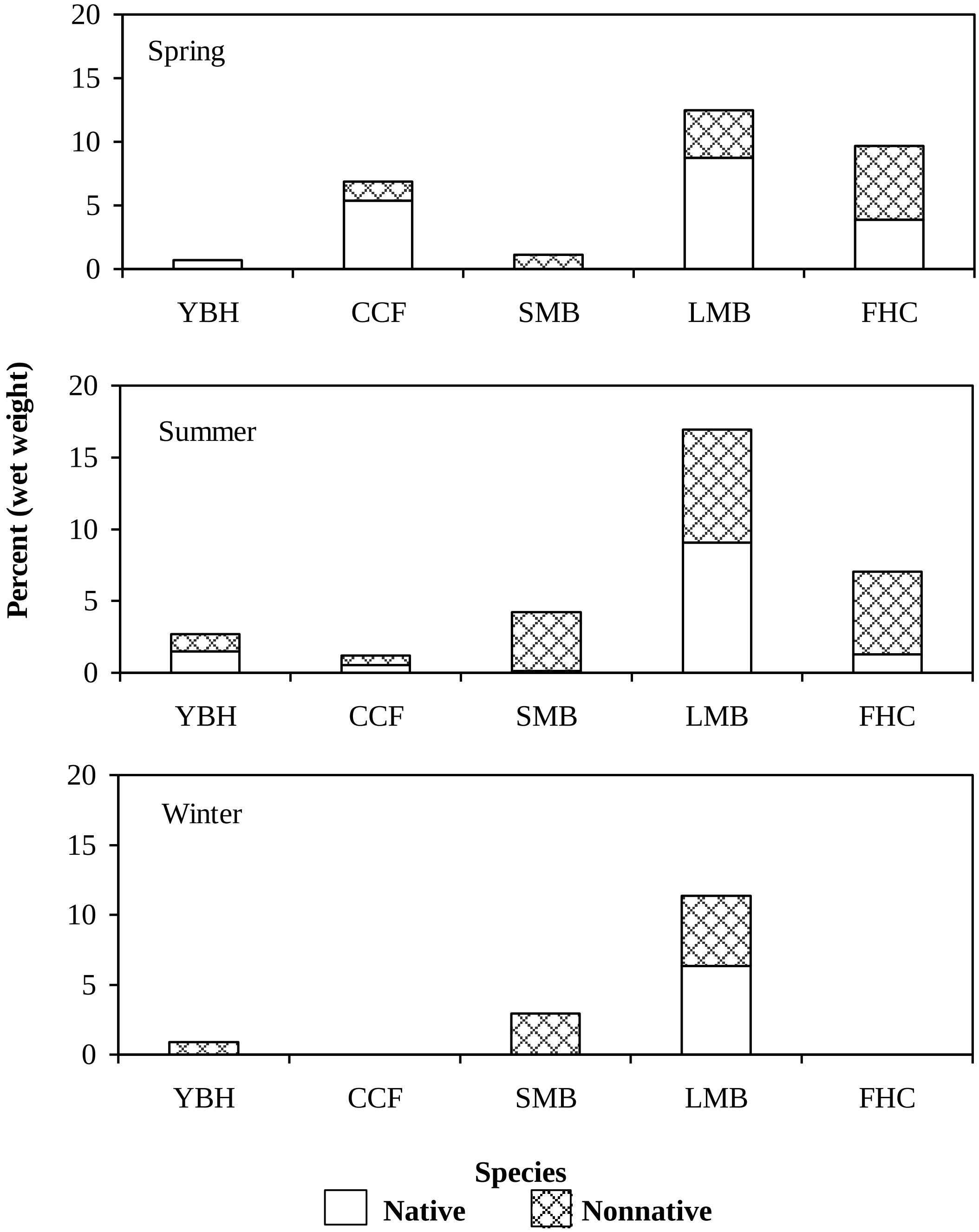
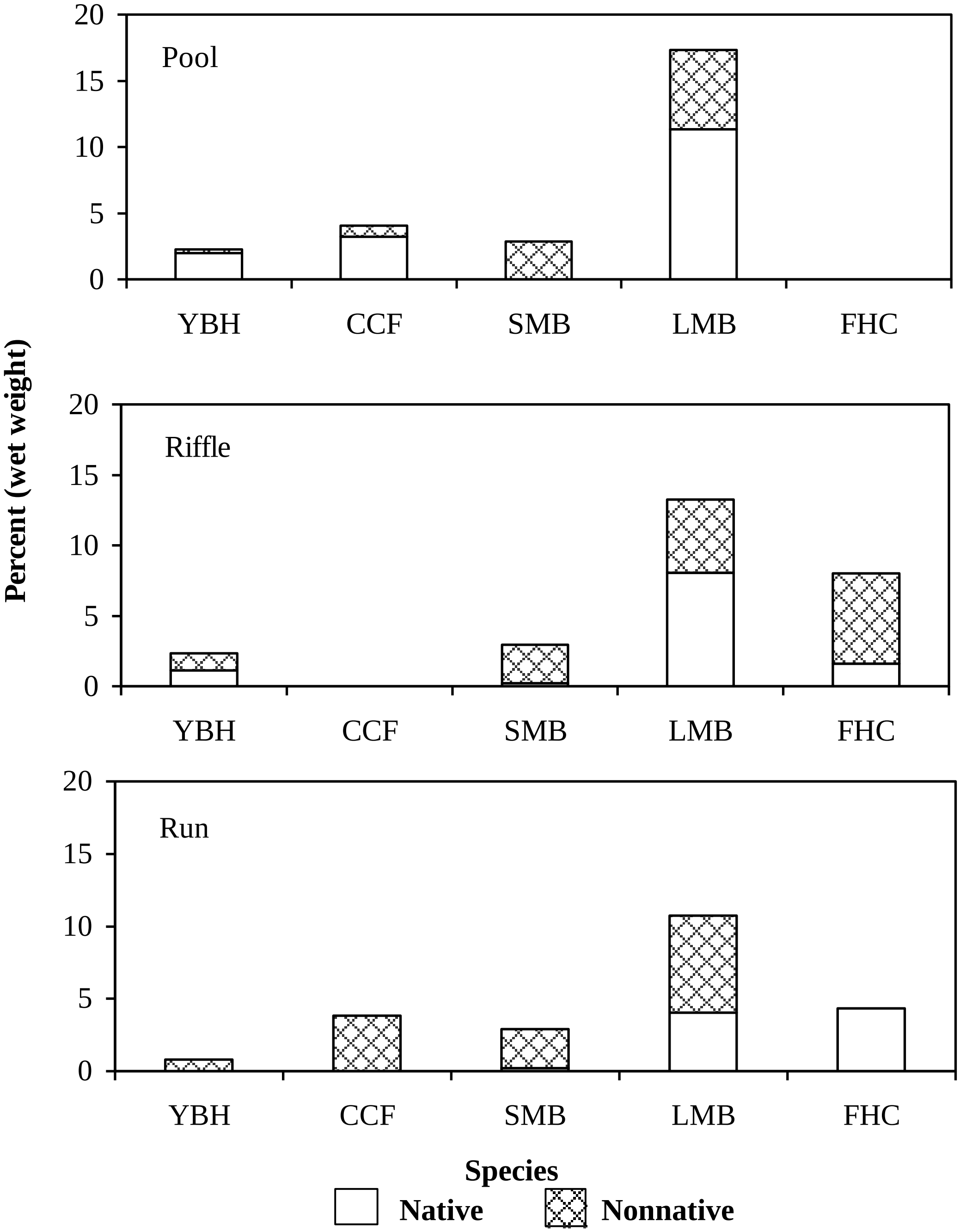


Figure 4.-Percent by weight of native and nonnative fish in the diet of largemouth bass (LMB), flathead catfish (FHC), channel catfish (CCF), smallmouth bass (SMB), and yellow bullhead (YBH) by environment.



APPENDIX B

Consumption Rates of Native Fishes by Nonnative Fishes in the Verde River, Arizona

Rates of Consumption of Native Fish by Nonnative Fishes in the Verde River, Arizona

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Key Words: Bioenergetics, rainbow trout, largemouth bass, channel catfish, flathead catfish, smallmouth bass, yellow bullhead catfish, predation

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Abstract

Largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieui*, channel catfish *Ictalurus punctatus*, flathead catfish *Pylodictis olivaris*, yellow bullhead *Ameiurus natalis*, and rainbow trout *Oncorhynchus mykiss* were sampled throughout the Verde River from March 2002 to January 2003 to examine trends in prey fish consumption. The Wisconsin bioenergetics model (Hanson et al. 1997) was used to quantify variation in daily ration of fish, including native fish consumed by largemouth bass, smallmouth bass, channel catfish, flathead catfish, yellow bullhead, and rainbow trout. Largemouth bass had the highest overall daily ration of fish and native fish, more than twice that of any other species. The daily ration of fish consumed by largemouth bass was highest below Bartlett Dam where native fish densities were the highest and when native fishes were spawning (spring and summer). Finally, daily ration of juvenile largemouth bass (< age 1) was higher than other juvenile nonnative fishes, which corresponds with overlap in use of habitat with age 0 native fishes. Although fish were a small percentage of the diet of rainbow trout, they had the second highest daily ration of fish (exclusively nonnative), while all other species had similar lower daily rations of fish and native fish. Largemouth bass and rainbow trout had the highest consumption rate of fish in the Verde River; by decreasing the abundance and distribution of these species, managers may be able to increase the abundance and distribution of native fishes. Future research is needed to determine what methods will be most effective in reducing densities of largemouth bass and to determine stocking locations and densities for rainbow trout to reduce the potential predation impacts on native fishes.

Introduction

The introduction of nonnative fishes across the desert Southwest have had detrimental effects on native fishes through competition, hybridization, disease transfer, and predation (Rinne and Minckley 1991; Lassuy 1995; Marsh and Douglas 1997). As a result many native fishes are federally listed under provisions of the Endangered Species Act (ESA) of 1973.

Predation from nonnative sport fishes is hypothesized to be one of the primary causes of native fish declines in the Verde River and across the Southwest (Rinne and Minckley 1991; Lassuy 1995; Marsh and Douglas 1997). Within the Verde River, native fish have been documented in the diets of various nonnative fishes (Brouder et al. 2000; Leslie et al. *in prep.*, this issue), however the rate of consumption of native fishes by nonnative fishes has not been quantified. By identifying the consumption rate of native fishes by nonnative fishes managers will be able to evaluate the potential effects of increasing (stocking) or decreasing (mechanical removal) the biomass of nonnative fishes will have on the native fishes in the Verde River.

We estimated the consumption rate of fish and native by largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieui*, channel catfish *Ictalurus punctatus*, flathead catfish *Pylodictis olivaris*, rainbow trout *Oncorhynchus mykiss*, and yellow bullhead *Ameiurus natalis,* in the Verde River. These species were chosen for analysis based on the percentage of their diet composed of fish and native fish (Leslie et al. *in prep.*). Rainbow trout were specifically chosen because they are the only nonnative species that is currently being stocked into the Verde River. By quantifying consumption rates of native fishes by nonnative piscivores we will identify (1) which species and age classes of nonnative fishes exhibit the highest daily consumption rates (2) the season when consumption rates of native fishes were the highest and (3) the geographic region in which consumption is primarily occurring.

This information allows managers to assess which species and age classes are having the greatest predatory impact on native fishes and make management decisions accordingly. By focusing control and removal efforts on the specific species and age classes that have the highest consumption rates of native fishes, managers have been able to greatly reduce the potential predation on native fishes and increase the abundance and distribution of native fishes (Foerster and Ricker 1941; Meachum and Clark 1979; Smith and Tibbles 1980; Friesen and Ward 1999; Koonce et al. 1993; Tyus and Saunders III 2000).

Methods

The Verde River, located within the Gila River Basin, flows approximately 300 km from Sullivan Lake to its confluence with the Salt River. For a detailed description of the study area and sample design, see Leslie et al. (*in prep.*).

Study design

We used the Wisconsin bioenergetics model (Hanson et al. 1997) to calculate consumption rates of prey fish for primary predators in the Verde River (largemouth bass, smallmouth bass, channel catfish, flathead catfish, yellow bullhead, and rainbow trout; as determined by Leslie et al., *in prep.*) by section of river, season, and age class.

We divided the river into four major sections based on degree and type of anthropogenic impacts (see Leslie et al. *in prep.*, for map). Section I, flowed approximately 69 km from Sullivan Dam to Clarksdale and was largely free of anthropogenic impacts. Section II, flowed 49 km from Clarksdale to Beasley Flats, and was the most developed section of the river, characterized by many irrigation diversions, sites of ground water pumping and considerably altered riparian vegetation. Section III, federally designated as “Wild and Scenic” in 1984 under the Wild and Scenic Rivers Act, flowed 90 km from Beasley Flats to Horseshoe Dam. Section IV, flowed 41 km from below Bartlett Dam to the Salt River, and had regulated flow and a larger volume than other sections.

We delineated three seasons based on observed growth rates of nonnative fishes and fluctuations in water temperature. Spring was designated as March through May (simulation day 1 to 94), summer was June through September (day 95 to 220), and winter was October through February (day 221 to 365). Days of simulation for age 0 fish started on the first day we captured them. Our sampling ended in January 2003; however, we ran our simulations from March 2002 to March 2003 to represent consumption rates of fish across the entire year. For purposes of our simulations, diet composition, temperature, and growth rate estimates were assumed to be constant for each species from January 2003 through February 2003

We delineated three age classes for largemouth bass, smallmouth bass, channel catfish, flathead catfish and yellow bullhead based on length frequencies for each species. Consumption rates were not determined by age class for rainbow trout because age 1 fish were stocked into the Verde River and they are assumed to not be reproducing or surviving through the summer (Roger Sorensen, Arizona Game and Fish Department, personal communication).

Bioenergetics model simulations

The Wisconsin bioenergetics model estimates the daily consumption rates of each prey species by each predator through balanced energy equations that take into account each predator's specific physiological parameters, energy densities (Joules/gram) of prey, proportion of the diet made of different prey, growth rates of the predator, timing of and energy spent on reproduction by each species, and the temperature regimes in which they occur.

Physiological parameters

We used physiological parameters for consumption, respiration, waste loss, and predator energy density that were included in the bioenergetics model for largemouth bass, smallmouth bass, and rainbow trout (Shuter and Post 1990; Rand et al. 1993; Rice et al. 1993, respectively). We used physiological parameters described by Blanc and Margraf (2002) for channel catfish. We used channel catfish as a surrogate species for flathead catfish and yellow bullhead because physiological parameters were not available for these species. We borrowed energy densities for prey species from the literature (Table 1).

Diet composition

We used diet information collected by Leslie et al. (*in prep.*) for diet composition inputs into the model. We used section- and species-specific length frequencies to separate diet composition data into age classes at each sample site. We pooled diet composition across each pool, riffle and run at each sample site to increase sample size and because we were unable to determine in which environment the prey items were consumed.

Diet data were pooled for all rainbow trout and the bioenergetics model was run for the spring stocking season (January through May). We used Diet data from April and May 2002 and January 2003 for the spring simulation using the bioenergetics model. We collected only one trout during the summer season so we only analyze consumption rates during the spring.

Growth rates

Growth rates for age 0 and age 1 fish were calculated from length frequency data (Devries & Frie 1996) for all fishes except rainbow trout. Length frequency data were not reliable for age 2+ fish so the average size of age 2+ fish was calculated using length frequency data and used as the average length of age 2+ at the beginning of our study. We did not use a weighted average because the data was normally distributed with no obvious outliers. We calculated the average growth per day of age 2+ fish using mark-recapture data from tagged age 2+ fish. We multiplied growth per day by the number of days during each season to calculate the average length of each species at the beginning and end of each subsequent season (Table 2). The winter growth rate of age 1 channel catfish in Section IV was used to calculate winter growth for age 2+ channel catfish because no age 2+ channel catfish were marked or recaptured during winter. We developed length-weight regressions for each species to convert growth in length to growth in weight for input into the bioenergetics model.

We assumed no growth for rainbow trout during our simulation because water temperature was above optimal temperature for growth (25°C; Sublette et al. 1990), and rainbow trout generally do not to survive in the Verde River long enough to experience growth (Roger Sorensen, Arizona Game and Fish Department, personal communication). Also the average weights of all rainbow trout captured were very similar to average weights of stocked fish (215 g) so we assumed they were not gaining or loosing a significant amount of weight while residing in the Verde River.

Reproduction

We accounted for energy costs associated with spawning for age 2+ largemouth bass, smallmouth bass, flathead catfish, channel catfish and yellow bullheads. The bioenergetics model requires inputs on the day of spawning and the proportion of fish mass that is lost on that day (gonado somatic index (GSI)). We calculated the spawning day for each species based on the water temperature at which they spawn (Table 3: Sublette et al. 1990) and the GSI for each species was borrowed from the literature (Timmons et al. 1980; Davis 1986; Davis 2000).

Temperature regime

The temperature regimes for each section were calculated (Figure 1) from water temperature measurements taken from each pool, riffle, and run. Water temperatures were measured mid-morning at median depth of the water column. While water temperatures can fluctuate throughout the day we assumed we were capturing the median water temperature because temperatures tend to peak in the late afternoon and are generally coldest in the early morning. We calculated average water temperature for each month (Figure 1) by averaging site-specific water temperatures within each section. Temperature profiles were the same for all age classes and species within a section.

The model interpolated values of diet composition, thermal experience, and growth between sample dates. The model was run only for age classes of nonnative fishes where prey fish were found in the diet; otherwise daily ration was entered as zero.

Analysis

We used one-way analysis of variance (ANOVA) and linear combinations to test for and quantify differences in mean daily ration of fish and native fish by species and age class of nonnative fish, section of river, and season. We did not test for interactions between section of river, environment, and season because we did not capture fish in each environment and season within each section.

Piscivores are opportunistic (Hodgson and Kitchell 1987); they are not seeking out specific species of native fish to feed upon. We viewed the daily ration of fish (native and nonnative) consumed by nonnative fishes as the highest possible predation rate that could occur on native fishes (longfin dace, Sonora sucker and desert sucker) if they were readily available as prey. The daily ration of native fishes is the actual daily consumption of native fishes we observed.

Results

Daily ration

Largemouth bass had the highest average daily ration of fish and native fish (Figure 2: ANOVA, $F_{5,106} = 5.49$, $P < 0.01$; $F_{5,106} = 5.95$, $P < 0.01$, respectively). The average daily ration of fish by largemouth bass was 5.2 mg/g (SE = 1.44) greater than the daily ration of fish by all other species (linear combinations, $F_{1,106} = 12.73$, $P < 0.01$). Their daily ration of native fish was 2.9 mg/g (SE = 1.04) greater than the daily ration of native fish consumed by any other species (linear combinations, $F_{1,106} = 7.83$, $P < 0.01$).

Rainbow trout had the second highest daily ration of fish, all of which were nonnative prey fish (Figure 2). Flathead catfish had the second highest daily ration of native fishes, followed by yellow bullhead, channel catfish, and smallmouth bass (Figure 2). Flathead catfish, yellow bullhead, channel catfish, and smallmouth bass had similar low consumption rates of fish.

Spatial trends

The highest daily rations of fish and native fish consumed by piscivores occurred below Bartlett Dam, in Section IV (Figure 3; ANOVA, $F_{3,107} = 4.03$, $P = 0.01$; $F_{3,107} = 8.02$, $P < 0.01$, respectively). The daily ration of fish by nonnative fishes was 3.4 mg/g (SE = 1.09) higher in Section IV than in any other sections of the river (linear combinations, $F_{1,107} = 11.27$, $P < 0.01$). The daily ration of native fish by nonnative fishes was 3.5 mg/g (SE = 0.71) higher in Section IV than in any other section (linear combinations, $F_{1,107} = 23.89$, $P < 0.01$).

Within Section IV, largemouth bass had the highest daily ration of fish and native than other species; within other sections the daily ration of fish was not significantly different by species (Figure 3; ANOVA, $F_{3,28} = 6.58$, $P < 0.01$; $F_{3,28} = 5.86$, $P < 0.01$). The daily ration of fish consumed by largemouth bass was 12.1 mg/g (SE = 2.75) higher than the daily ration of other species in Section IV (linear combinations, $F_{1,28} = 19.41$, $P < 0.01$). Likewise, the daily ration of native fish consumed by largemouth bass was 8.3 mg/g (SE = 2.03) higher than the daily ration by other species in Section IV (linear combinations, $F_{1,28} = 16.71$, $P < 0.01$).

Seasonal variation

The average daily ration of fish consumed by nonnative fishes was lowest during winter (Figure 4; ANOVA, $F_{2,108} = 4.64$, $P < 0.01$). During the winter, the average daily ration of fish was 3.1 mg/g (SE = 1.05) lower than the daily ration of fish consumed by nonnative fishes during spring and summer (linear combinations, $F_{1,108} = 8.58$, $P < 0.01$). The average daily ration of native fishes was not significantly different by season (ANOVA, $F_{2,108} = 2.18$, $P < 0.12$), the daily ration was 1.4 mg/g (SE = 0.73) lower in winter than in spring and summer (linear combinations, $F_{1,108} = 3.75$, $P = 0.05$). The daily ration of native fish was the highest for all piscivores during the spring (Figure 4).

Largemouth bass had the highest daily ration of fish and native fish during summer and winter than any other species (Figure 4; ANOVA, $F_{4,37} = 10.31$, $P < 0.01$; $F_{4,37} = 3.77$, $P = 0.01$; $F_{4,37} = 2.28$, $P = 0.07$; $F_{4,37} = 2.59$, $P = 0.05$, respectively). The daily ration of fish consumed by largemouth bass was 10.5 mg/g (SE = 1.69) greater than the daily ration of fish consumed by other species during the summer, and 0.8 mg/g (SE

= 0.21) greater during the winter (linear combinations, $F_{1,37} = 38.75$, $P < 0.01$; $F_{1,33} = 14.31$, $P < 0.01$, respectively). The daily ration of native fish consumed by largemouth bass was 4.3 mg/g (SE = 1.45) greater than the daily ration of fish consumed by other species during the summer, and 0.5 mg/g (SE = 0.15) greater during the winter (linear combinations, $F_{1,37} = 8.62$, $P < 0.01$; $F_{1,33} = 9.81$, $P < 0.01$, respectively).

Age relations

There were no statistical significant differences in daily ration of fish or native fish consumed by various age classes of largemouth bass (Figure 5; ANOVA, $F_{2,24} = 0.97$, $P = 0.39$; $F_{2,24} = 0.44$, $P = 0.65$, respectively), smallmouth bass ($F_{2,24} = 0.42$, $P = 0.89$; $F_{2,24} = 1.04$, $P = 0.37$), channel catfish ($F_{2,24} = 2.09$, $P = 0.22$; $F_{2,24} = 0.78$, $P = 0.51$), yellow bullhead ($F_{2,24} = 0.42$, $P = 0.66$; $F_{2,24} = 1.27$, $P = 0.30$), or flathead catfish ($F_{2,24} = 0.37$, $P = 0.69$; $F_{2,24} = 0.59$, $P = 0.56$).

Within each age class, largemouth bass had the highest daily ration of fish and native fish compared to other species (Figure 5; linear combinations, $F_{1,25} = 8.69$, $P < 0.01$; $F_{1,34} = 10.86$, $P < 0.01$; $F_{1,37} = 4.47$, $P = 0.04$, respectively). Age 0 and 1 largemouth bass also had the highest daily ration of native fishes of all other species (Figure 5; linear combinations, $F_{1,25} = 4.00$, $P = 0.05$; $F_{1,34} = 5.62$, $P = 0.02$, respectively). The difference in daily ration among piscivores was greatest within age 0 fish; the daily ration of fish by age 0 largemouth bass was 8.51 mg/g (SE = 2.89) greater than the daily ration of fish consumed by other age 0 fish. Additionally they were the only species to consume native fishes.

Discussion

By focusing management and research efforts on the species and age classes of predators that have the highest consumption rates of native fishes, managers have been able to increase the abundance and distribution of native fishes. Salmon *Oncorhynchus* spp., populations have benefited from control efforts on northern pikeminnow *Ptychocheilus oregonensis,* (Foerster and Ricker 1941; Friesen and Ward 1999; Tyus and Saunders III 2000), and artic char *Salvelinus alpinus* (Meachum and Clark 1979), while many native fishes have benefited from control efforts on lamprey *Petromyzon marinus*, in the Great Lakes (Smith and Tibbles 1980; Koonce et al. 1993).

Data on consumption rates of native fishes suggest that the abundance and distribution of native fishes in the Verde River might be increased if future management efforts reduce the abundance of largemouth bass and rainbow trout. Predation by other species is also important; however, their daily ration of prey fish is less than half of that by largemouth bass and rainbow trout. If the average size of the other piscivores were to increase or if they are at high densities, they could also have a large predatory impact on the abundance and distribution of native fishes. Consumption rates alone are not enough to determine the impact of predation by nonnative fishes; the abundance of native and nonnative fishes must also be considered. This topic will be further discussed by C. Velez (*in prep.*).

Current data indicate that management and research efforts could have the greatest impact on the abundance and distribution of native fishes by focusing on largemouth bass below Bartlett Dam. Largemouth bass had the highest consumption rate of fish (native and nonnative) below Bartlett Dam where densities of native fish were highest (Velez et al. *in prep.*); the highest consumption rate of fish in spring and summer when native fishes are spawning; and of all age 0 and 1 piscivores, they had the highest daily ration of fish at ages 0 and 1 when habitat use overlaps with young of the year native fishes.

A more extensive study focusing on rainbow trout may be warranted before stocking practices are changed in the Verde River. Our consumption rate estimates are based on the diet of only 32 rainbow trout, and we found no evidence of them consuming native fishes. However, rainbow trout are opportunistic feeders (Hodgson and Kitchell 1987), and they had the second highest consumption rate of fish. They have the potential to have a large predatory impact on the abundance and distribution of native fishes if they are stocked in areas where native fishes are in high densities or are spawning.

Limitations of data

To make inference about the spatial, seasonal and age variation in consumption rates of fish by predators in the Verde River we made several assumptions. The primary assumption in determining predator demand for prey is that food is not limiting, thus consumption is equivalent to demand (Ney 1990). While food can often be limiting in closed systems (Ney 1990), we feel that if prey availability was a limiting factor in our study, then prey would be equally limiting to all species and the trends in consumption rates would not be affected.

The Wisconsin bioenergetics model requires numerous physiological input parameters that are often difficult to measure accurately. The validity of consumption estimates depends on the accuracy of the input parameters. We assumed that values of physiological parameters we borrowed from the literature were representative of fishes in the Verde River. Parameter estimates are routinely borrowed from the literature and used in the bioenergetics model. While the parameter estimates may not be the exact values experienced in the field, they are useful for showing trends in predator consumption (Ney 1990; Hanson et al. 1996).

We also made several assumptions to be able to draw inference to the Verde River from our sample data. We assumed that: the diet and growth rates of fishes and the temperature regimes at our sampling sites (which were randomly chosen from available access points) were representative of the Verde River; electrofishing provided a representative sample of species and age class of piscivores; three consecutive sampling days at three sites were representative of a month within a given section; and there was no diel variation in the proportions of prey consumed by these piscivores. We feel that our estimates were representative of the general trends in consumption rates of fish and native fish that are occurring in the Verde River. While there are fluctuations in data across sites and years, the bioenergetics model is widely used and allows the evaluation of trends in consumption rates (Kitchell et al. 1977; Stewart et al. 1981; Ney 1993; Schindler et al. 1993).

Management implications

We recommend a more extensive study focusing on the predation impact of rainbow trout on native fishes and the stocking practices of rainbow trout before changing stocking practices. Based on current stocking records, 21,772 kg of rainbow trout were stocked into the Verde River in 2002. If every trout survived to feed for one day, they could consume 78 kg of prey fish (based on daily ration of 3.57 mg prey fish/g/day). Survival of stocked fish varies; angling records indicate that approximately 80% of rainbow trout are killed within the first week of being stocked into the Verde River (Andy Clark, Arizona Game and Fish Department, personal communication). We observed rainbow trout in the Verde River in August; these fish lived for at least four months because the last date of stocking was in April. Rainbow trout have the potential to severely impact the abundance and distribution of native fish population because stocking of rainbow trout overlaps with the peak of spawning activities by native fishes. Future research is needed to determine the best stocking locations, dates, and size of fish to stock into the Verde River to reduce the predation impact they could have on the abundance and distribution of native fishes.

Future research is also needed to determine what methods will be most effective in reducing densities of largemouth bass in the Verde River and if these efforts are effective in increasing the abundance and distribution of native fishes. Complete removal of largemouth bass from the Verde River may be impossible or undesirable. Researchers have been successful in increasing prey abundances by altering age structure and density of predators by increasing harvest through reward programs (bounties), changing fishing regulations and by physical removal efforts (Ney 1990; Beamesderfer 1996; Tyus and Saunders III 2000). These management actions may be useful in decreasing the demand for prey fish and increasing native fish abundance and distribution.

Increased stocking of native fishes combined with removal efforts of largemouth bass may increase the abundance and distribution of native fishes in the Verde River (Ney 1990). Currently razorback suckers (*Xyrauchen texanus*) and Colorado pikeminnow (*Ptychocheilus lucius*) greater than 300 mm are currently being reintroduced into the Verde River. These larger fish are assumed to be large enough to escape predation by nonnative fishes (Jahrke & Clark 1999); during our study the average size of prey fish consumed was 32 mm long, and 99% of the prey fish consumed were less than 100 mm. Brouder et al. (2000) also found the majority of native fishes preyed upon ranged in length from 34-90 mm. If the size of razorback suckers and Colorado pikeminnow stocked was reduced, it may be possible to increase the number of fishes that can be stocked into the Verde River. Stocking of other native species may also help increase their abundances and distributions throughout the Verde River.

Researchers are currently conducting nonnative removal studies on the upper Verde River (Section I) and appear to be getting increased abundance of young suckers (John Rinne, personal communication). Continued research is needed to test the effect of removing the primary piscivores from the Verde River on the abundance and distribution of native fishes. Research is also needed to determine the annual exploitation rate of largemouth bass that will provide the greatest reduction in predation while not resulting in increased predation, growth or reproduction in surviving largemouth bass or other predators.

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Table 1.- Prey energy densities (J/g wet weight) used in the bioenergetics models.

Species	Closest Surrogate	Energy Density (J/g)	Source
Longfin dace	Fathead minnow	4488	Bryan et al. (1996)
Sonora sucker	White sucker	3696	Bryan et al. (1996)
Desert sucker	White sucker	3696	Bryan et al. (1996)
Unknown sucker	White sucker	3696	Bryan et al. (1996)
Nonnative fish	Average of species	4543	Cummings & Wuycheck (1971); Miranda & Muncy (1989); Bryan et al. (1996)
Unknown fish		4605	Miranda & Muncy (1989)
Insects		3140	Hewett & Johnson (1992)
Plants	Algae	992	Kitchell & Windell (1970)
Crayfish		3140	Cummins & Wuycheck (1971)
Amphibians	Larval fish	4000	Hanson & Johnson (1997)

Table 2.- Seasonal growth used in bioenergetics simulations, in terms of initial and final weights for each season, for each age-group of largemouth bass (LMB), smallmouth bass (SMB), channel catfish (CCF), yellow bullhead (YBH), and flathead catfish (FHC), March 2002-2003.

		Initial weight (g) for:				
Age	Day	LMB	SMB	CCF	YBH	FHC
				Section I		
0	94	*	2.50	*	-	-
	220	*	8.02	-	6.68	-
	365	*	10.74	-	11.37	-
1	1	*	13.95	-	-	-
	94	*	19.72	*	14.21	-
	220	*	48.23	-	28.96	-
	365	*	59.83	-	-	-
2+	1	*	80.38	-	-	-
	94	*	88.96	*	-	125.50
	220	*	114.46	-	68.29	126.57
	365	*	-	-	75.35	-
				Section II		
0	94	2.46	1.44	-	-	-
	220	15.31	12.28	-	-	-
1	1	11.59	13.95	-	-	-
	94	22.13	26.71	-	-	-
	220	37.19	51.93	-	-	-
	365	44.62	59.83	-	-	*
2+	1	159.10	31.30	-	-	-
	94	182.47	36.28	-	-	-
	220	218.87	51.72	-	-	-
	365	266.28	-	-	-	*
				Section III		
0	94	2.46	2.50	-	-	3.47
	220	11.59	10.74	-	-	12.85
	365	17.41	-	-	-	-
1	1	13.37	26.71	-	*	-
	94	33.79	44.69	-	-	19.15
	220	62.08	59.83	-	-	41.08
2+	1	239.60	88.79	-	*	-
	94	271.58	97.92	-	-	102.21
	220	317.80	-	-	-	103.17
	365	377.77	-	-	-	-
				Section IV		
0	1	3.64	*	*	*	*
	94	3.98	*	-	4.82	5.88
	220	22.13	*	-	17.39	10.20
	365	24.76	*	-	-	-
1	1	24.76	*	5.65	11.37	10.20
	94	37.19	*	13.62	24.76	15.83
	220	67.02	*	32.83	33.51	-
	365	83.26	*	39.52	-	-
2+	1	292.82	*	215.41	-	178.07
	94	326.80	*	317.39	68.29	179.04
	220	380.71	*	506.03	82.78	180.34
	365	446.35	*	583.36	-	-

* No diet data - Simulation not run

Table 3.- Water temperature (°C) when spawning begins and the calculated first day of spawning used in bioenergetics simulations for age 2+ largemouth bass, smallmouth bass, channel catfish, yellow bullhead and flathead catfish by section of river from March 2002 to March 2003.

	Largemouth bass		Smallmouth bass		Channel catfish		Yellow bullhead		Flathead catfish	
Section	°C	Day	°C	Day	°C	Day	°C	Day	°C	Day
I	18	-	15	68	21	-	20	80	24	158
II	18	64	15	50	21	-	20	-	24	-
III	18	31	15	31	21	-	20	-	24	107
IV	18	18	15	-	21	174	20	37	24	100

- Simulation not run

Figure 1. - Thermal experience for largemouth bass, smallmouth bass, channel catfish, flathead catfish, yellow bullhead, and rainbow trout used in bioenergetics modeling for March 2002 to February 2003. Model simulations began on March 1, 2002 (day 1) and ran through March 1, 2003 (day 365).

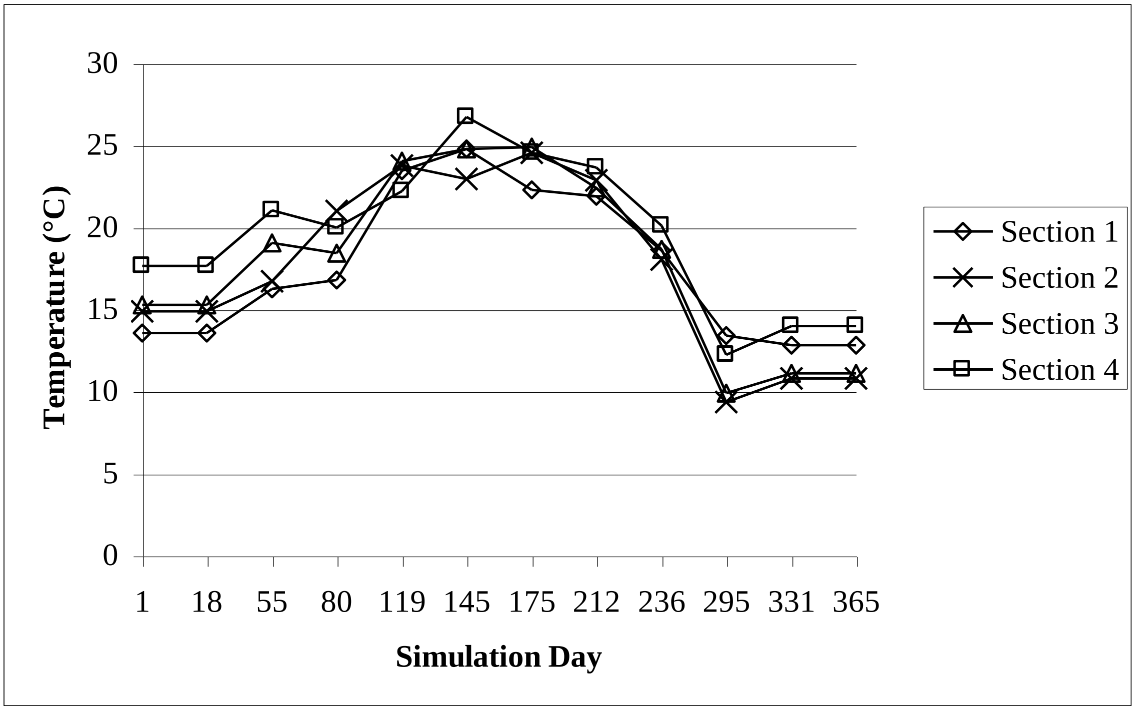
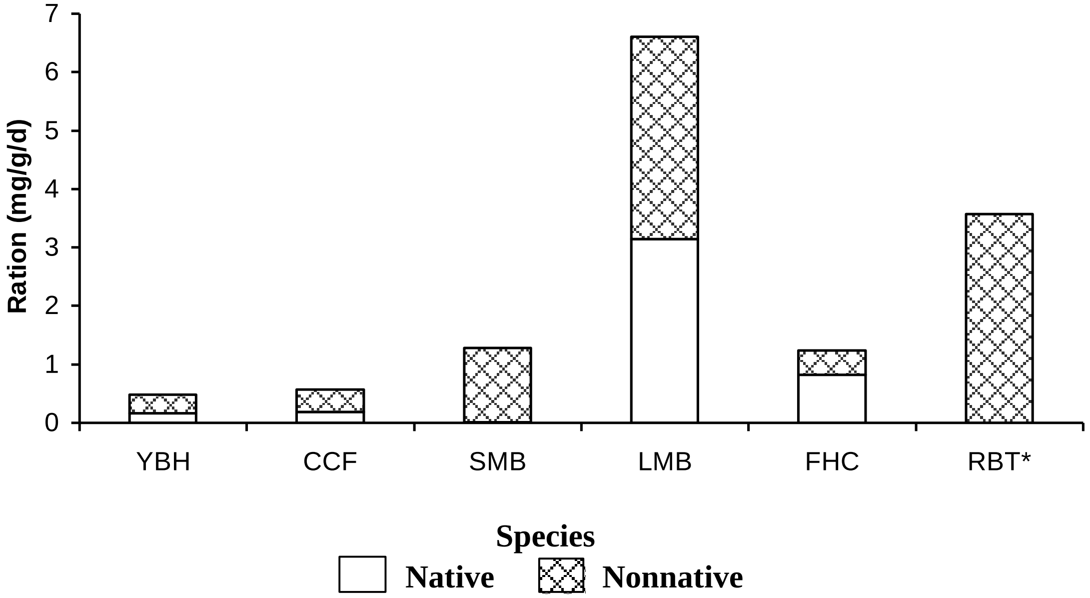


Figure 2. – Average daily ration (mg of prey per gram of predator per day) of yellow bullhead (YBH), channel catfish (CCF), smallmouth bass (SMB), largemouth bass (LMB), flathead catfish (FHC), and rainbow trout (RBT) feeding on native and nonnative prey fish in the Verde River, Arizona, March 2002-2003.



* Daily ration based on spring data only

Figure 3.- Average daily ration of native and nonnative fish (mg of prey per gram of predator per day) by section of river, of largemouth bass (LMB), smallmouth bass (SMB), channel catfish (CCF), flathead catfish (FHC), and yellow bullhead (YBH) in the Verde River, March 2002-2003.

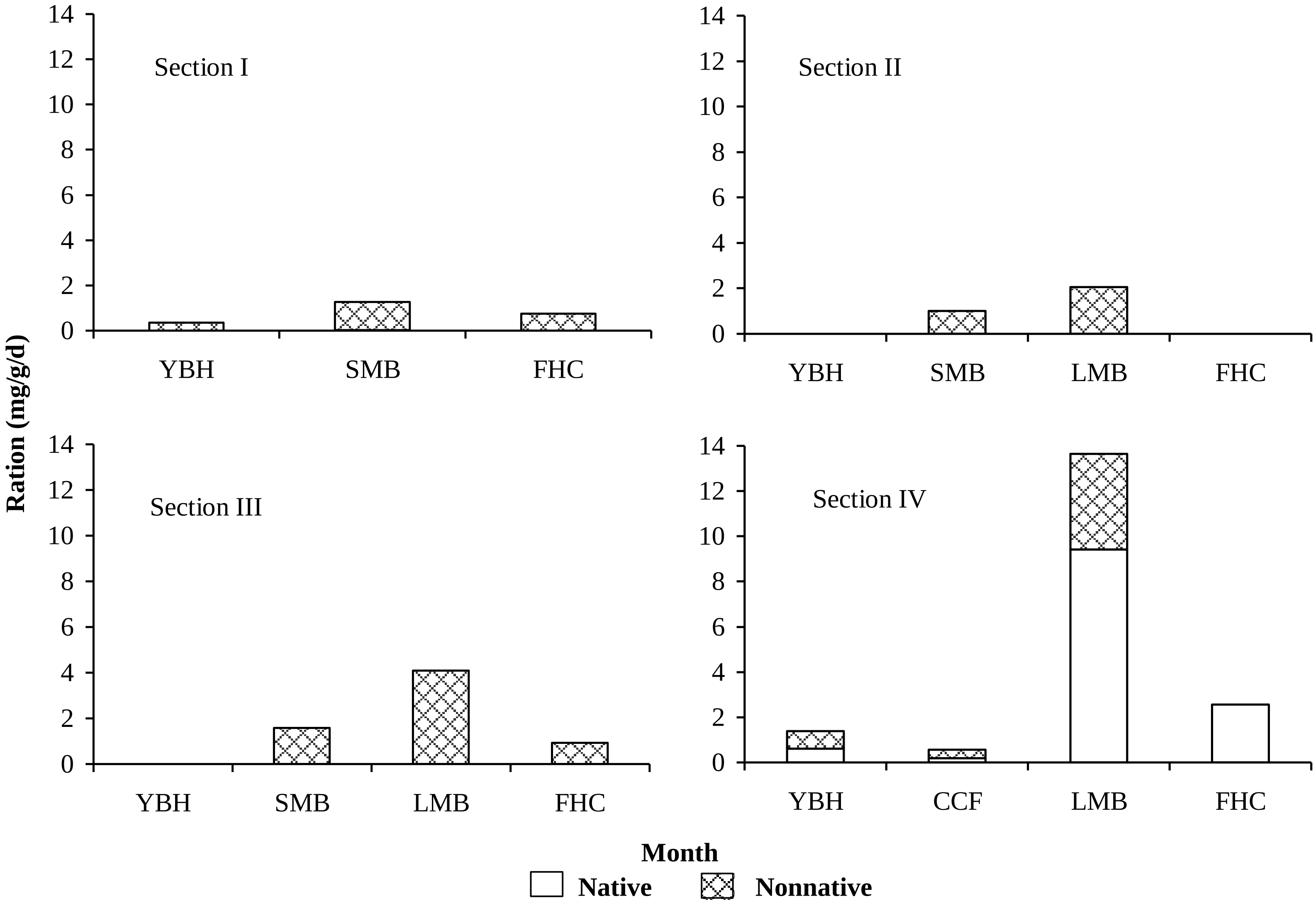


Figure 4.- Average daily ration (mg of prey per gram of predator per day) by season, of largemouth bass (LMB), smallmouth bass (SMB), channel catfish (CCF), flathead catfish (FHC), and yellow bullhead (YBH) feeding on native and nonnative prey fish in the Verde River, Arizona, March 2002-2003.

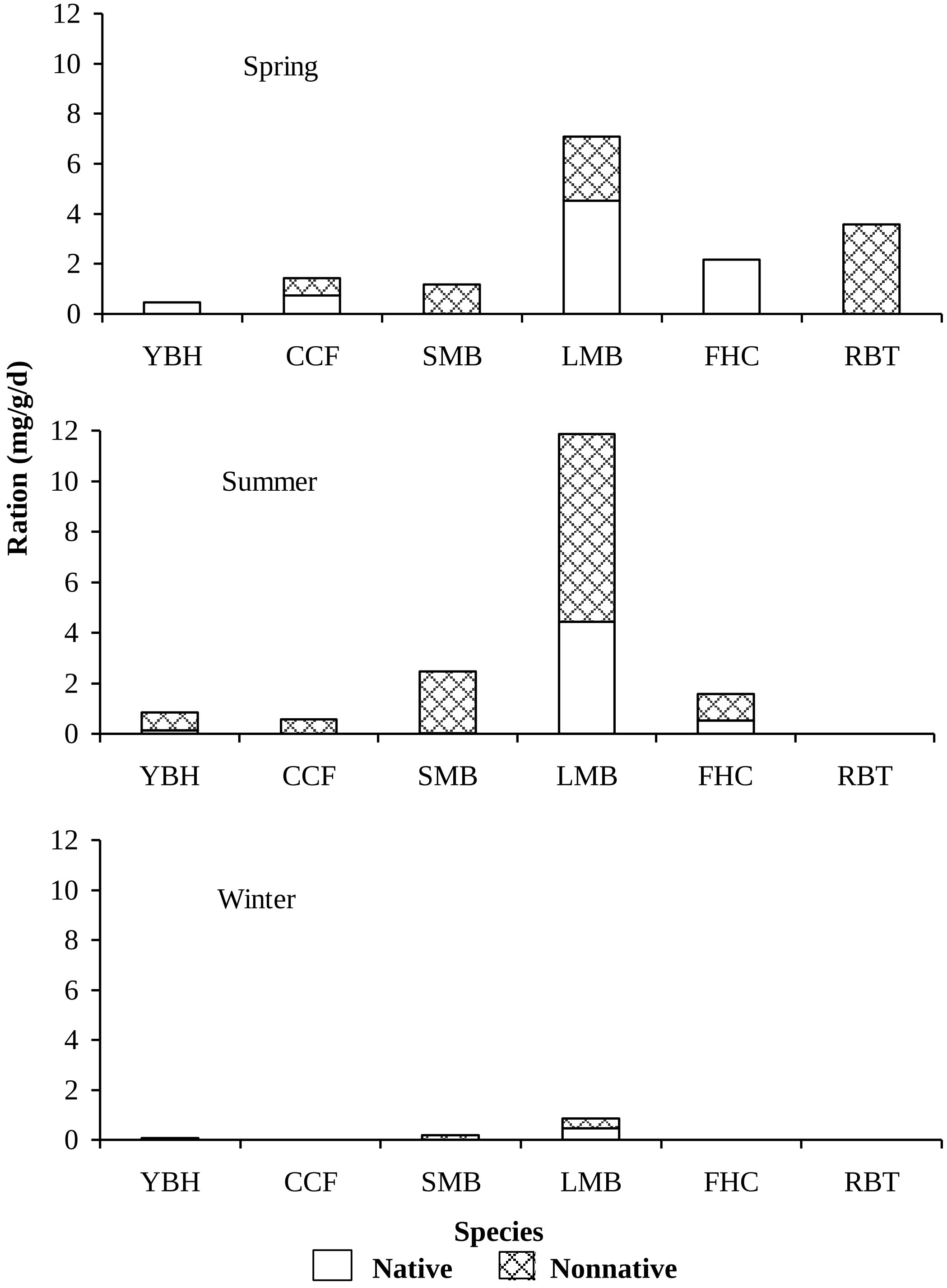


Figure 5.- Average daily ration (mg of prey per gram of predator per day) by age class, of largemouth bass, smallmouth bass, channel catfish, flathead catfish, and yellow bullhead feeding on native and nonnative prey fish in the Verde River, Arizona, March 2002-2003.

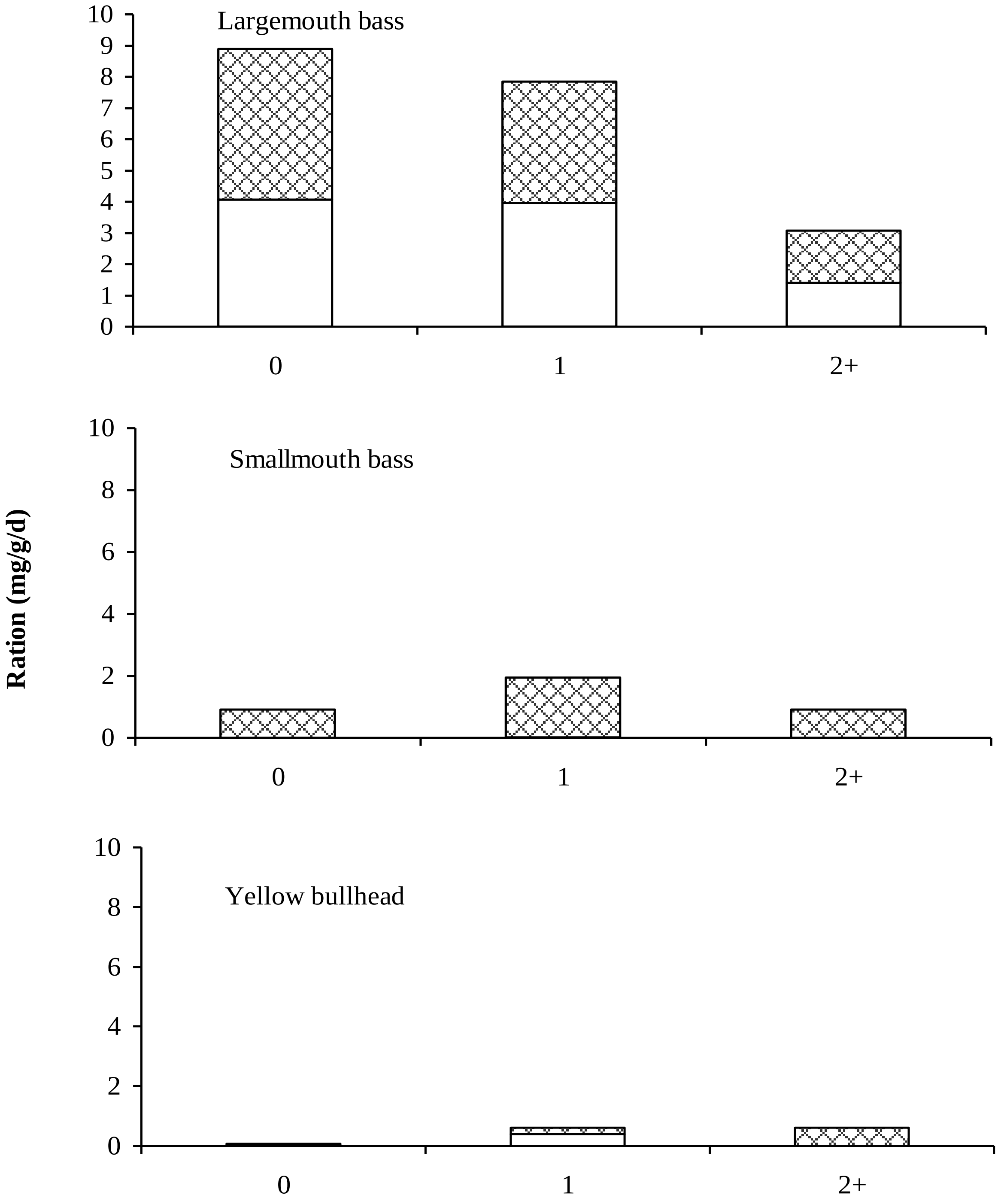
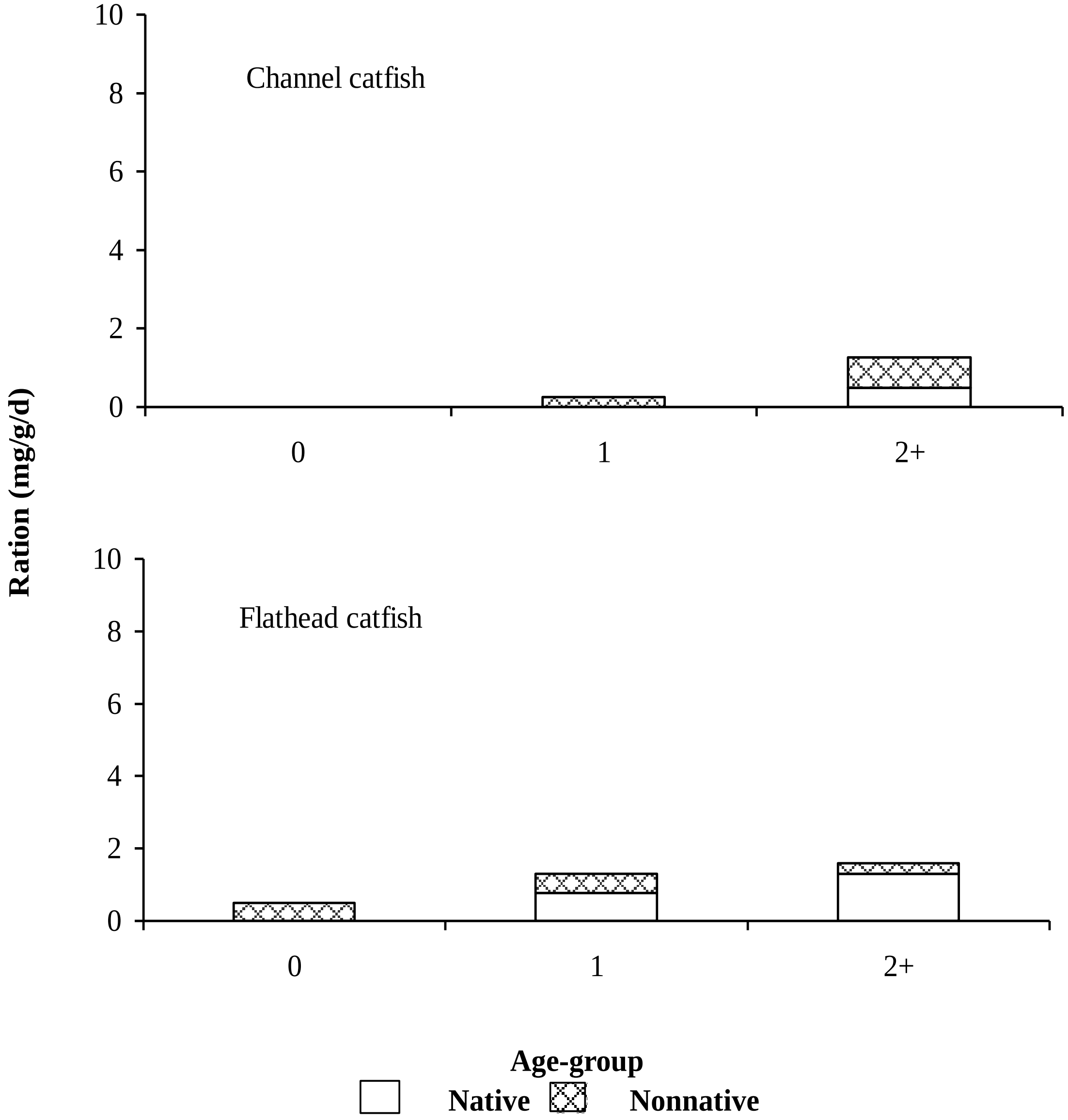


Figure 5 cont.- Average daily ration (mg of prey per gram of predator per day) by age group, of largemouth bass, smallmouth bass, channel catfish, flathead catfish, and yellow bullhead feeding on native and nonnative prey fish in the Verde River, Arizona.



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