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ARTICLE

Nonnative Fish Control in the Colorado River in Grand Canyon, Arizona: An Effective Program or Serendipitous Timing?

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Abstract

The federally endangered humpback chub *Gila cypha* in the Colorado River within Grand Canyon is currently the focus of a multiyear program of ecosystem-level experimentation designed to improve native fish survival and promote population recovery as part of the Glen Canyon Dam Adaptive Management Program. A key element of this experiment was a 4-year effort to remove nonnative fishes from critical humpback chub habitat, thereby reducing potentially negative interactions between native and nonnative fishes. Over 36,500 fish from 15 species were captured in the mechanical removal reach during 2003–2006. The majority (64%) of the catch consisted of nonnative fish, including rainbow trout *Oncorhynchus mykiss* (19,020), fathead minnow *Pimephales promelas* (2,569), common carp *Cyprinus carpio* (802), and brown trout *Salmo trutta* (479). Native fish (13,268) constituted 36% of the total catch and included flannelmouth suckers *Catostomus latipinnis* (7,347), humpback chub (2,606), bluehead suckers *Catostomus discobolus* (2,243), and speckled dace *Rhinichthys osculus* (1,072). The contribution of rainbow trout to the overall species composition fell steadily throughout the study period from a high of approximately 90% in January 2003 to less than 10% in August 2006. Overall, the catch of nonnative fish exceeded 95% in January 2003 and fell to less than 50% after July 2005. Our results suggest that removal efforts were successful in rapidly shifting the fish community from one dominated numerically by nonnative species to one dominated by native species. Additionally, increases in juvenile native fish abundance within the removal reach suggest that removal efforts may have promoted greater survival and recruitment. However, drought-induced increases in river water temperature and a systemwide decrease in rainbow trout abundance concurrent with our experiment made it difficult to determine the cause of the apparent increase in juvenile native fish survival and recruitment. Experimental efforts continue and may be able to distinguish among these factors and to better inform future management actions.

Modifications to river ecosystems are a ubiquitous feature of human-occupied landscapes. Such modifications and the often large-scale changes in physical and biotic processes have prompted a recent increase in river restoration projects and an active dialogue between scientists and policy makers on both river restoration science and the appropriate measures of river restoration success (Poff et al. 2003; Palmer et al. 2005). Although such research efforts have led to increased understanding

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of the structure and function of river ecosystems, scientists frequently are unable to predict with great certainty the outcome of specific restoration activities. Partly because this uncertainty can lead to skepticism and mistrust on the part of policy makers, adaptive management (Holling 1978; Walters 1986) has been widely advocated as a strategy to guide restoration programs (Poff et al. 2003). Adaptive management recognizes that predictions of system response to restoration activities are uncertain, and this strategy therefore seeks to use thoughtful and deliberate application of management actions to learn about system behavior and to determine successful restoration policies. After recognition of degraded conditions in the Grand Canyon reach of the Colorado River downstream of Glen Canyon Dam (GCD; NRC 1987), the Glen Canyon Dam Adaptive Management Program (GCDAMP; formed in 1996) has attempted to use adaptive management for river restoration.

A focal objective of the GCDAMP is conservation of the native fishes that are endemic to this basin, particularly the humpback chub *Gila cypha*, which is federally listed as endangered. Beginning in January 2003, the GCDAMP initiated a multiyear program of experimentation to test policies that were specifically designed to conserve Grand Canyon native fishes by improving rearing conditions in the main-stem Colorado River. As originally conceived, the experiment sought to manipulate three factors that were thought to influence the juvenile rearing success of native fishes in the Colorado River: (1) nonnative fish abundance (Olden and Poff 2005), (2) GCD discharge patterns (Osmundson et al. 2002), and (3) GCD release water temperature (Robinson and Childs 2001). Levels of these factors were to be varied according to a factorial design over 16 years to determine which factors (and which interactions) exerted the most control over native fish recruitment and to inform subsequent management policies (Coggins et al. 2002).

Although managers did not fully adopt this long-term program of experimentation, they did implement a modified version of both the recommended flow manipulations and the nonnative fish control treatments. The U.S. Fish and Wildlife Service biological opinion for humpback chub (USFWS 1994) originally conceived the manipulation of flows to stabilize nearshore rearing conditions and mimic the seasonal hydrograph to improve survival rates of native fish; however, managers instead chose to increase the extent of hourly fluctuations from GCD during winter months. The intent of these flows, termed "nonnative suppression flows," was to reduce survival rates for early life stages of nonnative salmonids and thereby improve rearing conditions for native fish. The nonnative fish control experiment consisted of actively removing the nonnative fish from a 15.2-km Colorado River reach that was deemed critical habitat for humpback chub.

To assess these management actions, three scientific investigations were initiated and are presented as three companion papers in this issue. The first study (described in the present article) focused on quantifying the extent to which nonnative populations were depleted in the mechanical removal reach and the numerical response of the fish community to nonnative fish removal. The second study (Yard et al. 2011, this issue) focused on quantifying the predatory impacts of rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* on native fishes and investigating the influence of temperature and turbidity on the foraging behavior of these nonnative species. The third study (Korman et al. 2011, this issue) focused on the efficacy of the nonnative suppression flows in reducing survival rates of the early life history stages of rainbow trout.

For several decades, the fish community in the Grand Canyon reach of the Colorado River has been dominated numerically by two nonnative salmonids: the rainbow trout and brown trout (Gloss and Coggins 2005). Because introductions of nonnative salmonids adversely affect native invertebrate (Parker et al. 2001), amphibian (Knapp and Matthews 2000), and fish (McDowall 2003, 2006) communities across the globe, determining whether and under what environmental conditions nonnative salmonids may limit native fish recruitment is a key information need for the GCDAMP. Interactions with various nonnative fishes are widely implicated in the decline of southwestern native fishes (Minckley 1991; Tyus and Saunders 2000). Predation by nonnative salmonids, particularly brown trout, on native fishes in Grand Canyon has been demonstrated (Valdez and Ryel 1995; Marsh and Douglas 1997), and rainbow trout predation on native fishes has also been documented in other southwestern U.S. systems (Blinn et al. 1993). Besides causing direct mortality through predation, both rainbow trout and brown trout have exhibited other negative interactions with native fishes in western U.S. river systems, including interference competition, habitat displacement, and agonistic behavior (Blinn et al. 1993; Taniguchi et al. 1998; Robinson et al. 2003; Olsen and Belk 2005).

Removal of nonnative organisms to potentially benefit native species is most often conducted in small streams (e.g., Meyer et al. 2006), lakes and reservoirs (e.g., Hoffman et al. 2004; Vrendenburg 2004; Lepak et al. 2006), and terrestrial environments (e.g., Erskine Ogden and Rejmánek 2005; Donlan et al. 2007). However, recently much effort has been expended by state and federal fishery managers to remove or reduce nonnative fishes in the Colorado River basin as an aid to native fish recovery (Tyus and Saunders 2000). Unfortunately, little documentation is available to evaluate the efficacy of these efforts despite the high costs and expectations associated with their implementation (Mueller 2005). This study describes an effort to evaluate the efficacy of a nonnative fish removal program that was intended to benefit native fishes. Given the ecological and management interest in nonnative species removals, this portion of the GCDAMP also represents an important example of the first phase of active adaptive management (Parma et al. 1998) applied to benefit a focal biological resource, the humpback chub. Specifically, the objectives of this study were to (1) evaluate the effectiveness of nonnative control efforts in the main-stem Colorado River and (2) characterize changes in the fish community during nonnative control efforts. Note that Coggins and Yard

(2010) prepared a synopsized version of this work, which was more appropriate for consideration by GCDAMP committees.

METHODS

Mechanical removal reach: study areas and field protocols.—The Little Colorado River (LCR) inflow reach of the Colorado River (Figure 1) extends from river kilometer (RKM) 90.8 to RKM 106.0 (as measured downstream from RKM 0 at Lees Ferry) and is recognized as having the highest abundance of adult and juvenile humpback chub in the Colorado River (Valdez and Ryel 1995). Due to the availability of spawning and rearing habitat in the LCR, the LCR inflow reach also has a relatively high abundance of other native fishes, including the flannelmouth sucker *Catostomus latipinnis*, bluehead sucker *Catostomus discobolus*, and speckled dace *Rhinichthys osculus*. Given the importance of this reach for native fishes, the LCR inflow reach was selected for the testing of nonnative mechanical removal efforts and was divided into six river sections, which are labeled A–F (Figure 2). Sections A and B are the downstream-facing right and left shores extending from RKM 90.8 to RKM 99.2. Sections C and D are the right and left shores between RKM 99.2 and RKM 100.2 and include the LCR confluence and the mixing zone below the LCR. Sections E and F are the right and left shores situated downstream of the LCR confluence and extend from RKM 100.2 to RKM 106.0. The study area was stratified into these six sections to control for the effect of the LCR's discharge into the main-stem Colorado River; sections A and B are unaffected by this tributary, and it is believed that sections E and F are a sufficient distance downstream of the mixing zone to be uniformly affected (Figure 2). Sections C and D include the LCR confluence and are differentially affected by LCR discharge throughout their lengths. Within river sections A–B and E–F, the shoreline was divided into 500-m sites. The number of sites within each river section was 19 each in sections A and B and 13 each in sections E and F. Sections C and D constituted single sites. Note that shoreline distances are considerably longer than the thalweg distances as calculated from aerial imagery (U.S. Geological Survey, unpublished data) owing to geomorphic irregularities, such as tributary deltas.

From January 2003 to August 2006, 23 field trips were conducted to remove nonnative fish in serial depletion passes by using boat electrofishing within the mechanical removal reach. The majority of these trips removed fish during either four or five depletion passes; the exceptions were in August 2003 (2 passes), September 2003 (3 passes), and July 2004 (6 passes). All sites within sections A–B, C, and E–F were sampled during each pass. Section D, which encompassed the LCR confluence, was not sampled during any of the trips because of concerns about equipment damage associated with high water conductivity coming from the LCR and possibly high native fish abundance near the LCR confluence. All electrofishing was conducted at night, and two nights were required to complete each depletion pass for the entire reach. Electrofishing crews

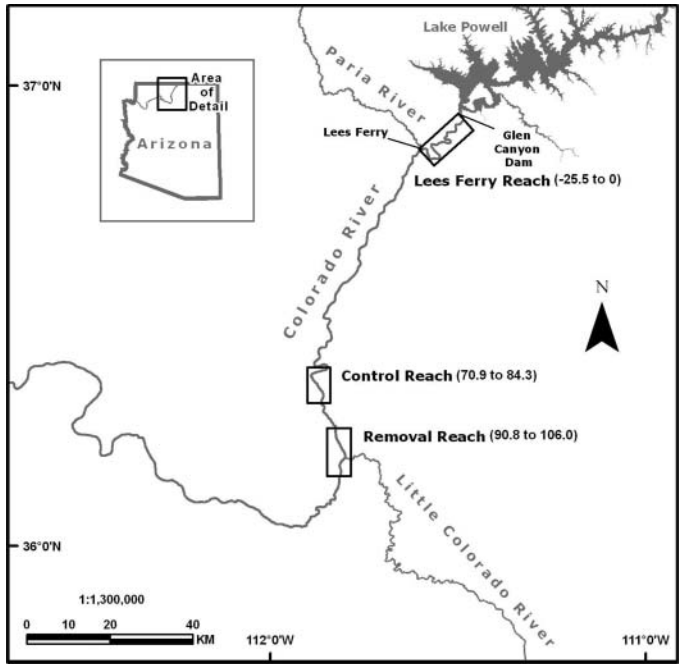

FIGURE 1. Map of the Colorado River within Grand Canyon, Arizona. The location of the Lees Ferry, control, and mechanical removal reaches are depicted. The number of river kilometers downstream from Lees Ferry (i.e., river kilometer 0) is indicated (in parentheses) for each reach.

consisted of a boat operator and a single netter. Two boat types (4.9-m rubber-hulled sport boat and 4.9-m aluminum-hulled sport boat) and two types of electrofishing control units (Coffelt Mark XXII and Smith-Root Mark XXII) were used in this study. Based on results reported by Speas et al. (2004) using similar sampling techniques, we estimated that the effective sampling zone was from the shoreline to approximately 4.5 m offshore. In an attempt to standardize among boat and control unit types, current output was adjusted to produce 5,000 W of power during all electrofishing operations. Nonnative fish were euthanized, and their total lengths (TLs) and weights (g) were recorded. Native fish were measured (TL), and those larger than 150 mm TL received passive integrated transponder tags.

To determine whether changes in the fish community within the mechanical removal reach were related to environmental influences rather than to the mechanical removal, a control reach was established upstream of the removal reach in an area of high rainbow trout density (RKM 70.9–84.3; Figure 1). This reach was stratified into sixty 500-m sites (30 on each shoreline). During most trips, 24 sites (approximately 40% of the total shoreline) were randomly chosen and sampled by using capture methods identical to those outlined above for the mechanical removal reach. Exceptions occurred in January 2003, when 25 sites were sampled, and in August 2003 (due to inclement weather), when 11 sites were sampled. All captured nonnative fish were identified and measured (TL); each individual that was 200 mm TL or larger received a uniquely numbered

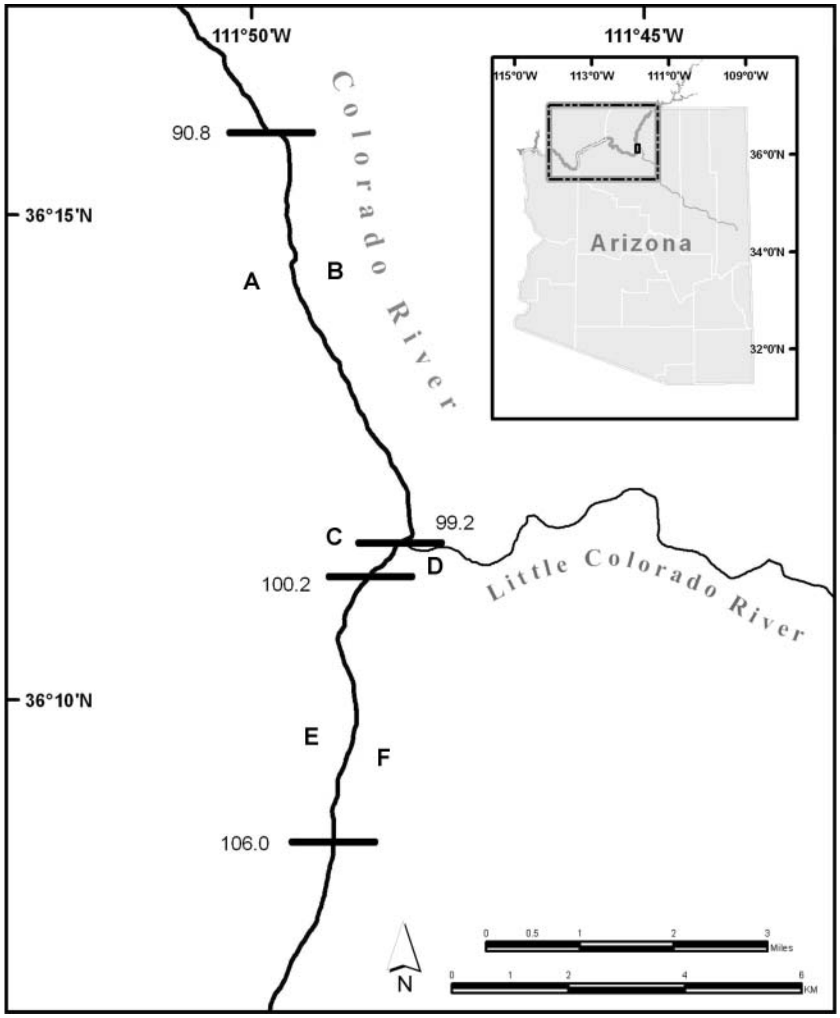

FIGURE 2. Map of the mechanical removal reach in the Colorado River within Grand Canyon, Arizona, illustrating the reach sections. The number of river kilometers downstream from Lees Ferry (i.e., river kilometer 0) is indicated at demarcation lines.

external T-bar anchor tag, and the left pelvic fin was removed prior to release. All fish captured in the control reach were released alive. Mark–recapture data were used to estimate abundance, capture probability, and apparent survival rate.

Mechanical removal reach: data analysis.—Following the methods of Dorazio et al. (2005), we used a hierarchical Bayesian modeling (HBM) framework to estimate rainbow trout abundance and capture probability from data collected among the serial removal passes. This framework assumes that the overall population is a collection of subpopulations (defined below), each with different abundance and capture probability during removal efforts. Subpopulation abundance and capture probability are sampled from common population-level distributions conditional on unknown hyperparameters (i.e., parameters that govern the population-level distributions). This hierarchical structure allows for a model-based aggregation of data among subpopulations that can be thought of as intermediate between analyses that operate on data pooled over all subpopulations and those that operate on each subpopulation independently. The structure allows information to be shared among subpopulations, particularly those subpopulations for which the data are sparse or uninformative, in some cases leading to unlikely parameter estimates. In these situations, the subpopulation parameter values are more heavily influenced by the population distribution and are thus pulled or shrunk (Gelman et al. 2004) towards the population distribution means. The amount of shrinkage is a function of both the difference between subpopulation and population distribution means and the population distribution variance.

We defined closed subpopulations corresponding to fish within each mechanical removal site, and we assumed that the observed numbers of removals from site i (1,. . ., I) on removal pass j (1,. . ., J) were drawn from a multinomial distribution with the number of trials equal to the site abundance (N_i) and cell probability vector $\overline{\pi}_i = \left\{\pi_{i,1}, \pi_{i,2}, ..., \pi_{i,J}\right\}$. If we first assume that capture probability is constant among removal passes within each site i, then the cell probability for site i in the jth depletion pass is given by

$$\pi_{ij} = \theta_i(1 - \theta_i)^{(j-1)}, \quad (1)$$

where θ_i is the constant capture probability in site *i*. The likelihood for the overall model is given as

$$L\left(N_i, \bar{\pi}_i \,|\bar{x}_i\right) = \frac{N_i!}{c_i\left(N_i - x_{i.}\right)!}\left(1 - \theta_i\right)^{J_i(N_i - x_{i.})}\prod_{j=1}^{J}\left(\pi_{i,j}\right)^{x_{ij}}, \quad (2)$$

where x_{ij} is the number of fish captured in site *i* and depletion pass *j*, $x_{i.} = \sum_{j=1}^{J_i} x_{ij}$ is the total number of fish captured in site *i*, and $c_i = \prod_{j=1}^{J_i} x_{ij}!$.

Equation (2) is the familiar Zippin (1956) estimator, which assumes that capture probability θ_i is constant within a site across passes within a trip. To cast this model in a HBM framework, we assumed that capture probability for a set of sites is sampled from a common distribution. The set of sites could either be all sites within the removal reach or a subset of sites belonging to a common stratum. Because there is good reason to believe that electrofishing capture probability is influenced by abiotic factors, such as turbidity (Reynolds 1996), and because there is frequently higher turbidity below the LCR confluence (Yard 2003), we chose to stratify the overall removal reach into sites upstream of the LCR confluence (sections A and B) and sites downstream of the confluence (sections C, E, and F) and to fit separate distributions to each stratum. Similarly, fish abundance typically differs upstream versus downstream (Gloss and Coggins 2005) of the LCR confluence, so separate distributions of abundance were also used.

Following Dorazio et al. (2005), we assumed that the site-specific capture probabilities were sampled from beta distributions in each stratum as $\theta_{i,k} \sim \text{Beta}(\alpha_k, \beta_k)$, where *k* is 1 for the upstream stratum or 2 for the downstream stratum and where α_k and β_k are the hyperparameters. The mean (μ_k) of the beta distribution is $\alpha_k/(\alpha_k + \beta_k)$, and the variance is $\mu_k(1 - \mu_k)/(\tau_k + 1)$, where τ_k is the similarity parameter and is equal to $\alpha_k + \beta_k$. We assumed that the site-specific abundances were sampled from Poisson distributions with mean and variance λ_k. For convenience, μ, τ, and ψ (where $\psi = \log_e\lambda$) were estimated for each stratum. We chose diffuse and uninformative prior distributions for each hyperparameter as follows: $\mu_k \sim \text{Uniform}(0, 1)$; $\tau_k \sim \text{Uniform}(0, 100)$; $E(\psi_k) \sim \text{Normal}(\text{mean} = 0, \text{SE} = 10)$; and $\text{SE}(\psi_k) \sim \text{Uniform}(0, 10)$.

For each trip, we used the resulting posterior distributions of λ_k and θ_k to characterize the abundance and capture probability for each stratum. Net immigration between any two trips was computed as the difference between the stratum abundance estimated at the end of one trip and the abundance estimated at the beginning of the subsequent trip. Daily net immigration rate was estimated as the net immigration divided by the elapsed time (d) between subsequent trips. All of the HBM analyses were executed in program R (R Development Core Team 2007) and WinBUGS (Lunn et al. 2000). For each trip analyzed, we summarized the distribution of each parameter among 20,000 Markov-chain Monte Carlo samples with a thinning frequency of 10 and a discard of the first 10,000 burn-in samples. We examined convergence by using the potential scale reduction factor of Gelman and Rubin (1992).

Control reach: data analysis.—Abundance of rainbow trout within the control reach was assessed by using electrofishing catch rate and mark–recapture-based open-population estimators. Because all rainbow trout that were marked with external tags were also given a secondary fin clip, our estimators of apparent survival rate (i.e., survival rate decremented by immigration rate; hereafter referred to as survival rate), capture probability, and abundance were conditional on estimated tag loss. Thus, although the basic observation and likelihood models used to estimate the key population parameters are given below in equations (6) and (7), we begin our overall model description with the tag loss models.

To estimate tag loss, we predicted the proportion of fish recaptured at each trip that would still retain their external tags. This proportion is not influenced by survival rate or capture probability under the assumption that survival rate and capture probability are independent of tag retention. We further assumed that tag loss rate during the first month after initial tagging would be different from the rate experienced in subsequent months. This allows for the possibility that the tag loss rate is higher initially (e.g., as a result of improper placement) but then declines. The predicted number of tagged fish in month *t* is

$$\hat{T}_t = S\left[\hat{T}_{t-1}(1 - l_2) + F_{t-1}(1 - l_1) + R_{t-1}(1 - l_1)\right], \quad (3)$$

where *S* is the monthly survival rate; $\hat{T}_t$ is the number of tagged fish available for capture just prior to sampling in month *t*; l_2 is the monthly secondary tag loss rate; F_{t-1} is the number of newly tagged fish in month $t - 1$; l_1 is the monthly initial tag loss rate (suffered in the month after tagging); and R_{t-1} is the number of fish that had lost their tags prior to month $t - 1$ and were retagged in month $t - 1$. Conversely, the predicted number of fish that lost their tags in month *t* is

$$\hat{L}_t = S\left[\hat{L}_{t-1} - R_{t-1} + \hat{T}_{t-1}(l_2) + F_{t-1}(l_1) + R_{t-1}(l_1)\right], \quad (4)$$

where $\hat{L}_t$ is the number of fish that lost their tags and are available for capture just prior to sampling in month *t*. The predicted tag retention rate ($\hat{\eta}_t$) of recaptured fish in the population in month *t* is then

$$\hat{\eta}_t = \frac{\hat{T}_t}{\hat{T}_t + \hat{L}_t}. \quad (5)$$

Note that equations (3) and (4) are linked by the R term such that when previously tagged fish are recaptured without a tag, they are fitted with new tags and thus are decremented from L and added to T. To estimate l_1 and l_2, we minimized the sum of squares between observed and predicted retention rates among the 22 sampling occasions after the first occasion. It is worth noting that because S appears in each term of equation (5), there is no need to estimate S in order to estimate tag loss rates.

We used a two-stage design to estimate key rainbow trout population parameters. In the first stage, we estimated monthly survival rate ($\hat{S}_t$) and capture probability ($\hat{p}_t$) conditional on tag loss rates, generally following a "single age recoveries only" model (Brownie et al. 1985). However, following the method of Coggins et al. (2006) and for computational simplicity, we assumed that observed recaptures followed a Poisson distribution rather than a multinomial distribution. Under this structure, the complete capture history is not used and the predicted numbers of fish that are recaptured with tags in month t from releases in a previous month e is

$$\hat{r}_{e,t} = (F_e + R_e)\,(1 - l_1)\,(1 - l_2)^{(t-e-1)} \left(\prod_{i=e}^{t-1} \hat{S}_i \right) \hat{p}_t. \qquad (6)$$

To reduce the number of parameters to be estimated, we set the monthly survival rate among months that were not sampled equal to the survival rate of the next sampled month. Assuming that the observed numbers of fish released in month e and recaptured with tags in a subsequent month t (i.e., $r_{e,t}$) represent independent samples from Poisson distributions with means given by equation (6), the log-likelihood function (ignoring terms involving only the data) is

$$\log_e L\left(r \mid \overline{p}\,,\, \overline{S}\right) = \sum_{e=1}^{22} \sum_{t>e}^{23} \left[-\hat{r}_{e,t} + r_{e,t} \log_e\left(\hat{r}_{e,t}\right) \right], \qquad (7)$$

where $\overline{p}$ and $\overline{S}$ are the unknown capture probability and monthly survival rate vectors to be estimated. The model was implemented in a Microsoft Excel spreadsheet by using Solver (Ladson and Allan 2002) as the nonlinear search procedure. As measures of uncertainty, 95% likelihood profile confidence intervals were computed for $\overline{p}$ and $\overline{S}$ using PopTools (Hood 2000). With the estimates of monthly survival rate and capture probability thus available, the abundance of 200-mm-TL and larger rainbow trout was estimated in the second stage by dividing the numbers of fish captured by the capture probability. Approximate 95% confidence intervals on these abundance estimates were calculated by using the confidence bounds on the capture probability estimates.

RESULTS

Over 36,500 fish representing 15 species were captured in the mechanical removal reach during 2003–2006 (Table 1). The majority (64%; 23,266) of these fish were nonnative, primarily consisting of rainbow trout (19,020), fathead minnow (2,569), common carp (802), and brown trout (479). Native fish (13,268) contributed 36% of the total catch and included flannelmouth suckers (7,347), humpback chub (2,606), bluehead suckers (2,243), and speckled dace (1,072). The contribution of rainbow trout to the overall catch composition (native and nonnative species) fell steadily throughout the study period from a high of approximately 90% in January 2003 to less than 10% in August 2006 (Figure 3). Overall, the catch percentage contributed by nonnative fish exceeded 95% in January 2003 and fell to less than 50% after July 2005. Owing to particularly large catches of flannelmouth suckers and humpback chub in September 2005, the nonnative contribution to the catch in that month was less than 20%. Although the catch of nonnative fish generally fell during the study, catches of nonnative cyprinids (dominated by fathead minnow) increased in 2006.

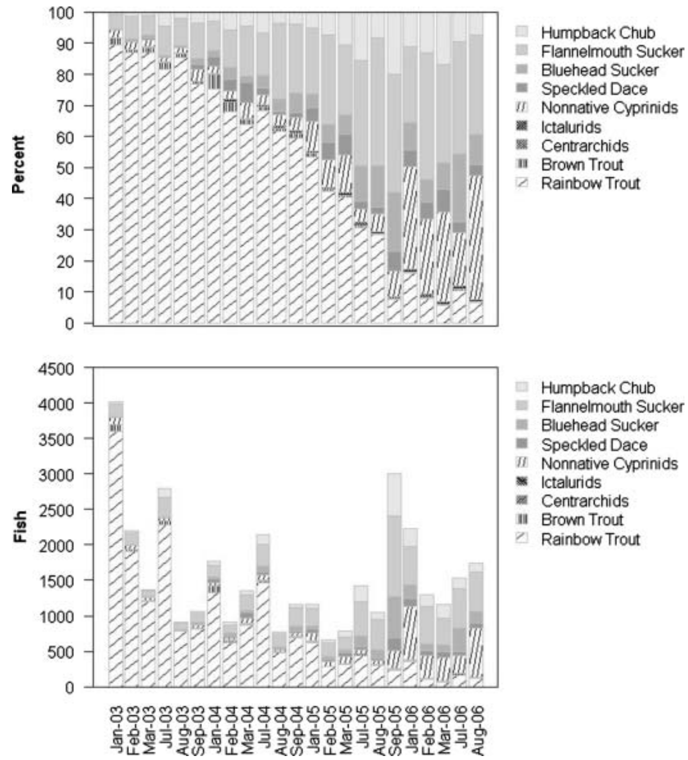

FIGURE 3. Upper panel, percent composition and lower panel, number of fish (by species or species group) captured with electrofishing in the mechanical removal reach of the Colorado River during 2003–2006 (nonnative cyprinids = fathead minnow, common carp, and red shiner; ictalurids = black bullhead and channel catfish; centrarchids = green sunfish, smallmouth bass, and striped bass).

Based on HBM, the estimated abundance of rainbow trout in the entire removal reach ranged from a high of 6,446 (95% credible interval [CI] = 5,819–7,392) in January 2003 to a low of 617 (95% CI = 371–1,034) in February 2006, which translates to a 90% reduction over this time period (Table 2). Between February 2006 and the final removal effort in August

TABLE 1. Electrofishing catch of native and nonnative fish species in the mechanical removal reach of the Colorado River within Grand Canyon, Arizona, 2003–2006.

		Native species[a]					Nonnative species[b]										
Trip date	Removal passes	BHS	FMS	HBC	SPD	SUC	BBH	BNT	CCF	CRP	FHM	GSF	PKF	RBT	RSH	SMB	STB
Jan 2003	5	8	188	26	7	2		87		80	17		1	3,605			
Feb 2003	5	18	165	26	2			24		33	21			1,913	1		
Mar 2003	5	11	89	13	8		3	21	1	22	8		1	1,195	1		
Jul 2003	5	12	267	124	6	3	4	63		29	4			2,278	1		
Aug 2003	2	4	79	17		5	2	12		14				779			
Sep 2003	3	19	119	37	18	4	1	11		31	4		2	818	1		
Jan 2004	4	32	169	51	53	3	3	88		23	18			1,330			
Feb2004	4	37	110	52	34		9	29	1	9	13			622			
Mar 2004	5	24	218	61	92	3	5	22		18	44		6	867			
Jul 2004	6	84	296	142	47		9	29	1	26	32		9	1,464	3		
Aug 2004	4	33	190	27	7		6	7		16	6		3	480	2		
Sep 2004	4	72	258	43	19		11	17		29	13			687	5		
Jan 2005	4	54	244	61	52		8	14		27	72		1	623	9		
Feb 2005	4	38	191	49	39		3	4	1	14	39		2	283	2		
Mar 2005	4	51	176	82	51		8	4		14	73		3	318	4		
Jul 2005	4	159	480	220	38	1	17	9	2	45	9	1		432	2		2
Aug 2005	4	124	419	86	24	24	9	4		36	17		1	295	4		
Sep 2005	4	576	1,140	600	187	4	14	7		47	190			230	15		
Jan 2006	4	197	545	249	115	1	23	9		38	685			357	13		
Feb 2006	4	98	529	171	70		15	5		10	300		1	103			
Mar 2006	4	96	365	196	84		12	2		8	322	1	1	66	2		
Jul 2006	4	331	554	145	56		15	8		64	192		2	159	2		
Aug 2006	4	165	556	128	63	9	13	3	1	169	490		34	116	1	1	
Total		2,243	7,347	2,606	1,072	59	190	479	7	802	2,569	2	67	19,020	68	1	2

[a]BHS = bluehead sucker; FMS = flannelmouth sucker; HBC = humpback chub; SPD = speckled dace; SUC = unidentified sucker.

[b]BBH = black bullhead *Ameiurus melas*; BNT = brown trout; CCF = channel catfish *Ictalurus punctatus*; CRP = common carp *Cyprinus carpio*; FHM = fathead minnow *Pimephales promelas*; GSF = green sunfish *Lepomis cyanellus*; PKF = plains killifish *Fundulus zebrinus*; RBT = rainbow trout; RSH = red shiner *Cyprinella lutrensis*; SMB = smallmouth bass *Micropterus dolomieu*, STB = striped bass *Morone saxatilis*.

2006, the estimated rainbow trout abundance increased by approximately 700 fish (i.e., from 617 in February to 1,297 [95% CI = 481–2,825] in August). Although this increase was more than double the February 2006 estimate, the August 2006 estimate was much less precise. The estimated abundance in the downstream stratum of the mechanical removal reach was approximately 30% of the abundance estimated for the upper stratum (Figure 4). The estimated capture probability ranged from 4% to 34% in the upper stratum (Figure 4) and was generally less in the lower stratum (range = 2–19%).

Estimates of rainbow trout net immigration rate indicated that the fish were moving into both strata within the removal reach at a higher rate during 2003–2004 than during 2005–2006 (Figure 5). Additionally, net immigration was apparently lowest in July–September and highest in January–March, particularly during 2003. During 2005–2006, a net immigration rate different than zero was suggested for only two time intervals in the downstream stratum and for only one time interval in the upstream stratum. However, because these estimates are the difference between two distributions (each with its own error), the net immigration estimates were imprecise for many of the time periods (Figure 5).

In total, 11,221 fish representing eight species were captured during control reach sampling (Table 3). The majority of fish captured were rainbow trout (95%), followed by flannelmouth suckers (3%) and brown trout (1%). A general pattern of decreasing rainbow trout abundance was observed throughout the study, particularly after spring 2005 (Figure 6). Initial (l_1) and secondary (l_2) monthly tag loss rate estimates were 0.11 (95% CI = 0.0–0.43) and less than 0.01 (95% CI = 0.00–0.05), respectively, suggesting that most tag loss occurred shortly after tagging. Rainbow trout abundance within the control reach was estimated at between 5,000 and 10,600 fish during 2003–2004 and between 2,000 and 5,300 during 2005–2006 (Table 4; Figure 6). This analysis in combination with the catch rate assessment (Figure 6) suggests that rainbow trout abundance declined by

TABLE 2. Estimated abundance of rainbow trout in the mechanical removal reach of the Colorado River at the beginning of each month, 2003–2006 (95% CI = 95% Bayesian credible interval). The upper stratum includes sections A and B; the lower stratum inclueds sections C, E, and F (Figure 2).

	Total reach abundance		Upper stratum abundance		Lower stratum abundance	
Trip date	*N*	95% CI	*N*	95% CI	*N*	95% CI
Jan 2003	6,446	5,819–7,392	4,977	4,519–5,640	1,469	1,168–1,996
Feb 2003	3,073	2,802–3,492	2,437	2,226–2,778	637	489–879
Mar 2003	2,372	1,939–3,014	2,023	1,606–2,671	349	289–485
Jul 2003	5,253	4,249–7,616	3,614	3,164–4,183	1,639	902–3,776
Aug 2003	1,574	1,253–2,199	1,237	1,001–1,652	336	178–845
Sep 2003	3,008	1,964–4,197	2,399	1,438–3,507	609	345–1,187
Jan 2004	2,207	1,953–2,635	1,684	1,472–2,002	523	385–851
Feb 2004	1,611	1,098–2,809	845	732–1,026	767	293–2,009
Mar 2004	1,425	1,227–1,710	1,075	925–1,325	350	269–516
Jul 2004	3,445	2,533–5,284	1,718	1,566–1,925	1,727	856–3,627
Aug 2004	932	734–1,536	677	515–1,266	255	183–455
Sep 2004	2,459	1,647–3,752	1,980	1,296–3,290	479	199–1,060
Jan 2005	989	819–1,275	722	675–786	266	115–539
Feb 2005	869	519–1,785	386	317–516	483	142–1,388
Mar 2005	975	636–1,548	782	498–1,377	193	80–427
Jul 2005	1,626	742–5,837	736	560–1,085	891	128–5,056
Aug 2005	690	498–1,080	415	339–549	275	115–638
Sep 2005	697	460–1,291	411	288–601	286	108–893
Jan 2006	710	514–1,121	502	386–719	208	100–580
Feb 2006	617	371–1,034	479	258–879	138	61–290
Mar 2006	669	280–1,460	367	154–860	302	69–992
Jul 2006	726	376–2,210	538	251–1,853	188	89–410
Aug 2006	1,297	481–2,825	767	262–2,087	530	136–2,090

one-half or more between the first and last 2 years of the study. Capture probability ranged from 3% to 13% and showed no strong temporal pattern (Figure 6). Estimated monthly survival rate ranged from a low of approximately 0.72 to a high approaching 1.00. The lowest survival rates were observed during 2004–2005 (Figure 6).

The abundance of rainbow trout declined both in the mechanical removal reach and in the control reach over the study period; however, the pattern of decline was dissimilar between reaches. In the mechanical removal reach, the largest decline (62%) occurred between January 2003 and September 2004 and the decline was relatively constant during the remainder of the study (Figure 7). In contrast, rainbow trout abundance in the control reach declined at an approximately constant rate throughout the study. These patterns indicate that removal efforts affected abundance in the mechanical removal reach predominantly during 2003 and 2004.

Another difference between the mechanical removal and control reaches involved the seasonal patterns in rainbow trout abundance. In the removal reach, a pattern of declining abundance during each 3-month period of removal efforts (e.g., January–March) was followed by an increase in abundance at the beginning of the next series of removal efforts (e.g., July–September), particularly during 2003–2004 (Figures 4, 7). This pattern would be expected if the removal rate was greater than the immigration rate only during each removal series. This pattern was not evident in the control reach for either the catch rate estimate or the abundance estimate (Figures 6, 7), suggesting that mechanical removal was influencing the abundance of rainbow trout in the removal reach. Overall, these observations suggest that starting in 2005, there was a systemwide disruption in the pattern of net immigration, most likely from upstream sources, into the removal reach and possibly into the control reach.

DISCUSSION

Mechanical Removal: Effective Program?

Our results suggest that the mechanical removal program was successful in reducing the abundance of nonnative fishes, particularly rainbow trout, in a large segment of the Colorado River in Grand Canyon. However, maintenance of low rainbow trout abundance in the removal reach was also facilitated by reduced immigration rates during 2005–2006 and a systemic decline in rainbow trout abundance. A common feature of this study and other successful attempts to apply nonnative

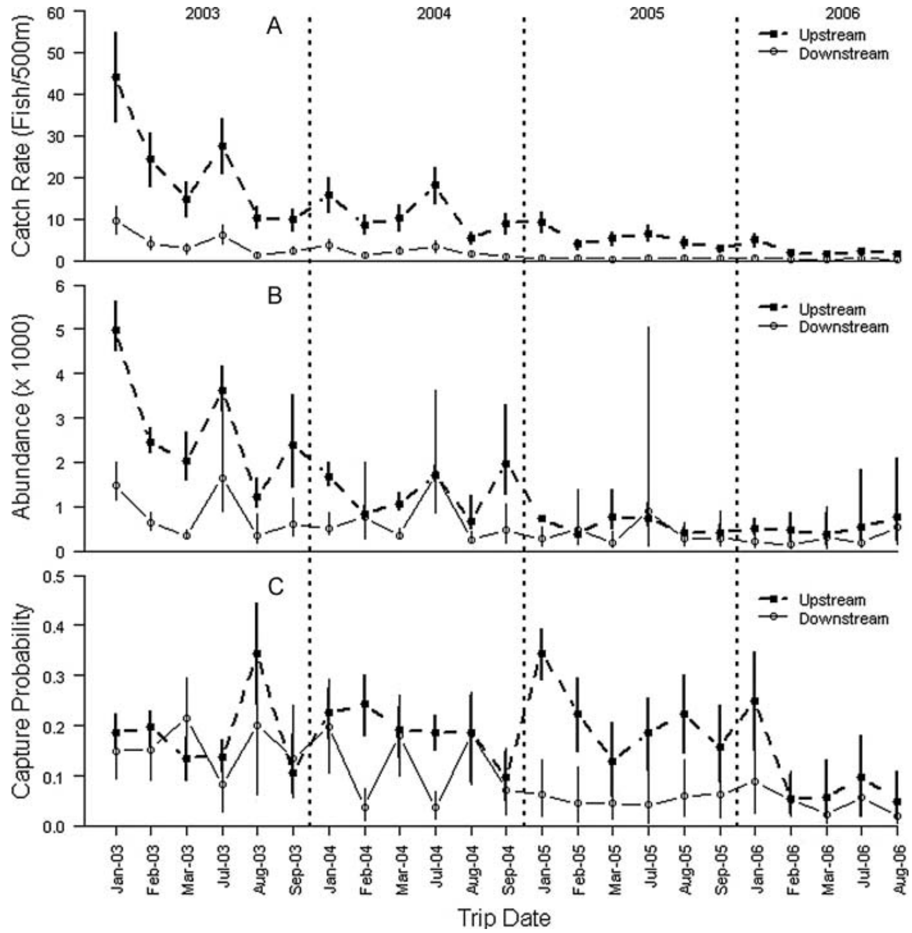

FIGURE 4. Estimated monthly **(A)** catch rate, **(B)** abundance, and **(C)** capture probability of rainbow trout in upstream and downstream strata (see Methods) within the mechanical removal reach of the Colorado River, 2003–2006. Error bars represent 95% Bayesian credible intervals.

mechanical removal is the significant and sustained removal effort. Bigelow et al. (2003) demonstrated that population-level changes were not evident in removal efforts aimed at nonnative lake trout *Salvelinus namaycush* in Yellowstone Lake until the latter years of a 4-year study, when additional support for the project (e.g., funding and equipment) allowed for increases in total removal effort and efficiency. Similarly, objectives for the removal of nonnative brook trout *Salvelinus fontinalis*, golden trout *Oncorhynchus mykiss aguabonita*, and rainbow trout from small, high-altitude lakes in the Sierra Nevada were achieved with year-round gill-net fishing (Knapp et al. 2007). In combination with increased predation from native predators, Hein et al. (2006, 2007) demonstrated effective control of nonnative rusty crayfish *Orconectes rusticus* by using mechanical removal but only with sustained and significant removal effort. The need for sustained "maintenance" control of nonnative species is typical (Pine et al. 2007) as many such species demonstrate high resilience and are well adapted to their introduced environment, as evidenced by their invasion success (often human aided) and the warranted need for management action. Considering the high net immigration rates of rainbow trout into the mechanical removal reach during 2003–2004, much smaller and possibly undetectable reductions in overall abundance would have been realized if removal efforts had been significantly less (e.g., 1 removal trip/year).

Serendipitous Timing: What Led to the Decline of Rainbow Trout in the Control Reach?

The decline of rainbow trout abundance observed in the control reach was probably precipitated by at least two factors. First, rainbow trout abundance in the Lees Ferry reach (i.e., from GCD at RKM −25.5 to Lees Ferry at RKM 0) of the Colorado River increased during approximately 1992–2001 and then steadily fell during 2002–2006 (Makinster et al. 2007). With the exception of limited spawning activity in select tributaries of the Colorado River in Grand Canyon, rainbow trout reproductive activity appears to be limited mainly to the Lees Ferry reach (Korman et al. 2005). Examination of length frequency distributions of rainbow trout captured by electrofishing from GCD to RKM 90.8 during 1991–2004 also supports the idea that Lees Ferry is the primary spawning site, as the juvenile size-class of

TABLE 3. Electrofishing catch of native and nonnative fish by species in the control reach of the Colorado River, 2003–2006. Species codes are defined in Table 1.

		Native species					Nonnative species			
Trip date	Control sites	BHS	FMS	HBC	SPD	SUC	BBH	BNT	CRP	RBT
Jan 2003	25		1					10	1	444
Feb 2003	24		1					8		548
Mar 2003	24		1					5		888
Jul 2003	24		2					8	1	416
Aug 2003	11							4	1	256
Sep 2003	24		7			1		7	2	1,036
Jan 2004	24							5		702
Feb 2004	24		1					3	1	434
Mar 2004	24	2	3					14		851
Jul 2004	24		9	1				2		491
Aug 2004	24		6					9		346
Sep 2004	24		4			2		8	1	498
Jan 2005	24		1					1		503
Feb 2005	24		4		1			9		476
Mar 2005	24	1	5					9		540
Jul 2005	24	1	34					11		277
Aug 2005	24		21					5		332
Sep 2005	24	1	72		1			2	1	284
Jan 2006	24	2	31		1			2	1	277
Feb 2006	24		53					4	2	243
Mar 2006	24		23					5		336
Jul 2006	24	5	47	1	12			2	5	176
Aug 2006	24	10	52	1			1	1	1	294
Total		22	378	3	15	3	1	134	17	10,648

rainbow trout is largely absent from collections downstream of RKM 16.1 (Coggins and Yard 2010). Thus, it is reasonable to conclude that at least for the last 10–15 years, the natal source of most rainbow trout in this system has been the Lees Ferry reach, and the decline beginning in 2002 may have reduced dispersion to downstream locations.

The second possible factor in the decline of rainbow trout abundance within the control reach is that from September 2004 to January 2005, the discharge and sediment load from the Paria River (an ephemeral but major tributary near RKM 0) increased to the point outlined by GCDAMP to trigger an experimental flow from GCD as a potential strategy for rebuilding depleted sandbars in the Colorado River (U.S. Geological Survey, unpublished data). It is possible that the high-flow event and the associated period of elevated turbidity influenced rainbow trout density downstream of the Paria River confluence, perhaps through elevated mortality rates. Estimated rainbow trout survival rates in the control reach generally support the notion that rainbow trout experienced diminished survival rates during late 2004 and early 2005 (Figure 6).

This hypothesis is further supported by considering that the density of rainbow trout is not uniform in the Colorado River below GCD and that distribution patterns are likely influenced by food resources and foraging efficiency (Gloss and Coggins 2005). Rainbow trout density generally declines with downstream distance from GCD but exhibits punctuated declines below the confluences of the Paria River and the LCR. The densities of algae and invertebrates in the Colorado River also decline along this gradient (Kennedy and Gloss 2005), suggesting a possible linkage between distance from the dam and primary production. A major factor that is likely influencing these algal and fish distributional patterns is the sediment delivery from tributaries and the subsequent effects of elevated turbidity in downstream sections of the Colorado River. Yard (2003) demonstrated that these tributary inputs of sediment periodically limit the availability of light for aquatic primary production. Trout are predominantly sight feeders; thus, high turbidity and reduced prey levels are likely to adversely affect foraging efficiency by decreasing prey encounter rates (Barrett et al. 1992).

Other Species

Beginning in September 2005, large increases in the catch of nonnative fathead minnow and black bullheads were observed

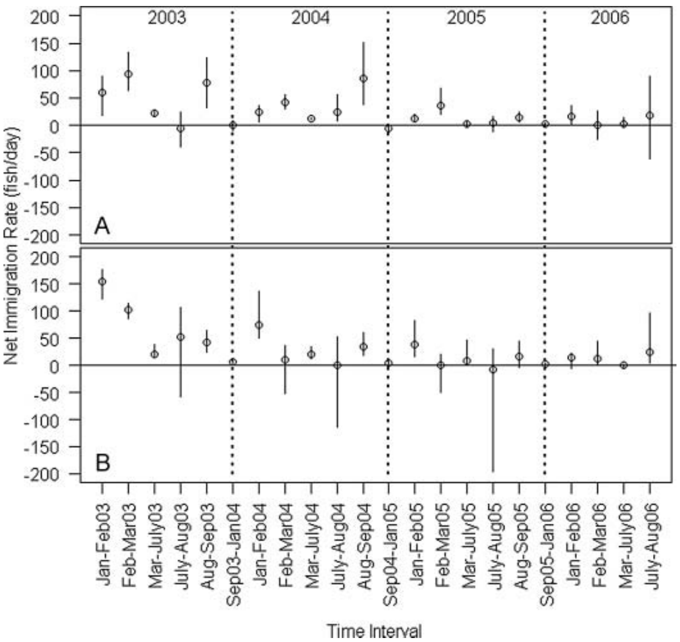

FIGURE 5. Net immigration rate of rainbow trout into the **(A)** upstream stratum and **(B)** downstream stratum within the mechanical removal reach of the Colorado River between January 2003 and August 2006. Positive values of net immigration rate imply that the fish were moving into the removal reach; negative values imply that fish were moving out of the reach. Error bars represent 95% Bayesian credible intervals.

TABLE 4. Estimated abundance of rainbow trout in the control reach of the Colorado River at the beginning of each month, 2003–2006 (95% CI = 95% profile likelihood confidence interval).

	Total abundance	
Trip date	*N*	95% CI
Feb 2003	5,058	3,500–7,262
Mar 2003	10,571	8,064–14,136
Jul 2003	10,106	6,572–16,367
Aug 2003	8,819	5,494–13,593
Sep 2003	8,051	6,004–10,860
Jan 2004	9,952	6,491–15,662
Feb 2004	8,998	5,570–15,024
Mar 2004	7,939	5,379–11,798
Jul 2004	8,758	5,895–13,254
Aug 2004	6,981	4,519–11,171
Sep 2004	7,208	4,733–10,795
Jan 2005	4,138	2,853–6,090
Feb 2005	4,527	3,344–6,202
Mar 2005	5,253	3,939–6,907
Jul 2005	3,163	1,967–5,245
Aug 2005	3,247	2,126–4,900
Sep 2005	2,955	1,877–4,604
Jan 2006	4,032	2,502–6,694
Feb 2006	2,992	1,957–4,804
Mar 2006	2,518	1,594–3,443
Jul 2006	2,131	1,113–4,062

in comparison with the previous 17 trips, suggesting that immigration, survival, or both increased in the mechanical removal reach for these species. Since fathead minnow and black bullheads have not been captured with any regularity in the control reach or in other sampling conducted upstream of RKM 70.8 (U.S. Geological Survey, unpublished data), it is reasonable to conclude that their source is not upstream. Stone et al. (2007) documented the presence of these species and other warmwater nonnative species in the LCR approximately 132 km upstream from the confluence and suggested that this tributary was the probable source of fathead minnow, black bullheads, and six other nonnative fishes that were frequently encountered in the lower LCR and the Colorado River. Thus, one possible explanation for the elevated catch of fathead minnow and black bullheads in the mechanical removal reach is an elevated emigration rate of these fishes from the LCR. Alternatively, increasing water temperature, particularly in 2005 (Figure 8), and the concurrent reductions in rainbow trout biomass may have influenced the survival and activity of these fishes, causing them to be more abundant and more susceptible to capture.

Recommendations for Future Mechanical Removal Operations

We recommend that further effort be spent in more thoroughly documenting the preferred habitats of target nonnative species. This information would be useful in effectively distributing removal effort among habitat types that contain the highest densities of nonnative species. Bigelow et al. (2003) described the use of hydroacoustic surveys to better target areas of high lake trout abundance and thereby increase the efficiency of the control program. Another possible technique to better determine these high-density areas in the mechanical removal reach would be to employ a finer-scale, shoreline-habitat-based delineation of removal sites rather than the coarse 500-m sites used in the present study. Serial depletion data could then be analyzed with the HBM to include a habitat covariate for density. This approach has been successfully used to describe patterns in the density of organisms as a function of habitat characteristics (Royle and Dorazio 2006).

Adaptive Management in Grand Canyon: The Future

This study documents the implementation of an ecosystem-scale adaptive management experiment aimed at testing the efficacy of a particular management policy (i.e., nonnative fish control) in order to improve the status of native fish resources in Grand Canyon. Although this study focuses on the efficacy of implementing the policy, the more interesting, important, and difficult questions are related to evaluating whether the policy will have the intended effect. If nonnative salmonids are a significant, uncompensated mortality source for native fish that are attempting to rear in the main-stem Colorado River, then (1) the

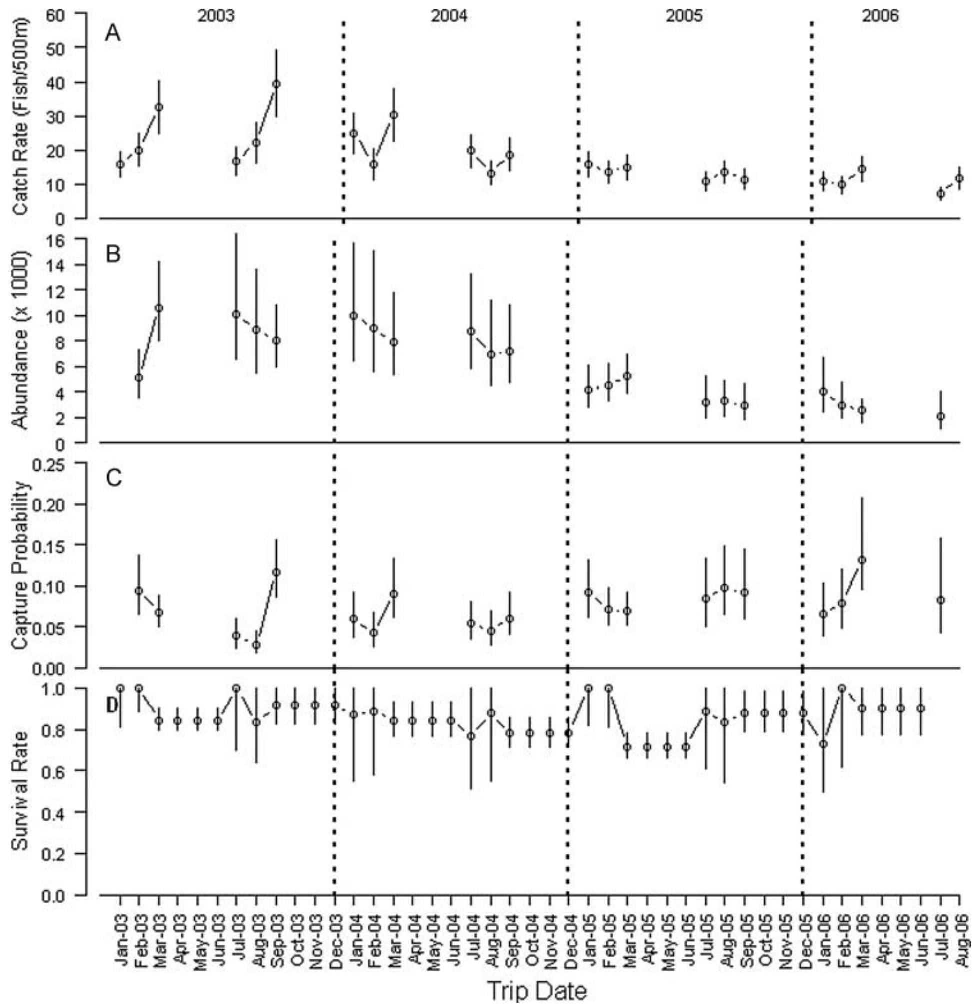

FIGURE 6. Estimated monthly **(A)** catch rate, **(B)** abundance, **(C)** capture probability, and **(D)** survival rate of rainbow trout in the control reach of the Colorado River, 2003–2006. Error bars represent 95% profile likelihood confidence intervals.

survival rate and abundance of juvenile native fish in the main stem should have increased during 2003–2006 and (2) humpback chub recruitment associated with the 2003–2006 brood years should increase.

There are some indications that the abundance of native fishes increased in the removal reach during 2003–2006 (Figure 3), suggesting increased survival rate, increased production of juvenile fish, or both. Additionally, the most recent humpback chub stock assessment suggests an increasing trend in recruitment beginning with the brood years after approximately 1998, and the 2003 brood year appears to be particularly strong (Figures 8–9 in Coggins and Walters 2009). However, Coggins and Walters (2009) cautioned that recruitment is particularly difficult to estimate for this population, so subsequent assessments that produce recruitment estimates for the 2005–2006 brood years will be critical for policy evaluation. While these early signs of increasing survival and recruitment are encouraging, they are not adequate to infer the success of the nonnative removal policy—primarily because of the nearly perfect correlation between the unplanned increases in release water temperature and the magnitude of the nonnative fish reduction (Figures 4, 8). Since water temperature is also a controlling factor affecting humpback chub growth and survival (Gloss and Coggins 2005; Coggins and Pine 2010), it is possible that increased water temperature could have led to increased native fish rearing success even without concurrent nonnative species control efforts. As such, it is not yet possible to singly evaluate the relative contribution of either factor to juvenile humpback chub rearing success or recruitment. However, current information does support continued evaluation of a management policy of low nonnative species abundance and increased water temperature.

Mechanical removal was effective at reducing nonnative salmonid abundance based on a very intensive 4-year field effort. However, this success appears to have been aided by a systemwide decline in rainbow trout abundance, which resulted in lower immigration into the removal reach during the final 2 years

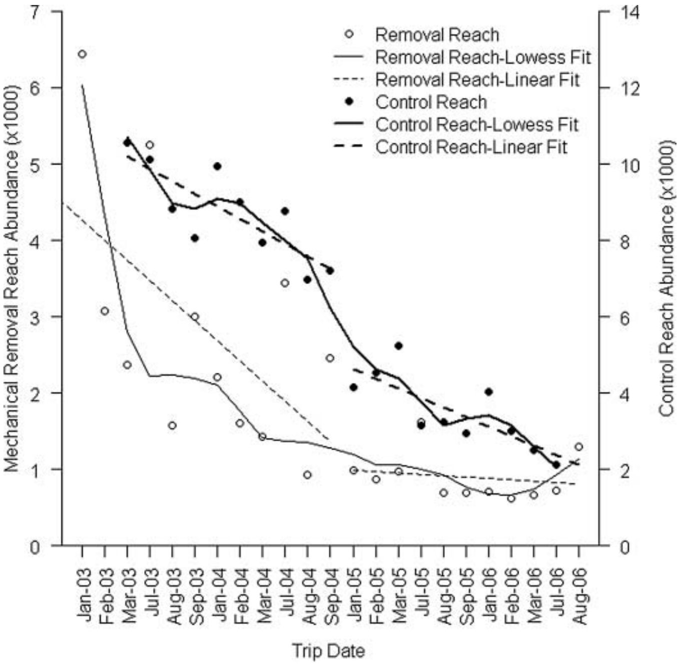

FIGURE 7. Estimated rainbow trout abundance in the mechanical removal and control reaches of the Colorado River at the beginning of each trip during 2003–2006. The solid lines represent locally weighted polynomial regressions (lowess) fitted to each time series. The dashed lines represent linear regressions fitted separately to the 2003–2004 and 2005–2006 portions of the time series.

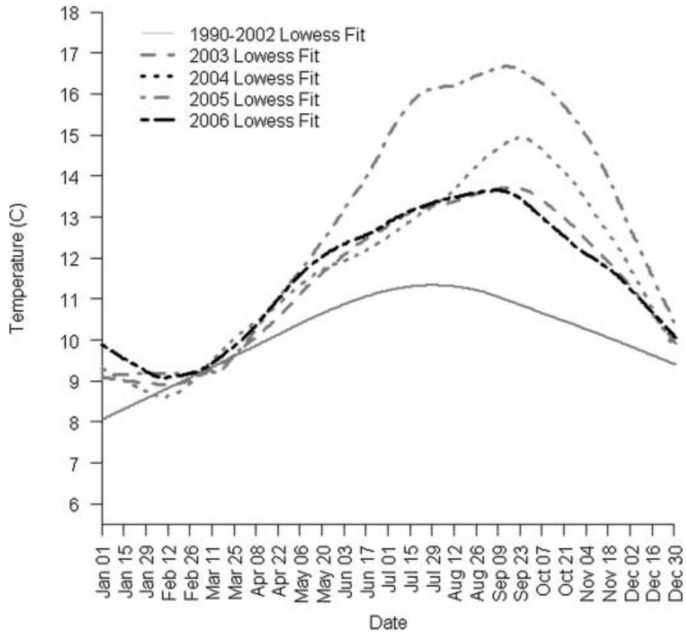

FIGURE 8. Daily mean water temperature (°C) observed in the Colorado River (~river kilometer 99.2) during 1990–2006. Lines indicate locally weighted polynomial regression (lowess) fits to the indicated data set.

of the study. We are uncertain whether the level of effort we deployed would be as effective at sustaining depressed rainbow trout numbers during a period of increasing rainbow trout abundance in the Lees Ferry Reach; however, we suspect that it would not. With the information on rainbow trout capture probability collected during this study, it is a simple task to compute the frequency and intensity of mechanical removal efforts that are required to counteract any particular immigration rate into the removal reach. For example, if future removal efforts consist of four depletion passes with a 15% capture probability, each trip will remove approximately 50% of the rainbow trout that are present at the beginning of the trip. If the immigration rate and the time lag until the next removal effort allow an equivalent number of rainbow trout to migrate back into the reach, the abundance will be held approximately constant from the beginning of one trip to the next. If the immigration rate declines or if the time interval between removal efforts is shortened, then the abundance will tend to decrease. Alternatively, if the immigration rate increases or if the time interval between removal efforts is lengthened, the abundance will tend to increase. Thus, the efficacy of removal will always be dependent on immigration rate, capture probability, and the frequency and intensity of removal efforts. As such, the efficacy of a particular control strategy (i.e., frequency and intensity of removal efforts) is dynamic and must be periodically evaluated based on abundance estimates and removal numbers to assess whether reduction goals are being met.

Recent data on rainbow trout abundance in the Lees Ferry and control reaches indicate that an increase in abundance is underway (Makinster et al. 2007). We predict that this increase will result in increased rainbow trout abundance in the removal reach via an increased immigration rate. If future GCDAMP objectives call for the maintenance of depressed rainbow trout abundance in the removal reach, some additional control effort will probably be required. However, the nonnative species control program implemented during 2009 represented an 80% reduction in effort as compared with the annual effort expended during 2003–2006. Because the immigration rate was probably higher than that observed during the period of this study, the 2009 reductions in nonnative abundance were probably short lived. Thus, recent removal efforts are unlikely to meet GCDAMP objectives unless such efforts are conducted in concert with flow regimes that are targeted at reducing (or at least not stimulating) rainbow trout recruitment in the Lees Ferry reach (Korman et al. 2005).

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