

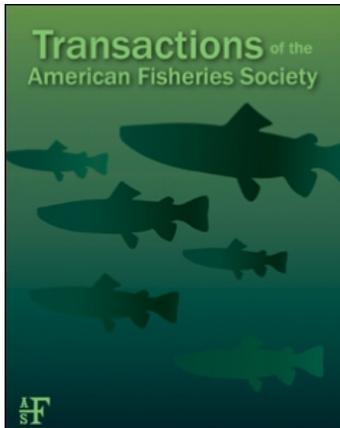
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### Trout Piscivory in the Colorado River, Grand Canyon: Effects of Turbidity, Temperature, and Fish Prey Availability

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ARTICLE

## Trout Piscivory in the Colorado River, Grand Canyon: Effects of Turbidity, Temperature, and Fish Prey Availability

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### Abstract

Introductions of nonnative salmonids, such as rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*, have affected native fishes worldwide in unforeseen and undesirable ways. Predation and other interactions with nonnative rainbow trout and brown trout have been hypothesized as contributing to the decline of native fishes (including the endangered humpback chub *Gila cypha*) in the Colorado River, Grand Canyon. A multiyear study was conducted to remove nonnative fish from a 15-km segment of the Colorado River near the Little Colorado River confluence. We evaluated how sediment, temperature, fish prey availability, and predator abundance influenced the incidence of piscivory (IP) by nonnative salmonids. Study objectives were addressed through spatial (upstream and downstream of the Little Colorado River confluence) and temporal (seasonal and annual) comparisons of prey availability and predator abundance. Data were then evaluated by modeling the quantity of fish prey ingested by trout during the first 2 years (2003–2004) of the mechanical removal period. Field effort resulted in the capture of 20,000 nonnative fish, of which 90% were salmonids. Results indicated that the brown trout IP was higher (8–70%) than the rainbow trout IP (0.5–3.3%); however, rainbow trout were 50 times more abundant than brown trout in the study area. We estimated that during the study period, over 30,000 fish (native and nonnative species combined) were consumed by rainbow trout (21,641 fish) and brown trout (11,797 fish). On average, rainbow trout and brown trout ingested 85% more native fish than nonnative fish in spite of the fact that native fish constituted less than 30% of the small fish available in the study area. Turbidity may mediate piscivory directly by reducing prey detection, but

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**this effect was not apparent in our data, as rainbow trout IP was greater when suspended sediment levels (range = 5.9–20,000 mg/L) were higher.**

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Introductions of nonnative salmonids, such as rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*, have affected native fishes worldwide in unforeseen and undesirable ways. Nonnative fishes are of concern because through competition and predation, they have had strong and adverse effects on native fishes (Fausch 1988; Crowl et al. 1992; Blinn et al. 1993; Ruzycski et al. 2003; Baxter et al. 2007) and aquatic communities (Flecker and Townsend 1994; Baxter et al. 2004). The legacy of these effects is only now being understood and acknowledged (Minckley and Deacon 1991; Behnke 1992; Simon and Townsend 2003; McDowall 2006). Studies of the effects of nonnative salmonids on native fishes have tended to focus on competition more than predation, perhaps because piscivory can be rare and hence difficult to quantify in the scope of most investigations. The success of salmonids in the wide range of environments where they have been introduced appears to be mediated by various factors, including flow regime (Fausch et al. 2001; Propst et al. 2008), temperature (Taniguchi et al. 1998), drought (Closs and Lake 1996), and turbidity (Blinn et al. 1993; Stuart-Smith et al. 2004).

Introduced salmonids, particularly rainbow trout and brown trout, often thrive in regulated rivers downstream of dams because dam effects on flow, temperature, and turbidity can favor these fishes. Rainbow trout and brown trout were historically introduced in smaller tributaries and headwater streams of the Colorado River basin with the expectation of developing recreational fisheries (Minckley 1991; Behnke 2002). Later, after the construction of multiple dams and the ensuing alterations in physical conditions, trout populations further extended their range (through stocking) beyond the headwater segments and downstream into the arid physiographic regions of the Colorado River (Blinn and Poff 2005). Although brown trout are more widely recognized as piscivores, both of these salmonids can pose a predatory threat to native fishes (e.g., Crowl et al. 1992; McDowall 2003); however, relatively few studies have actually quantified the incidence of piscivory by these species or the potential effects of such piscivory on native fish populations (Johnson et al. 2008).

A unique and highly endemic assemblage of fish evolved in the Colorado River (Minckley and Deacon 1968), which historically consisted of sediment-laden waters that were variable in flow and temperature (Carothers and Brown 1991). These physical conditions were typical of most unregulated southwestern rivers (Webb 1996). Earlier fish surveys and general research studies documented the partial extirpation and overall decline of the Grand Canyon native fish assemblage (Maddux et al. 1987; Minckley 1991; Coggins et al. 2006). Only four native species currently persist in Grand Canyon: the federally endangered humpback chub *Gila cypha* (USOFR 1967), the flannelmouth

sucker *Catostomus latipinnis*, the bluehead sucker *Catostomus discobolus*, and the speckled dace *Rhinichthys osculus*. Given its endangered status, the humpback chub is a species of special concern in Grand Canyon.

Possible explanations for the decline of Grand Canyon native fishes include the potential effects of main-stem dams and nonnative fishes (Minckley and Deacon 1968). Most studies have focused on understanding the effects of dam-induced habitat alterations on native fishes (e.g., Maddux et al. 1987; Valdez and Ryel 1995; Gorman and Stone 1999; Robinson and Childs 2001). To date, interactions between native and nonnative fish have not been the explicit focus of rigorous investigation, although several authors have described the potential effects of nonnative species, including rainbow trout and brown trout, on the native fishes of the Grand Canyon (Minckley 1991; Valdez and Ryel 1995; Marsh and Douglas 1997; Petersen and Paukert 2005).

In 2002, a significant decline in recruitment was detected for the Grand Canyon humpback chub population; this decline likely resulted from reduced survival of young fish (age < 3; Coggins et al. 2006). Various factors (e.g., piscivory, competition, habitat alterations, water temperature, parasites, and disease) were hypothesized as possible causal mechanisms for the decline; however, interactions with nonnative fish appeared to be the most likely and testable mechanism (Coggins 2008). Therefore, a large-scale, multiyear experimental program was designed under the auspices of the Glen Canyon Dam Adaptive Management Program (Gloss and Coggins 2005). The experimental program included two components: (1) systematic treatment with a widely fluctuating flow regime in winter to reduce reproduction and age-0 survival of nonnative trout (Korman et al. 2011, this issue) and (2) a localized treatment designed to selectively remove nonnative fish (mechanical removal) in a segment of the Colorado River near the confluence with the Little Colorado River (LCR; Coggins et al. 2011, this issue).

This companion paper reports on the dietary findings that resulted from the nonnative fish removal component conducted in the Colorado River near the LCR confluence. Our objectives were to (1) determine the incidence of piscivory (IP) by rainbow trout and brown trout and (2) determine how physical and biological factors (sediment, temperature, fish prey availability, and predator abundance) influenced the IP. These objectives were addressed through spatial (upstream and downstream of the LCR confluence) and temporal (seasonal and annual) comparisons of prey availability and consumption by nonnative trout. Based on our empirical findings, a piscivory model was then developed to estimate the quantity of fish prey consumed by nonnative trout during the first 2 years of the 4-year mechanical removal period (2003–2006).

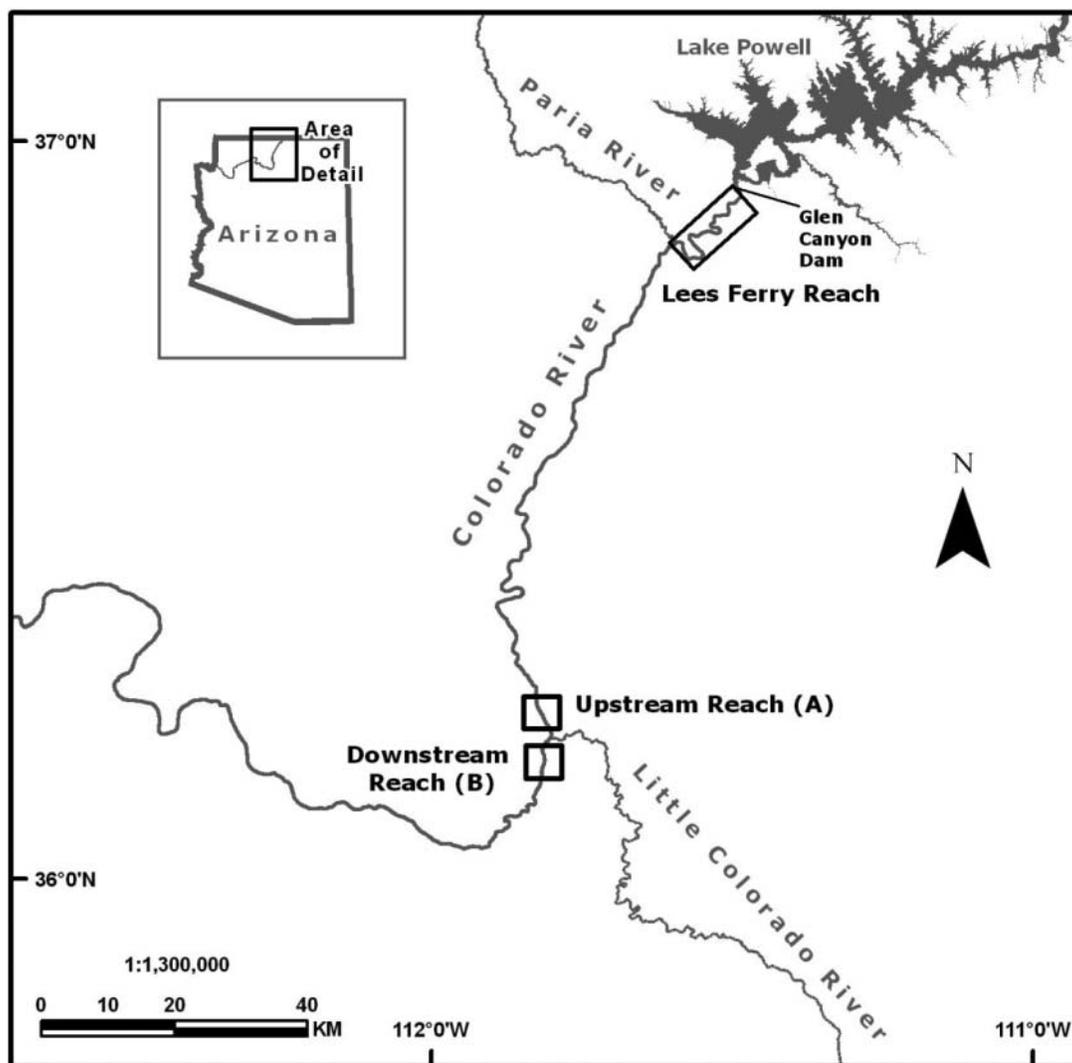


FIGURE 1. Map of the Colorado River, Grand Canyon, identifying the overall study area and sampling reaches upstream (A) and downstream (B) of the Little Colorado River confluence. The middle of the study area is located 99 km downstream from the Paria River and 123 km from Glen Canyon Dam (State Plane, Arizona Central 202, North American Datum of 1983).

## METHODS

*Study area.*—The mechanical removal study was undertaken in a 15-km segment of the Colorado River that encompasses the LCR confluence. Two separate study reaches were established upstream and downstream of the LCR confluence (Figure 1). In addition, a control site (without nonnative fish removal) was also established 16 km upstream of the mechanical removal area to determine whether changes in the fish community were related to the mechanical removal treatment (Coggins 2008; Coggins et al. 2011). The vicinity of the LCR confluence was selected as the study site for several reasons. First, the LCR is considered critical spawning and rearing habitat for native fishes, especially the humpback chub. Seasonal floods prompt the dispersal of

young fish from the LCR into the main-stem Colorado River (Clarkson and Childs 2000). Third, the LCR confluence is an area of strong overlap between nonnative trout and native fishes, which made it an ideal study site for investigating trout piscivory on native fishes in conjunction with the removal effort. Lastly, this study area exhibits both spatial and temporal variation in turbidity. Two major Colorado River tributaries are the Paria River (25 km downstream from Glen Canyon Dam) and the LCR (123 km downstream from the dam), which have distinct flow frequencies and sediment contributions that act in combination with flow releases from Glen Canyon Dam to affect turbidity levels in the main-stem Colorado River (Topping et al. 2005). As a result, the downstream study reach possesses higher turbidity

levels and more frequent episodes of high turbidity relative to the upstream study reach.

**Fish collection.**—All of the rainbow trout and brown trout that were caught and removed (2003–2004) were used for diet analysis. Six trips were conducted annually: three in the winter (January–March) and three in the summer (July–September). Each of the two study reaches was further subdivided into 500-m sampling units; the upstream reach contained 38 sampling units, and the downstream reach contained 27 units. Four to five depletion electrofishing passes were conducted per trip; the exceptions were in August 2003 (2 passes), September 2003 (3 passes), and July 2004 (6 passes). Four electrofishing boats were simultaneously used to sample both upstream and downstream study reaches. Two nights were required to complete each depletion pass for the entire study area. Two types of variable-voltage pulsators (Coffelt Mark XXII and Smith-Root Mark XXII) were used for electrofishing. The output current was standardized at 5,000 W of power (amps  $\times$  volts). All fish were identified to species and measured for weight and length. Native fish, which were less vulnerable to capture with electrofishing, were released when caught. Nonnative fish were euthanized and removed. The gastrointestinal tracts of all rainbow trout and brown trout were collected and preserved in a 95% solution of ethyl alcohol.

**Statistical analyses.**—Stomach contents were examined to determine the IP (i.e., presence or absence of piscivory) and stomach emptiness by using the entire gastrointestinal tract ( $n = 15,360$  rainbow trout and 400 brown trout stomachs). Stomach contents were separated and identified under a stereomicroscope (Leica L5). The IP was a count statistic representing the proportion of sampled predators with fish prey remains in their gastrointestinal tracts. We stratified our IP estimates between predator species (rainbow trout and brown trout) and study reaches (upstream and downstream). One-way and two-way analyses of variance (ANOVAs) were used to compare mean monthly IP estimates for rainbow trout and brown trout and to evaluate how this count statistic differed spatially (i.e., upstream versus downstream of the LCR confluence) and temporally (year and season). Based on the analyses (significance level  $\alpha = 0.05$ ), post hoc tests were performed by using the Tukey–Kramer procedure (unequal sample sizes). A modified Levene's test was used to detect departures from normality and equality of variances. For descriptive analyses, IP was estimated for both monthly and seasonal comparisons.

**Incidence of piscivory model.**—A combination of simple linear regression and multiple linear regression analyses was used to determine whether there were statistical relationships between daily IP and the following covariates: (1) mean daily temperature, (2) mean daily sediment concentration, (3) fish prey availability (native and nonnative species), and (4) daily predator abundance (combined rainbow trout and brown trout abundance estimate). We also tested for the effects of interactions between these covariates and IP. For each predator species, a linear regression model was selected from the set of potential

models by using Akaike's information criterion (AIC) as the selection criterion. The estimator used was

$$\hat{IP} = B_0 + B_1(x_1) + B_2(x_2) + B_3(x_1 \cdot x_2) \dots$$

where  $B_0$  is the constant;  $B_1$ ,  $B_2$ , and  $B_3$  are the regression coefficients; and  $x_1$ ,  $x_2$ , and  $x_3$  are the physical and biological covariates. We used AIC to compare a range of models for predicting IP (Burnham and Anderson 2002). We estimated model parameters and their variances by assuming normal error in Statistica (StatSoft 2009). Parameters were copied to Microsoft Excel to compute the total log likelihood for each model, which was then used to compute AIC. Models with AIC values that were similar to the model with the lowest AIC score were considered to have strong support (AIC difference [ $\Delta$ AIC] = 0–2), while those with larger AIC values were considered to have moderate support ( $\Delta$ AIC = 4–7) or essentially no support ( $\Delta$ AIC > 10).

**Physical and biological covariates.**—Water temperature was monitored at our study area; temperatures were averaged on a daily basis by using measurements made at 15-min intervals (Voichick and Wright 2007). Continuously monitored suspended sediment data (mg/L) were also remotely measured by using acoustic Doppler profilers (Melis et al. 2003; Topping et al. 2004) at two U.S. Geological Survey monitoring stations (upstream: gaging station 09383100 [123 km]; downstream: gaging station 09402500 [165 km]). These sediment data have compared well with other data collected by use of conventional sampling methods (i.e., integrated sediment samples collected from cableways with an isokinetic sampler; Melis et al. 2003).

Time adjustments were made to sediment data measured at gaging station 09402500. We back-calculated the difference in travel time between the downstream-most study reach and gaging station 09402500 (a linear distance of 38 km). Average water velocity (Wiele and Smith 1996) was used to estimate time differences with an unsteady-flow model (Wiele and Griffin 1997). Missing sediment concentration data were estimated by two methods: (1) for data missing at intervals greater than 15 min up to 2 d, we used a straight-line interpolation; and (2) for data missing at intervals greater than 2 d (i.e., September 2009 at gaging station 09383100), we used sediment rating curves established for the Paria River (Topping 1997) and the LCR (Randle and Pemberton 1987) and we estimated the sediment density mass rate. Travel time was back-calculated for each gaged tributary to the study reaches (upstream and downstream). Sediment density mass rates (kg/s) for each tributary were converted to a concentration (mg/L) by dividing the combined mass rates by the estimated flow discharge ( $m^3/s$ ) in the main stem (Wiele and Griffin 1997).

Fish prey availability was defined as the number of small fish (<150 mm total length [TL]) caught per shoreline length (km) by use of electrofishing gear. Electrofishing catch per unit effort (CPUE) indices were estimated for each trip ( $n = 12$ ) and were stratified spatially between the upstream and downstream

study reaches. We used linear interpolation to estimate daily abundance (CPUE) of native fish between sampling periods.

A hierarchical Bayesian modeling framework (Dorazio et al. 2005) was used to estimate rainbow trout and brown trout predator abundance and capture probabilities from the nightly catch data collected during serial depletion passes (see Coggins 2008 and Coggins et al. 2011, this issue for additional details on sampling design, methods, analyses, and efficacy of mechanical removal). Daily abundances of nonnative trout were calculated by using initial predator abundance estimates from each removal trip, and these same trip estimates were adjusted daily by taking the difference between the initial estimate and the observed number of nonnative fish that were removed nightly. Linear interpolation was used to estimate daily abundance levels between sampling periods.

**Fish prey consumption model.**—A model was developed to estimate the daily quantity of fish prey consumed by nonnative trout (Figure 2). Our model assumed a 1:1 correspondence between consumed and evacuated fish prey. The purpose of constructing this simulation model was to create a simplified version of the piscivorous interactions that occurred in this ecosystem in response to changes in predator and prey abundances and physical factors. The model estimated (1) average annual per capita

rates of consumption by rainbow trout and brown trout and (2) total number of fish prey consumed per predator species.

The model was used to predict digestion time ( $h$ ) so that an evacuation date could be determined for each ingested fish prey:

$$h = (DW_i - DW_e)/GER,$$

where  $DW_i$  is the initial dry weight of the ingested prey (g),  $DW_e$  is the dry weight at the time of evacuation (0.001 g), and GER is the predator's gastric evacuation rate. The GER was calculated as a function of water temperature ( $T$ ; °C) by using separate relationships for rainbow trout ( $\log_e GER_{RBT} = -5.439 + 0.224T$ ; Kawaguchi et al. 2007) and brown trout ( $GER_{BNT} = 0.053e^{0.0737T}$ ; He and Wurtsbaugh 1993).

Because fish remains were partially digested in the stomach, we were unable to determine species identification and an initial weight for all of the observed fish prey. A bootstrap technique was used to assign a species to each ingested fish prey by randomly sampling from our observed data for digested fish prey proportions. After the prey item was assigned to species, an initial length was then randomly selected from the known size distribution for that particular prey species based on electrofishing catches.

Each randomly selected TL was used as the initial length of the fish prey at time of consumption. Length selection ranged between the smallest observed sizes up to 150 mm TL. This process was repeated for all ingested fish prey. Size-class distributions were recalculated for each month to account for changes in catch frequencies between sampling trips. Linear interpolation was used to calculate daily CPUE values between trips. Length–weight relationships were used to estimate initial wet weight (g/fish prey), which was converted to  $DW_i$  by using a conversion factor (0.34; Elliot 1975). Length–weight relationships were obtained from the present study or from published literature (Carlander 1969; Schneider et al. 2000).

Based on  $h$ , each ingested fish was individually added to a daily evacuation date bin, which extended from the predator's capture date to the latest date that the fish prey's remains would still be in the predator's stomach. The daily sum of all fish prey evacuated on the current date ( $E_C$ ) was estimated as

$$\sum E_C = \sum E_T - \sum E_R,$$

where  $E_T$  represents the total number of consumed fish of each prey species binned for all evacuation dates (current and remaining evacuation dates) and  $E_R$  is the remaining number of consumed fish of each prey species that were assigned to future evacuation dates.

Physical and biological variables were used to inform a set of regressions that estimated the daily IP for both rainbow trout and brown trout. Based on the multiple linear regressions used for estimating IP, we estimated the 95% confidence interval (CI)

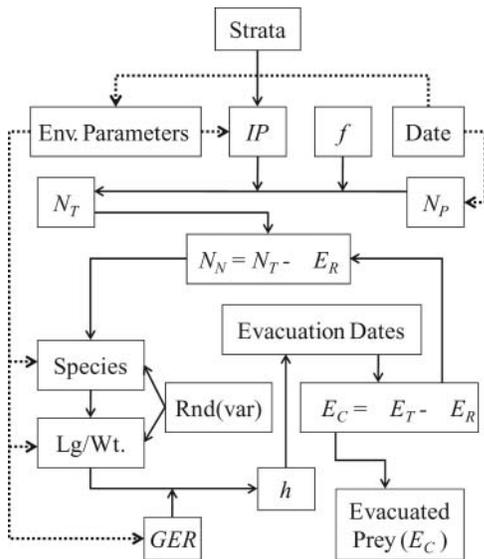


FIGURE 2. Prey evacuation model showing the sequential steps used in the process for estimating daily fish prey of nonnative rainbow trout and brown trout in the Colorado River (environmental [env.] parameters = sediment, temperature, and fish prey availability; IP = daily incidence of piscivory;  $N_P$  = predator population;  $f$  = average number of observed fish prey per predator;  $N_T$  = total number of ingested fish prey;  $N_N$  = daily estimate of newly ingested fish prey;  $E_R$  = remaining sum of fish prey for all prey species from future evacuation dates; Rnd[var] = random assignment of fish prey species and initial length [Lg] and weight [Wt.] at the time of consumption; GER = gastric evacuation rate;  $h$  = fish prey digestion time;  $E_C$  = daily sum of all fish prey evacuated on the current date;  $E_T$  = total numbers of consumed fish per prey species binned for current and remaining evacuation dates).

for each predicted estimate and then randomly sampled from the normal probability distribution ( $1.96 \cdot \text{SD}$ ) of that point estimate. This random estimation process for IP was then used to quantify the total number of ingested fish prey ( $N_T$ ) as

$$N_T = \text{IP} \cdot N_p \cdot f,$$

where  $N_p$  is daily predator abundance (L. G. Coggins, unpublished data) and  $f$  is the average number of observed fish prey per predator.

Although digestion rates are independent of fish prey size (He and Wurtsbaugh 1993), complete gut evacuation is faster for smaller prey and slower for larger prey. Thus, depending on prey size, some proportion of the same ingested fish initially accounted for on the previous day's estimate (the exception being the initial seed) would be present on subsequent days, leading to an overestimation of daily prey consumption. Therefore, the sum of  $E_R$  was used to convert the total number of ingested fish prey to a daily estimate of newly ingested fish prey ( $N_N$ ),

$$N_N = N_T - \sum E_R,$$

where  $N_T$  is the total number of ingested fish prey estimated for that day. This estimation process was performed daily over the entire period (2003–2004), where fish prey digestion times were once again recalculated for the next day's estimate of  $N_N$ . The model progressed forward by date, and all previous days' fish prey estimates ( $E_T$ ) were then revised by adding  $N_N$  to the remaining evacuation date bins. All negative values for  $N_N$  were considered to be unsuccessful piscivory events ( $N_N = 0$ ).

Considerable variability was included in the estimate of fish prey consumed; this was attributable to the randomization process used in selecting daily IP and individual fish prey size. Therefore, it required approximately 10,000 permutations to converge to a stable mean estimate of fish prey consumed. Confidence intervals for the mean estimate of consumed fish prey were estimated for each predator species. Model assumptions were (1) the number of evacuated fish prey was equal to the number of fish prey consumed, (2) probability of detecting IP was similar across sampling periods, (3) detection of IP in a given sampling period was independent of detection during all other sampling periods, (4) all salmonid fish were predaceous regardless of size, and (5) selection of fish prey was dependent on relative availability regardless of prey size (upper bound: 150 mm TL).

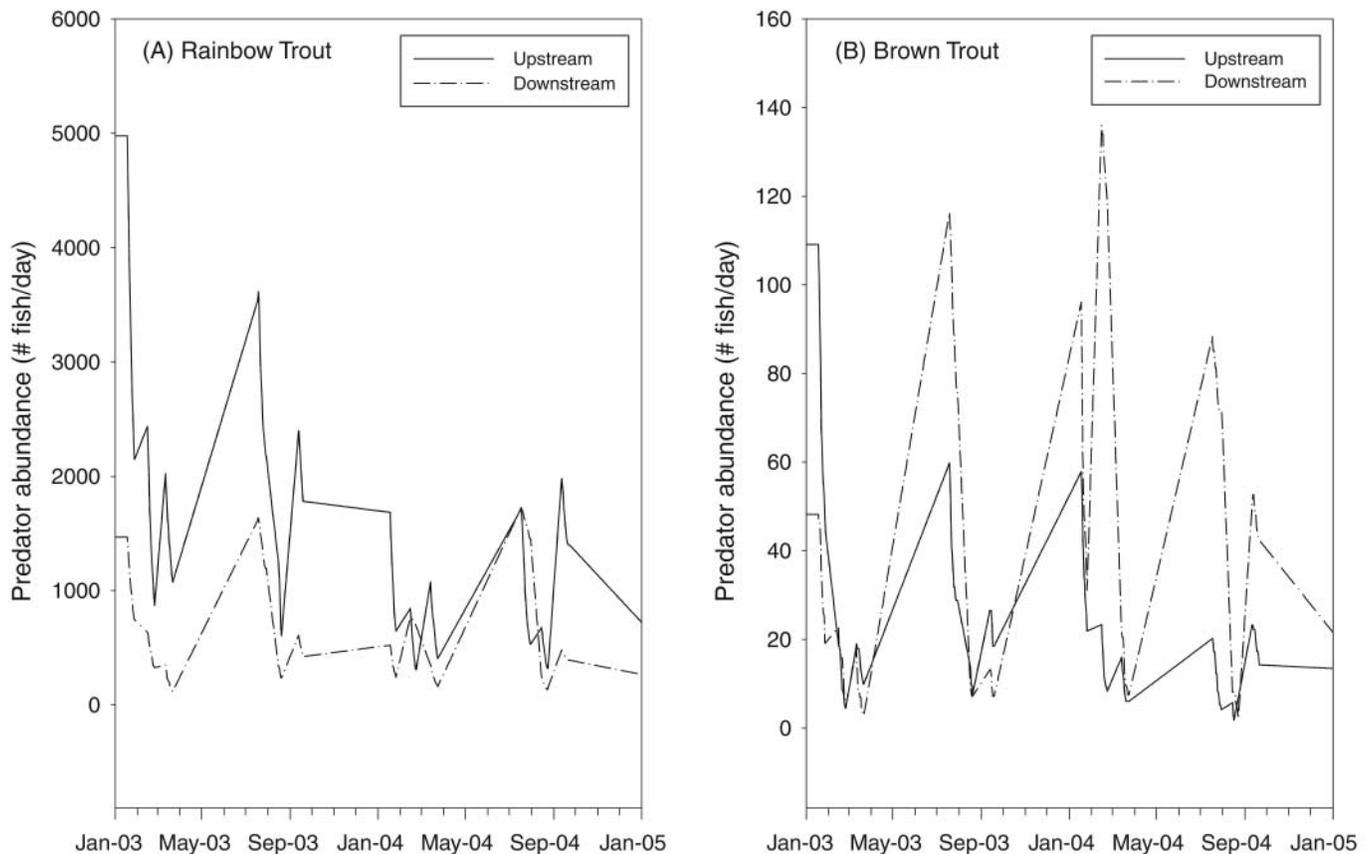


FIGURE 3. Daily abundance estimated for (A) rainbow trout and (B) brown trout in Colorado River study reaches upstream and downstream of the Little Colorado River confluence (see Coggins 2008 and Coggins et al. 2011).

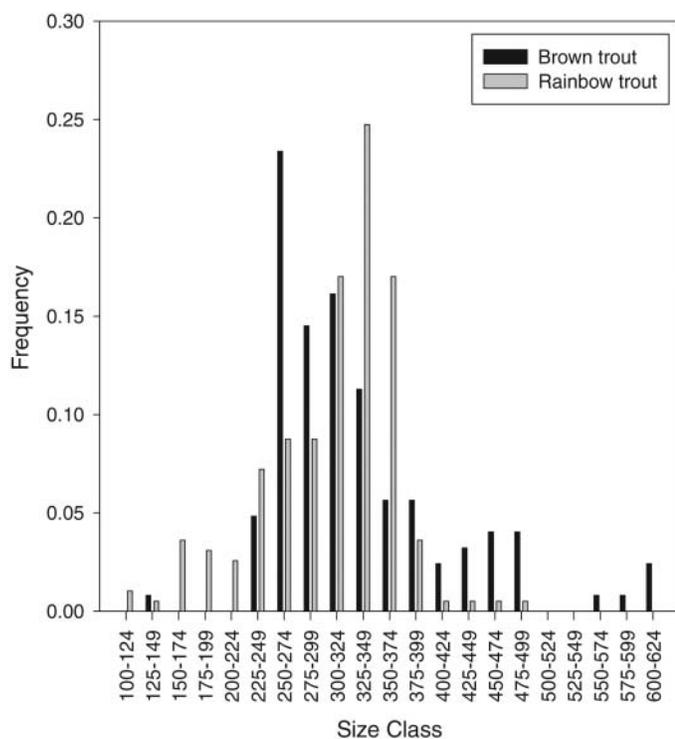


FIGURE 4. Predator size-class (total length, mm) distribution for rainbow trout and brown trout in Colorado River study reaches upstream and downstream of the Little Colorado River confluence.

## RESULTS

### Demographics

Rainbow trout were by far the most abundant fish in the catch, but their distribution was spatially uneven. The abundance estimates reported here were made only for the 15-km segment of the study area (Figure 1). Rainbow trout constituted 98% of salmonids in the catch (initial 2003 abundance estimate  $\pm$  95% CI = 6,446  $\pm$  946; Coggins et al. 2011) and had higher abundance in the reach upstream of the LCR (77%) than in the downstream reach (23%; Figure 3A). In contrast, brown trout (2% of the catch) were much less abundant (initial 2003 abundance estimate  $\pm$  95% CI = 156  $\pm$  29) and were more evenly distributed between upstream (55%) and downstream (45%) reaches (Figure 3B). The observed size range of piscivorous fish varied for both rainbow trout (105–436 mm TL) and brown trout (123–647 mm TL). The size-class distributions for observed predaceous trout (Figure 4) were similar to the overall size structure of the population, suggesting that all trout regardless of size were predaceous.

### Prey Proportions

Proportions of vertebrate prey ingested by rainbow trout and brown trout consisted of fish (90.3%), lizards (1.2%), birds (0.8%), bats (0.2%), other unidentifiable terrestrial vertebrates (2.5%), and vertebrates that could not be further discerned (5%). Stomachs in which evidence of piscivory was observed often

contained multiple fish prey (2–4 fish) at proportions of 6% for rainbow trout and 32% for brown trout. Only 22% of all fish prey remains were taxonomically identifiable at a species or family level (these fish prey proportions were used for the fish prey consumption model). Fish prey items that were identifiable included rainbow trout (7.3%), fathead minnow *Pimephales promelas* (7.8%), humpback chub (27.3%), speckled dace (15.2%), flannelmouth suckers (10.6%), bluehead suckers (3.0%), and other unidentifiable suckers (28.8%).

### Spatial and Temporal Comparisons of Piscivory

Mean monthly IP differed between the two nonnative trout species (one-way ANOVA:  $P < 0.01$ ; Table 1). Typically, rainbow trout IP was low and varied with location and season (two-way ANOVA:  $F_{3,20} = 13.9$ ,  $P < 0.01$ ). Post hoc tests revealed significant differences in rainbow trout IP between locations ( $P < 0.01$ ; upstream: 0.61%; downstream: 2.1%) and seasons ( $P < 0.01$ ; summer: 1.7%; winter: 1.05%) but not between years ( $P = 0.59$ ). In comparison, IP was highest for brown trout and varied between reaches and seasons (two-way ANOVA:  $F_{3,20} = 13.9$ ,  $P < 0.01$ ). Although post hoc comparisons indicated significant differences in brown trout IP by location ( $P < 0.01$ ; downstream: 36%; upstream: 11.6%), no differences were observed between seasons ( $P = 0.90$ ) or years ( $P = 0.60$ ).

### Effects of Physical and Biological Factors on Piscivory

For rainbow trout, there was a significant correlation ( $F_{3,86} = 25.5$ ,  $P < 0.001$ ) between IP and temperature, native fish prey availability, and sediment concentration. However, post hoc tests showed that rainbow trout IP was only correlated with increasing native fish prey availability ( $P < 0.001$ ) and increasing sediment concentration ( $P < 0.001$ ). There was no significant relationship between rainbow trout IP and temperature ( $P = 0.830$ ). Based on the above findings, we tested for an interaction effect ( $\alpha = 0.05$ ) by using the cross product of native fish prey availability and sediment concentration. For rainbow trout IP, a strong antagonistic interaction ( $F_{3,86} = 32.3$ ,  $P = 0.001$ ) was observed between sediment concentration (range = 5.9–20,000 mg/L; Figure 5) and native fish prey availability (CPUE range = 0.026–20.5 fish·km<sup>-1</sup>·trip<sup>-1</sup>; Figure 6). Rainbow trout IP increased with increasing native fish prey availability and with increasing sediment concentration up to 1,100 mg/L. Regardless of prey availability, further increases in sediment concentration beyond this level resulted in a decrease rather than an increase in rainbow trout IP.

In contrast, brown trout IP responded differently to these factors. Results showed a significant and positive correlation ( $F_{3,71} = 6.1$ ) between IP and either temperature ( $P = 0.003$ ) or native fish prey availability ( $P = 0.007$ ); however, no significant relationship existed between brown trout IP and sediment concentration ( $P = 0.835$ ). There was also no interaction effect between significant variables ( $P = 0.53$ ). The additive effect showed a 1.8-fold increase in brown trout IP with increasing temperature (range = 7.9–15.6°C) at low native fish prey

TABLE 1. Mean annual incidence of piscivory (IP) by rainbow trout and brown trout collected in Colorado River study reaches upstream and downstream of the Little Colorado River (LCR) confluence, 2003–2004 (CV = coefficient of variation).

Season and capture location relative to the LCR confluence	Total <i>n</i>	Piscivores <sup>a</sup>	IP (%)		
			Mean	SD	CV
<b>Rainbow Trout</b>					
Winter 2003					
Upstream	5,304	52	1.0	0.001	0.027
Downstream	1,219	25	2.1	0.004	0.081
Summer 2003					
Upstream	2,740	23	0.8	0.002	0.035
Downstream	730	24	3.3	0.007	0.132
Winter 2004					
Upstream	2,242	11	0.5	0.001	0.030
Downstream	543	7	1.3	0.005	0.097
Summer 2004					
Upstream	2,102	23	1.1	0.002	0.045
Downstream	480	16	3.3	0.008	0.164
<b>Brown Trout</b>					
Winter 2003					
Upstream	84	4	4.8	0.023	0.465
Downstream	47	16	34.0	0.069	1.382
Summer 2003					
Upstream	42	4	9.5	0.045	0.906
Downstream	40	28	70.0	0.072	1.449
Winter 2004					
Upstream	59	6	10.2	0.039	0.787
Downstream	75	42	56.0	0.057	1.146
Summer 2004					
Upstream	25	4	16.0	0.073	1.466
Downstream	28	9	32.1	0.088	1.765

<sup>a</sup> Number of predators with fish prey remains in their gastrointestinal tracts.

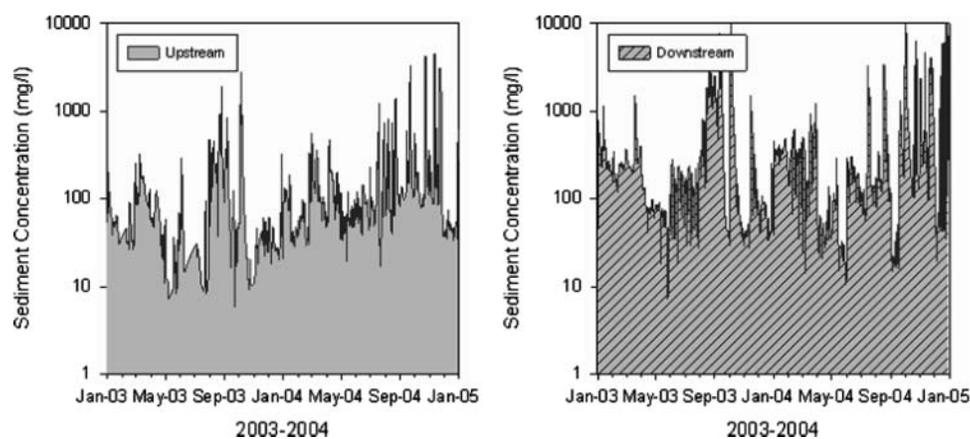


FIGURE 5. Mean daily suspended sediment concentrations (range = 5.9–20,000 mg/L) in Colorado River study reaches upstream and downstream of the Little Colorado River confluence. Sediment data (mg/L) were remotely measured by using laser-based sensors at two U.S. Geological Survey monitoring stations (upstream: gaging station 09383100; downstream: gaging station 09402500).

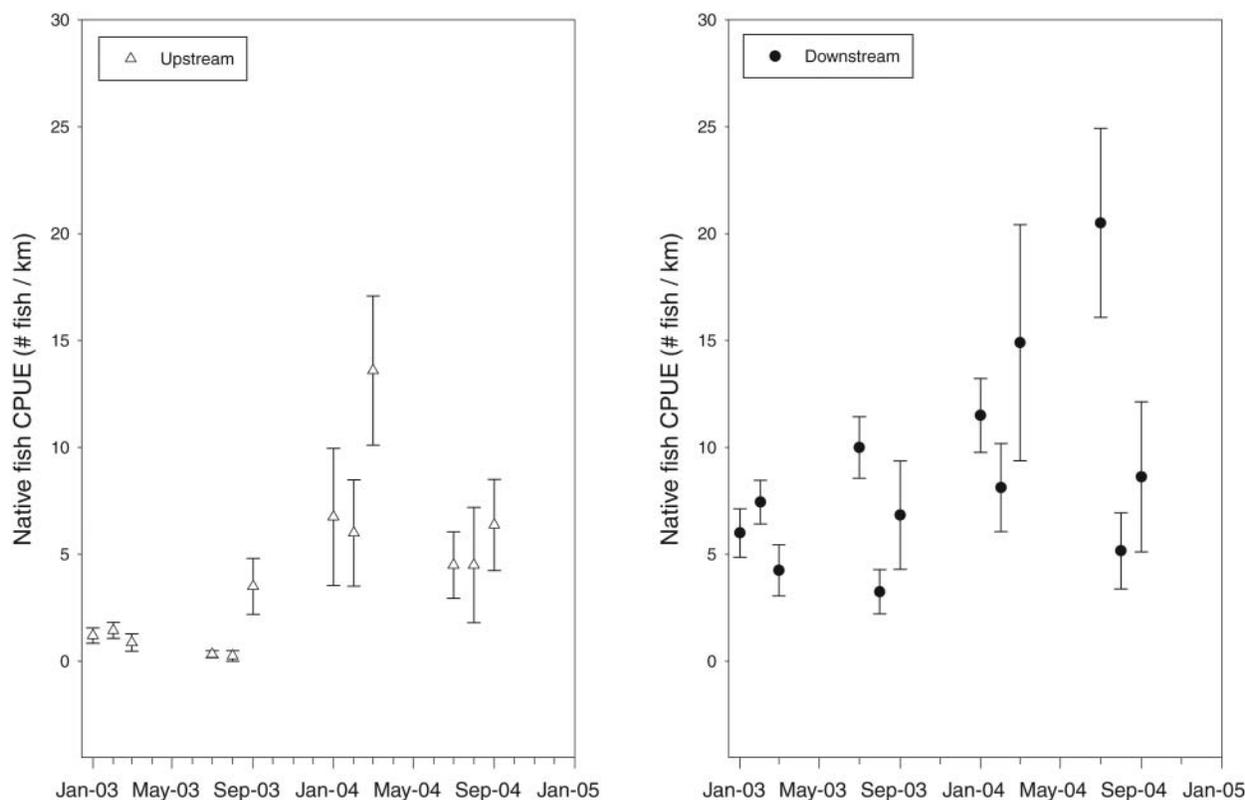


FIGURE 6. Mean ( $\pm 95\%$  confidence interval) availability (catch per unit effort [CPUE]; range =  $0.026\text{--}20.5\text{ fish}\cdot\text{km}^{-1}\cdot\text{trip}^{-1}$ ) of small ( $<150\text{ mm}$  total length) native prey fish captured by electrofishing in Colorado River study reaches upstream and downstream of the Little Colorado River confluence.

availability and a 1.3-fold increase with increasing native fish prey availability under higher temperatures.

We tested whether changes in predator abundance influenced daily IP for each predator species. Results indicated a significant and negative correlation between rainbow trout IP and predator abundance ( $F_{1,88} = 14.0$ ,  $P < 0.001$ ). In comparison, there was only a marginal negative relationship between brown trout IP and abundance ( $F_{1,73} = 3.2$ ,  $P = 0.075$ ). We also tested whether changes in native fish prey availability influenced the rainbow trout or brown trout IP independent of changes in predator abundance. Results indicated a significant and positive correlation between rainbow trout IP and native fish prey availability ( $F_{1,88} = 29.1$ ,  $P < 0.001$ ). A significant and positive correlation between brown trout IP and native fish prey availability was also observed ( $F_{1,73} = 8.1$ ,  $P = 0.006$ ).

### Modeling the Incidence of Piscivory

Based on evaluation with AIC, two different regression models were selected for estimating IP (Table 2). Among the 10 candidate models considered for rainbow trout, a model that included sediment concentration, fish prey availability, and a sediment  $\times$  prey availability interaction term (model 9 in Table 2) had the best out-of-sample predictive power (i.e., lowest AIC) for IP. This model explained over 50% of the variation in rainbow trout IP. There was moderate to essentially no sup-

port for the same model without the interaction term, and there was no support for the other remaining models. Among the 10 models considered for brown trout (i.e., models 11–20 in Table 2), a model that included temperature and fish prey availability (model 16) was selected as the most parsimonious based on its low AIC value. Unlike the analysis of rainbow trout models, several other models for brown trout (models 17 and 20) had strong support because of their low AIC values; however, these models were less simple and required more parameters. The remaining models (12, 13, 18, and 19) had moderate support for predicting brown trout IP.

Rainbow trout IP used in the simulation, based on the model with the lowest AIC value, was calculated from

$$\text{IP}_{\text{RBT}} = 0.01442 + 0.000036(S) + 0.002886(\text{CPUE}) - 0.000003(S \cdot \text{CPUE}),$$

where  $S$  is the mean daily sediment concentration (mg/L), CPUE is the native fish prey availability per trip, and  $S\cdot\text{CPUE}$  is the interaction term for the two independent variables. For brown trout, daily IP was estimated as follows:

$$\text{IP}_{\text{BNT}} = 0.138414 + 0.018434(T) + 0.008151(\text{CPUE}),$$

where  $T$  is mean daily water temperature ( $^{\circ}\text{C}$ ).

TABLE 2. Results of model selection based on Akaike's information criterion (AIC) used to compare a range of regression models for predicting incidence of piscivory by rainbow trout and brown trout. (Temp = Temperature; Sed = sediment concentration; Prey = native fish prey availability;  $B_0$ ,  $B_1$ ,  $B_2$  = regression coefficients; LogL log likelihood,  $K$  = number of model parameters;  $\Delta$ AIC = AIC difference). Models in bold had the lowest AIC value and therefore the best out-of-sample predictive power.

Model Number	Model	$B_0$	$B_1$	$B_2$	$B_3$	$R^2$	logL	$K$	AIC	$\Delta$ AIC
<b>Rainbow Trout</b>										
1	$B_0 + B_1(\text{Sed})$	0.026162	0.000021			0.328	203.7	2	-403	28
2	$B_0 + B_1(\text{Temp})$	0.003433	0.002671			0.039	187.6	2	-371	60
3	$B_0 + B_1(\text{Prey})$	0.021236	0.002537			0.294	198.7	2	-393	38
4	$B_0 + B_1(\text{Sed}) + B_2(\text{Temp})$	0.010519	0.000020	0.001417		0.339	204.5	3	-403	29
5	$B_0 + B_1(\text{Sed}) + B_2(\text{Prey})$	0.017919	0.000017	0.001966		0.470	214.3	3	-423	9
6	$B_0 + B_1(\text{Temp}) + B_2(\text{Prey})$	0.008032	0.001224	0.002434		0.257	199.1	3	-392	39
7	$B_0 + B_1(\text{Sed}) + B_2(\text{Temp}) + B_3(\text{Prey})$	0.013199	0.000017	0.000440	0.001933	0.471	214.4	4	-421	11
8	$B_0 + B_1(\text{Sed}) + B_2(\text{Temp}) + B_3(\text{Sed} \times \text{Temp})$	-0.007862	0.000106	0.002795	-0.000006	0.380	207.3	4	-407	25
9	<b><math>B_0 + B_1(\text{Sed}) + B_2(\text{Prey}) + B_3(\text{Sed} \times \text{Prey})</math></b>	0.014420	0.000036	0.002886	-0.000003	0.530	219.8	4	-432	0
10	$B_0 + B_1(\text{Temp}) + B_2(\text{Prey}) + B_3(\text{Temp} \times \text{Prey})$	0.005070	0.001477	0.003241	-0.000066	0.257	199.2	4	-390.3	41
<b>Brown Trout</b>										
11	$B_0 + B_1(\text{Sed})$	0.401566	0.000011			0.005	41.9	2	-80	15
12	$B_0 + B_1(\text{Temp})$	0.187905	0.019667			0.120	46.5	2	-89	6
13	$B_0 + B_1(\text{Prey})$	0.337666	0.008823			0.100	45.7	2	-87	7
14	$B_0 + B_1(\text{Sed}) + B_2(\text{Temp})$	0.187538	-0.000001	0.019734		0.120	46.6	3	-87	8
15	$B_0 + B_1(\text{Sed}) + B_2(\text{Prey})$	0.335361	0.000007	0.008735		0.102	45.8	3	-86	9
16	<b><math>B_0 + B_1(\text{Temp}) + B_2(\text{Prey})</math></b>	0.138414	0.018434	0.008151		0.205	50.4	3	-95	0
17	$B_0 + B_1(\text{Sed}) + B_2(\text{Temp}) + B_3(\text{Prey})$	0.136745	-0.000004	0.018697	0.008186	0.205	50.4	4	-93	2
18	$B_0 + B_1(\text{Sed}) + B_2(\text{Temp}) + B_3(\text{Sed} \times \text{Temp})$	-0.008145	0.000776	0.033804	-0.000056	0.180	49.2	4	-90	4
19	$B_0 + B_1(\text{Sed}) + B_2(\text{Prey}) + B_3(\text{Sed} \times \text{Prey})$	0.306553	0.000113	0.013798	-0.000015	0.151	47.9	4	-88	7
20	$B_0 + B_1(\text{Temp}) + B_2(\text{Prey}) + B_3(\text{Temp} \times \text{Prey})$	0.059762	0.025292	0.018851	-0.000925	0.290	50.6	4	-93	2

### Modeling of Fish Prey Consumption

Although rainbow trout were less piscivorous than brown trout, their greater abundance resulted in a cumulative piscivory effect that was much greater, representing 65% of the total fish consumed during the study period (2003–2004). The total number of fish prey evacuated during the first 2 years of the 4-year mechanical removal period (2003–2006) was 33,438 fish prey (rainbow trout: 21,641 fish prey; brown trout: 11,797 fish prey). Table 3 summarizes the estimated annual number of individuals of each prey species consumed by rainbow trout and brown trout within each study reach (upstream and downstream). The total number of consumed fish (2003–2004) partitioned among the different fish prey species included 3,412 flannelmouth suckers, 990 bluehead suckers, 9,278 other unidentifiable suckers, 5,339

speckled dace, 9,326 humpback chub, 2,669 fathead minnow, and 2,424 rainbow trout. The variability observed in mean fish prey estimates was due to the randomization process used for selecting IP, prey species, and initial weight.

Most of the piscivory by rainbow trout and brown trout occurred in the downstream reach (58%). Even though rainbow trout had a large cumulative piscivory effect, the annual per capita consumption rate was low overall; on average, each rainbow trout consumed 4 fish/year in the upstream reach and 10 fish/year in the downstream reach. In contrast, per capita rates of fish consumption by brown trout were much higher: 90 fish/year in the upstream reach and 112 fish/year in the downstream reach. The modeled simulation of daily evacuation rates of humpback chub prey (individuals/d) consumed by rainbow trout and brown

TABLE 3. Estimated number of fish prey evacuated annually by rainbow trout and brown trout in Colorado River study reaches upstream and downstream of the Little Colorado River confluence. Mean fish prey and 95% confidence intervals (CI) were estimated for the first 2 years (2003–2004) of the mechanical removal period.

Fish prey	Upstream reach				Downstream reach			
	2003		2004		2003		2004	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
<b>Rainbow Trout</b>								
Rainbow trout	426	(388–464)	336	(302–370)	339	(305–373)	462	(422–502)
Fathead minnow	429	(387–471)	433	(391–475)	343	(305–381)	529	(482–576)
Humpback chub	1,541	(1,460–1,622)	1,448	(1,369–1,527)	1,232	(1,163–1,301)	1,826	(1,736–1,916)
Speckled dace	857	(795–919)	868	(807–929)	686	(632–740)	1,058	(989–1,127)
Flannelmouth sucker	600	(552–648)	474	(431–517)	479	(436–522)	649	(599–699)
Bluehead sucker	171	(146–196)	141	(118–164)	137	(114–160)	190	(163–217)
Sucker (unidentified)	1,626	(1,547–1,705)	1,293	(1,225–1,361)	1,299	(1,232–1,366)	1,769	(1,688–1,850)
Total	5,650	(5,276–6,024)	4,993	(4,642–5,344)	4,515	(4,187–4,843)	6,483	(6,080–6,886)
<b>Brown Trout</b>								
Rainbow trout	167	(144–190)	89	(72–106)	272	(242–302)	333	(300–365)
Fathead minnow	169	(144–196)	108	(88–128)	279	(246–312)	378	(340–416)
Humpback chub	609	(562–656)	365	(328–402)	998	(938–1,058)	1,307	(1,234–1,380)
Speckled dace	339	(301–377)	216	(187–245)	557	(509–606)	758	(702–814)
Flannelmouth sucker	237	(207–267)	123	(102–144)	387	(349–424)	463	(423–504)
Bluehead sucker	68	(52–84)	37	(25–49)	111	(91–131)	135	(113–157)
Sucker (unidentified)	642	(597–686)	337	(304–370)	1,050	(992–1,108)	1,262	(1,199–1,325)
Total	2,232	(2,008–2,456)	1,275	(1,107–1,443)	3,654	(3,367–3,942)	4,636	(4,310–4,962)

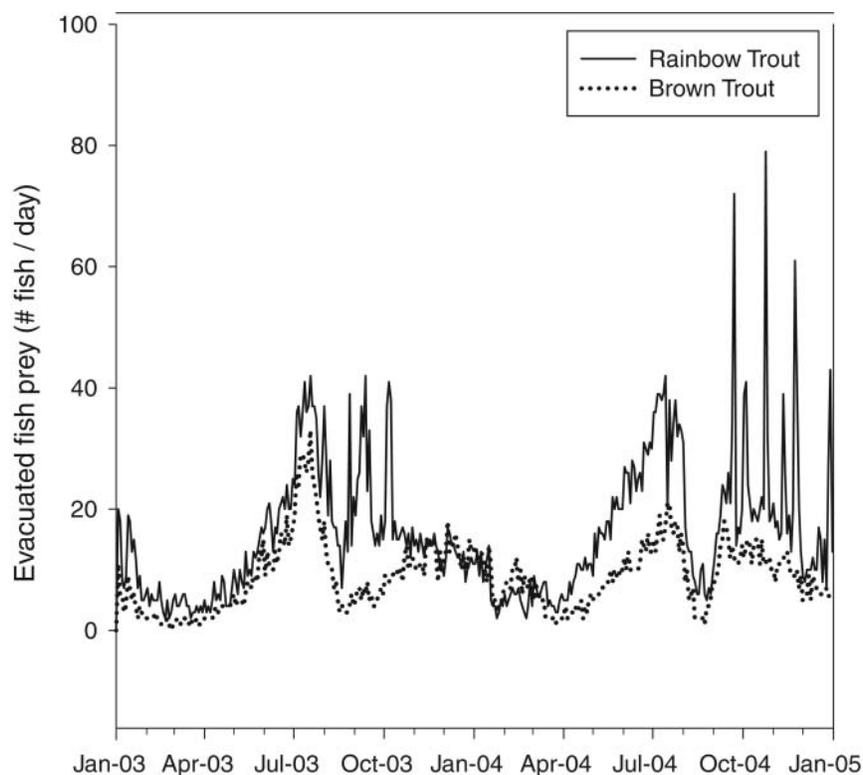


FIGURE 7. Daily rates of evacuation of humpback chub prey (<150 mm total length) consumed by rainbow trout and brown trout in the Colorado River near the Little Colorado River confluence (Figure 1) during the first 2 years (2003–2004) of the mechanical removal study.

trout is shown in Figure 7. Results indicated that daily consumption of juvenile humpback chub varied on a seasonal and annual basis. The differences in prey consumption were due to a combination of physical factors (turbidity and temperature; Figure 5), changes in predator abundance and distribution (upstream versus downstream; Figure 3), and prey abundances (Figure 6).

## DISCUSSION

This study confirms that both brown trout and rainbow trout inhabiting the Colorado River in Grand Canyon are piscivorous and consume native fish. In the case of the endangered humpback chub, the predation mortality caused by nonnative salmonids is likely a concern to managers charged with aiding in the recovery of this species. The present study found that brown trout IP was up to 70% in the study area depending on location and season, which supports the view that brown trout are aggressive piscivores (Crowl et al. 1992; McDowall 2006). The IP for rainbow trout (0.5–3.3%) was much lower than that for brown trout. However, rainbow trout were almost 50 times more abundant than brown trout, and thus our estimates suggest that rainbow trout predation accounted for more than half of the total number of fish consumed in the study area. Previous studies focusing on rainbow trout have frequently overlooked their potential role as piscivores because of the low incidence of fish prey in their diets, but the use of small sample sizes in dietary studies usually introduces the potential for underestimating the importance of piscivory (Angradi and Griffith 1990).

It is possible that piscivory could be a more important mechanism affecting native fishes than is generally recognized (McDowall 2003, 2006). Our study demonstrates that piscivory by rainbow trout and brown trout may be a large source of mortality for native fish in the Colorado River in Grand Canyon, which also corroborates prior findings by Marsh and Douglas (1997), who estimated similar risks of native fish mortality from predation by rainbow trout and brown trout. Even though about 20,000 nonnative trout were removed from the study area in 2003 and 2004, our modeling efforts suggest that rainbow trout and brown trout consumed over 30,000 fish prey in the study reaches during this same period. The majority of the humpback chub consumed by trout were young of the year and subadults (age < 3), and it seems likely that the loss of so many young fish will affect recruitment to the humpback chub population (Coggins and Walters 2009). On the other hand, we do not know whether predation is a large source of mortality at a population level since the total abundance of humpback chub recruits remains unknown (Coggins et al. 2006; Coggins and Walters 2009); other mortality sources and their rates are also unknown. Therefore, management efforts in reducing trout abundance to restore native fish populations may not have the desired response.

The availability of small fish as potential prey corresponded strongly with spatial and seasonal differences in piscivory by rainbow trout and brown trout. Native fish relative abundance

based on electrofishing was predominately higher in the downstream reach and in late summer, when seasonal dispersal from the LCR occurred due to flooding. Thus, greater IP was observed for both nonnative trout species in the turbid downstream reach, which also had a greater availability of small fish prey (<150 mm TL). A functional response to piscivory (Holling 1959) was plausible for both rainbow trout and brown trout in relation to changes in densities of native fish prey (Abrams 1993) and predator abundances (Murdoch 1971; Anderson 2001). It is likely that these two density-dependent processes had an effect on fish prey mortality. For example, prey availability and annual per capita consumption rates for trout were always greater in the more turbid downstream reach (i.e., annual consumption by rainbow trout and brown trout were respectively 2.5- and 1.24-fold greater downstream than upstream). Additionally, there was a negative correlation between IP and predator abundance such that piscivory increased as predator abundance decreased. Although the negative correlation was significant for rainbow trout, this compensatory response was only marginal for brown trout, possibly due to the smaller range in density for brown trout in this study.

Nonnative trout consistently consumed on average 85% more native fish than nonnative fish in spite of the fact that native fish made up less than 30% of the small prey fish available in the study area. The mechanisms responsible for this differential predation on native fish are uncertain (Ward and Bonar 2003), but vulnerability to predation may be higher for native fish because they lack a co-evolutionary history with these newly introduced predators (Townsend and Crowl 1991; Blinn et al. 1993). Other factors that may increase the relative vulnerability of native fishes include the colder water temperatures and lower turbidity of the main-stem Colorado River relative to its pre-dam state (Clarkson and Childs 2000; Ward and Bonar 2003). Additionally, smaller-sized, aggressive nonnative fishes (e.g., trout, fathead minnow, red shiner *Cyprinella lutrensis*, etc.) may relegate native fish to less-preferred or riskier habitat types (Blinn et al. 1993; Taniguchi et al. 1998; Walters et al. 2000; Ward and Bonar 2003), where the native fish may be more susceptible to predation by larger fish species or may experience slower growth (Walters and Korman 1999; Clarkson and Childs 2000).

The window of vulnerability would probably be shorter for native fishes if warmer water temperatures generate higher growth rates (Petersen and Paukert 2005). In the current thermal regime, the nonnative trout principally preyed upon juvenile and small-bodied fishes, yet we also observed that many trout were capable of consuming large adult fish (e.g., in one instance, a 610-mm brown trout consumed a 380-mm bluehead sucker). This size vulnerability might change under warmer temperature regimes depending on the divergence in growth rates between predators and fish prey (Ward and Bonar 2003; Petersen and Paukert 2005). Although humpback chub exhibit temperature-dependent growth (Coggins and Pine 2010), growth rates in the Colorado River under the temperature range observed (7.9–15.6°C) were probably not fast enough for

humpback chub to emerge from predation-vulnerable size-classes, especially since brown trout appeared to show increased piscivory with increases in temperature. Thus, there is a potential thermal tradeoff between increased fish prey growth and increased piscivory by brown trout.

Our findings show that humpback chub are vulnerable to trout predation at an individual level, but it is uncertain whether trout piscivory exerts a population-level effect on this endangered species. Likewise, it remains to be seen whether the humpback chub population has been positively affected by the mechanical removal of nonnative trout. We found that nearly 30% of the identifiable fish present in trout stomachs were humpback chub and that in spite of their low abundance, humpback chub appeared to be among the more likely prey fish to be consumed. Daily estimates of evacuated humpback chub ( $\leq 150$  mm TL) showed that more humpback chub were consumed during the second year (2004) of the mechanical removal study. For rainbow trout, the estimated increase in number of fish prey consumed appears to have been due to the interaction between sediment and prey availability, whereas for brown trout the increase was more related to prey availability and temperature. The increased predation was greatest in the downstream reach, where reductions in predator abundance were cumulatively lower.

Due to the interaction effect between turbidity and fish prey availability, it was difficult to separate the effects of these covariates on IP in this study. Both rainbow trout and brown trout exhibited higher piscivory in the more consistently turbid waters downstream of the LCR confluence, yet only rainbow trout piscivory was correlated with turbidity. However, unlike brown trout, rainbow trout were more abundant upstream than downstream and consequently had a greater cumulative piscivory effect even though the upstream reach was less turbid. Increased turbidity has been shown to reduce predation by visual feeders like trout (Guthrie and Muntz 1993); however, the decrease in visual detection (Strickler et al. 2005) may have been compensated for by the greater availability of small native fish that dispersed downstream of the LCR confluence (Holling 1959). It remains uncertain whether the observed increase in IP under increased turbidity was due to behavioral changes in the fish predators (Ginetz and Larkin 1976; Gradall and Swenson 1982) or in the fish prey (Miner and Stein 1996; Johnson and Hines 1999; Stone 2010).

Moreover, daily rainbow trout IP increased with increasing native fish prey availability and increasing sediment concentration up to 1,100 mg/L. Further increases in sediment concentration regardless of fish prey availability resulted in a decrease rather than an increase in IP. Reasons for this antagonistic interaction are uncertain, although physiological stress (i.e., increased ventilation rates and elevated levels of plasma cortisol; Redding et al. 1987; Newcombe and MacDonald 1991) and native fish response to turbidity (Johnson and Hines 1999; Stone 2010) are possible factors. Regardless of the mechanism, the positive predatory response to moderately high turbidity levels was a departure from the expected norm (Ginetz and Larkin

1976; Gradall and Swenson 1982; Miner and Stein 1996; Gregory and Levings 1998).

Our data suggest that brown trout typically employ an active foraging strategy that includes epibenthic feeding (e.g., amphipods and gastropods) as well as piscivory; this strategy may be better suited to (but is not necessarily limited to) turbid conditions (M. D. Yard, unpublished data). In contrast, our observations of rainbow trout diet suggest a heavy reliance on drifting invertebrate prey, and turbid conditions are known to make prey detection more difficult for sight feeders (Barrett et al. 1992). Consequently, the onset of turbid conditions may cause rainbow trout to move from territorial feeding lanes into the shallow shorelines and to switch from drift feeding to other foraging strategies that involve more active hunting or opportunistic predation (Shaw and Richardson 2001). Although brown trout were more equally distributed upstream and downstream of the LCR confluence, rainbow trout were nearly 80% more abundant upstream than downstream. Rainbow trout captured downstream of the LCR confluence exhibited reduced size and condition and more frequently had empty stomachs and lower gut fullness than their conspecifics sampled upstream (M. D. Yard, unpublished data).

Thus, trout feeding plasticity under varying turbidity may contribute to differences in piscivory between the two study reaches. Additionally, tributary flows and increased turbidity downstream of the LCR confluence often coincide with seasonal dispersal of young fish from the LCR into the main stem such that greater piscivory might be expected simply based on higher availability of fish prey. Increased turbidity should influence a predator's optical resolution and ability to discriminate between prey and suspended particles (Strickler et al. 2005). The resultant effect on prey size might lead to preferential consumption of larger prey items (macroinvertebrates and fish) and perhaps serves as compensation for the reduced reactive distance of predators (Vinyard and O'Brien 1976; Barrett et al. 1992). Conversely, reduced reactive distances may also affect the ability of fish prey to visually avoid predators during periods of high turbidity (Johnson and Hines 1999).

Management of sediment-routing processes within the Colorado River in Grand Canyon has been a focus of much effort in the past two decades (Walters et al. 2000). This effort has most often been couched in terms of maintaining sand beach features for both aquatic and terrestrial habitats (USDOI 1996), but its influence on turbidity and the potential for interactive effects on nonnative trout and their invertebrate prey (Petersen and Paukert 2005) and fish prey (Stone 2010) should also be considered and investigated further, albeit with some caution (Zipkin et al. 2009). Although turbidity may mediate the effects of nonnative trout on native fishes in Grand Canyon, the net consequence is uncertain. Our results suggest that increased turbidity and prey availability were associated with increased trout IP on native fishes, including the humpback chub. However, the role that suspended sediment and prey availability play in piscivory remains as indistinct as the turbid waters.

In conclusion, rainbow trout were less piscivorous than brown trout, but the greater abundance of rainbow trout resulted in a larger cumulative piscivory effect on the native fish community. Fish that are abundant like rainbow trout are frequently not piscivorous; fish that are highly piscivorous like brown trout are often uncommon and elusive to catch. Consequently, general studies on fish diet may either overlook (e.g., rainbow trout) or overemphasize (e.g., brown trout) the potential role of some nonnative species as predators of native fishes, especially if the numerical effect of predator abundance is not accounted for. Turbidity appears to mediate predation directly by reducing the visual detection of prey; nevertheless, the increase in availability of alternate prey (fish) or shifts in foraging strategy (active versus drift feeding) may offset the concealment gained from this cover. Conservation efforts (flow and sediment augmentation) that cause frequent or prolonged periods of turbidity make it unlikely that rainbow trout in particular would be able to persist below the LCR confluence without either emigrating or subsidizing their diet with larger prey items, like fish. On the other hand, brown trout appear to be better suited to the turbid conditions found near the LCR confluence and further downstream. Therefore, the use of turbidity as a predator control mechanism will probably have different transient and long-term effects on rainbow trout than on brown trout. Thus, despite the progress that has been made, which will inform adaptive management approaches, the responses of native and nonnative fish populations (and the aquatic food base that supports these higher trophic levels) to flow and sediment augmentation experiments remain uncertain.

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