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RESEARCH ARTICLE

Effects of Flow Restoration and Exotic Species Removal on Recovery of Native Fish: Lessons from a Dam Decommissioning

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Abstract

Flow diversion and invasive species are two major threats to freshwater ecosystems, threats that restoration efforts attempt to redress. Yet, few restoration projects monitor whether removal of these threats improve target characteristics of the ecosystem. Fewer still have an appropriate experimental design from which causal inferences can be drawn as to the relative merits of removing exotic fish, restoring flow, or both. We used a dam decommissioning in Fossil Creek, Arizona, to compare responses of native fish to exotic fish removal and flow restoration, using a before-after-control-impact design with three impact treatments: flow restoration alone where exotics had not been present, flow restoration and exotic fish removal, and flow restoration where exotics remain and a control reach that was unaffected by restoration actions. We show that removal of exotic fish dramatically increased native fish abundance. Flow restoration also increased native fish abundance, but the effect was smaller than that from removing exotics. Flow restoration had no effect where exotic fish remained, although it may have had other benefits to the ecosystem. The cost to restore flow ($12 million) was considerably higher than that to eradicate exotics ($1.1 million). The long-term influence of flow restoration could increase, as travertine dams grow and re-shape the creek increasing habitat for native fish. But in the 2-year period considered here, the return on investment for extirpating exotics far exceeded that from flow restoration. Projects aimed to restore native fish by restoring flow should also consider the additional investment required to eradicate exotic fish.

Key words: **dam decommissioning, exotic fish removal, invasive species, native fish, stream restoration, water diversion.**

Introduction

Stream ecosystems worldwide are threatened by water extraction, habitat alteration, spread of invasive species, and decline in water quality (Allan & Flecker 1993; Dynesius & Nilsson 1993; Richter et al. 1997). Freshwater species are among the most endangered groups of organisms worldwide (Miller et al. 1989; Williams & Miller 1990) with native fish in arid regions particularly threatened (Minckley & Deacon 1991; Moyle 1995; Olden & Poff 2005). More than $10 billion have been spent on stream restoration in the United States in the last decade, yet fewer than 10% of projects monitor if interventions are successful (Bernhardt et al. 2005; Palmer et al. 2005). Treating large restoration projects and other management interventions as ecological experiments is arguably the best way to understand ecosystems at scales relevant to policy (MacMahon & Holl 2001; Hart et al. 2002; Poff et al. 2003).

Although many streams face multiple threats, their relative magnitudes and the costs to reverse them are rarely quantified. This study capitalized on a large restoration program surrounding a hydropower decommissioning in Fossil Creek, Arizona, to illustrate how a simple cost-benefit analysis can guide restoration investments. Restoration included returning flow to the entire stream below the now defunct hydropower diversion dam and eradicating exotic fish from a 15-km subreach (Fig. 1). Fossil Creek is a model system to compare the costs and benefits of restoration interventions because (1) research prior to restoration estimated the magnitude of two ubiquitous threats (water diversion and exotic fish), yielding clear predictions of native fish responses to reversal of each threat; (2) the monetary costs of flow restoration and exotic fish removal were independent, enabling a simple cost-benefit analysis; and (3) native fish densities were measured before and after restoration to test predictions and quantify the benefits to native fish of restoration investments.

This study addressed the following questions: How did native fish respond to flow restoration and the removal of exotic species? What were the relative costs and benefits

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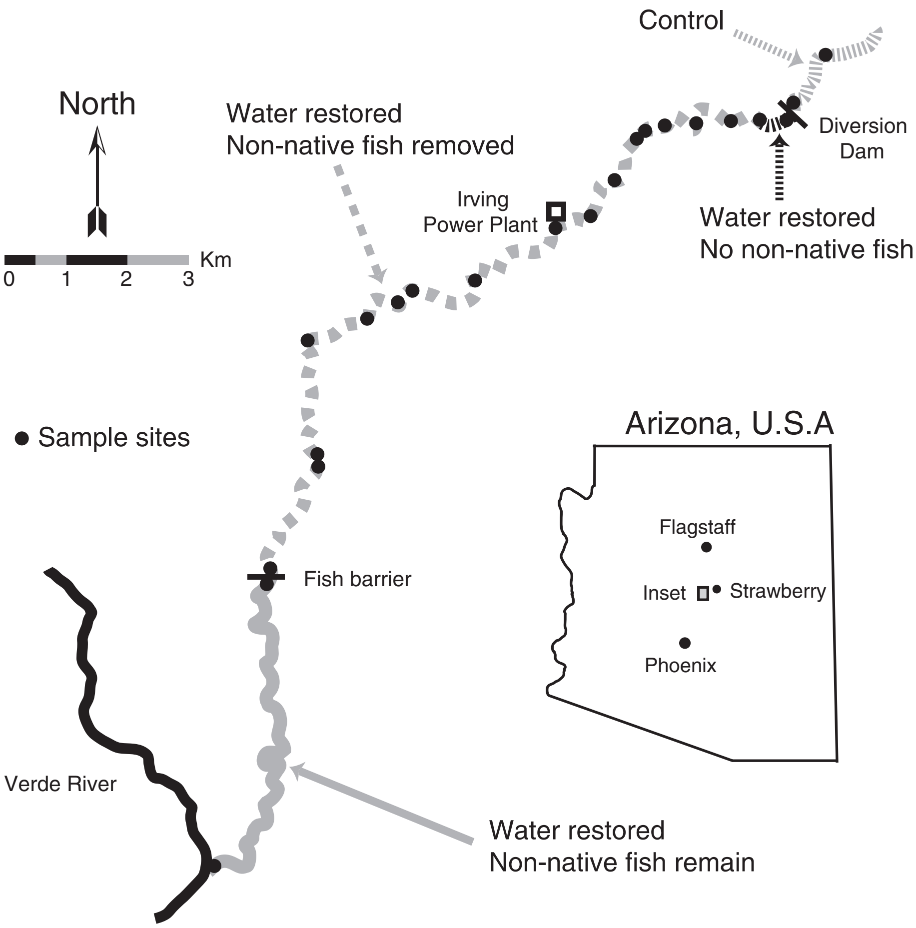

Figure 1. Map of the study area showing the now defunct Irving Power Plant. From 1909 to 2005, the majority of flow was diverted from the river, at the diversion dam, through a flume to two power plants, Irving and Childs. In 2004, exotic fish were removed from river km 1 to 16 where a fish barrier was constructed. Flow was restored in June 2005. The control reach above the dam always experienced full flows and was not invaded by exotic fish. Restoration treatments include (1) above dam control with full flows and no non-native fish; (2) flow restored—no non-native fish; (3) flow restored non-native fish removed; and (4) flow restored and non-native fish remain. Sample sites are denoted with a filled circle.

of flow restoration and exotic species removal on recovering native fish? Did pre-restoration threats assessments predict actual responses? Adaptive management requires that management proposals are accompanied by concise hypotheses predicting how ecosystems will respond to management interventions (Holling 1973). Yet, there are few examples in river restoration which complete a full adaptive management cycle from generating hypotheses about how ecosystems will respond to interventions, evaluating and learning from actual responses and applying the knowledge to future management actions both in the system that is tested and in other systems (Palmer et al. 2005). Here, we complete a full cycle using pre-restoration studies to generate predictions of how native fish would respond to increased flow and removal of exotics coupled with a cost-benefit analysis relating financial investments with fish recovery. Results from this study have the potential to guide river restoration projects where managers are considering improving habitat quality and or removing exotic fish.

Methods

Experimental Design

We used a modified before-after-control-impact (BACI) design to measure fish responses to restoration (Stewart-Oaten et al. 1986; Underwood 1991; Underwood 1994; Schmitt & Osenberg 1996). This design compared fish responses in reaches that experienced restoration actions with a control reach with no interventions. BACI designs are used to differentiate natural variability in fish densities from variability likely caused by restoration actions (Schmitt & Osenberg 1996). This study revisited predictions made and published as technical reports prior to restoration, as a "threats assessment" conducted in conjunction with the environmental impact assessment, required by the Federal Energy Regulatory Commission for the hydropower dam decommissioning (Marks et al. 2003; Marks et al. 2005). Predictions were based on fish distributions and stable isotope analysis of food web structure in pristine and disturbed reaches of Fossil Creek prior to restoration.

Study Site

The hydrology of the river was disturbed from 1915 to 2005 because a diversion dam and flume built less than 1 km downstream of the source springs diverted most of the flow to make hydroelectric power (Fig. 1). The reach above the dam remained relatively pristine with full flows (1,218 $L\,s^{-1}$) and no exotic fish, and served as a reference site. Water diversion below the dam created two distinct flow regimes. The 6.5 km reach directly below the dam received only seepage flow (5.6 $L\,s^{-1}$). The majority of flow was diverted through a flume to the Irving Power Plant where a portion was returned to the stream for a combined flow of 62.2 $L\,s^{-1}$ and the remaining flow was re-diverted to a second power plant (Childs) on the Verde River. This lower reach of partially diverted flows continued for 15 km to the confluence with the Verde River (Fig. 1). Exotic fish (primarily *Micropterus dolemieu* [smallmouth bass] and *Lepomis cyanellus* [green sunfish]), likely invaded from the Verde River, and were present in the lower 22 km of the river. The distribution of flows and non-native species prior to restoration resulted in three distinct reaches (1) full flows (1,218 $L\,s^{-1}$) and no non-native fish (control reach); (2) extreme water diversion with non-natives absent; (3) extreme and partial water diversion with non-natives present. Flow was restored to reaches two and three and non-native fish were removed from part of reach three, creating four restoration treatments: (1) control; (2) flow restored—no non-native fish; (3) flow restored—non-native fish removed, and flow restored non-native fish remain.

Unlike many dams, the Fossil Creek dam creates a very small reservoir (<1 acre), because water was immediately diverted through a flume and transported to two hydropower dams. Geomorphic studies indicate that the effects of the dam on flow, substrate, and channel width only extend 200 m above the dam (Monroe 2002; Schlinger et al. 2002). Most of the control reach was above this section and was not noticeably influenced by the dam. The dam was in place through the duration of this study so the only changes above the dam are due to natural variation. To test whether dependent variables in restored sites converge on the control, we used a two-way analysis of variance (ANOVA) designed to accompany the extended BACI design, where sample sites are nested within restoration treatments, and time (annual samples) is nested within "before or after" treatment (Keough & Quinn 2000). Although some researchers argue for using additional rivers as controls in BACI designs, there are no streams in the region with an intact assemblage of native fish. Because the focus of this research is to study changes in native species before and after restoration, it is imperative that species composition is similar among treatments. Fossil Creek has five native fish species, most of which are rarely found in nearby streams. Fish surveys conducted by our research team before (2004) and after (2006) restoration, in nearby streams, yielded only a few individuals of one native species, *Pantosteous clarki* (desert sucker) with more than 98% non-native fish. Sample sizes of native fish in these streams would be too low to determine how they varied during the duration of this study. Similarly, macroinvertebrate assemblages in Fossil Creek differ from those in other nearby streams (LeRoy & Marks 2006) making it difficult to compare food web structure across streams.

Pre-Restoration Threats Assessment. To estimate the relative magnitude of exotic species and flow diversion, we compared fish densities and food web structure, using stable isotopes, in the control reach with the disturbed reaches. Although this correlative design is not conducive to replication, it provides the best estimate available of the magnitude of threats in this system. We predicted that native fish densities would be reduced by both flow diversion and exotic species and that exotic species would alter native fish diets.

Restoration Interventions and Costs. Fifteen kilometers of stream was treated with antimycin A, to remove exotic fish, in fall 2004, 6 months before flow was restored (Weedman et al. 2005). Approximately 1,900 native fish were salvaged before chemical treatment, transferred by helicopter to a holding facility near the Irving Power Plant, and released back into the river following chemical treatment (Table 1). The number of fish captured is presented in Table 1. Because there were a few mortalities, the number of fish re-introduced was slightly lower than the number captured. Mortality was estimated at lower than 10% for all species (Weedman et al. 2005). A fish Aabarrier was built near river km 16 to prevent exotic fish from re-entering the stream, leaving the top 16 km of stream free of exotic fish and the bottom 7 km with exotic fish (Fig. 1). The barrier was designed and built by the Bureau of Reclamation as a drop barrier with roughly a 2-m drop that spans the entire channel (http://www.usbr.gov/lc/phoenix/biology/azfish/dropbarriers.html). Neither native nor exotic fish are able to cross the barrier when swimming upstream. The barrier was placed at this site because it was the most downstream site with a sufficiently constricted channel to build this type of barrier. The barrier was designed to have minimal effects on flow and appears much like a natural waterfall. The effects of chemical treatment on invertebrates were minimal and are reported in Dinger and Marks (2007). Flow was restored in June 2005 by re-diverting water around the dam. The flumes have been deconstructed and flow was increased from between 5.6 $L\,s^{-1}$ and 62.2 $L\,s^{-1}$ before restoration to 1,218 $L\,s^{-1}$ after restoration. Fossil Creek dam was operated as a run of the river dam with a diversion, so flow restoration here refers to return of base flow. Deconstruction of the hydropower plants and diversion dam is expected to be completed in 2010. The dam is being removed for safety and liability issues. With the dam still in place, it is possible to document the effects of increased flow decoupled from effects of dam removal, such as increased sediments or changes in water quality. The hydropower decommissioning will cost approximately $12.3 million (N. Svor, 2007, Arizona Public Service, Phoenix, AZ, personal communication). Although the restoration goals of decommissioning the facility were broad based and included improving stream and riparian habitat for multiple species, improving conditions for native fish was a major impetus behind the decision to decommission the facility (Marks 2007). The removal of exotic fish added $1.1 million to the cost and was a targeted intervention for reviving native fish (R. Clarkson 2007, United State Bureau of Reclamation, Phoenix, AZ, personal communication).

Fish Sampling. We estimated fish densities using snorkel surveys. Surveys were conducted twice prior to restoration (summer 2003, spring 2004) and four times after restoration (fall 2005, spring 2006, fall 2006, spring 2007). Twenty-three sites were sampled, although each site was not sampled each period (Fig. 1). Sites were chosen to provide coverage along the entire length of stream. Sites were 90- to 335-m long and contained both pool and riffle habitats. To minimize observer bias, surveys consisted of three snorkel passes through the entire length of the reach by independent observers. Individuals were trained to swim upstream slowly but continuously at similar rates. Fish samples were standardized to reach length. Individual fish were identified to species and categorized by length into three length categories (<100 mm, 100–200 mm, and >200 mm). Because the two chub species (*Gila robusta* and *G. nigra*) are morphologically similar, no attempt was made to distinguish between these two species during snorkel surveys and they were all counted as chub. Likewise, no attempt was made to distinguish between speckled dace (*Rhinichthys osculus*) and longfin dace (*Agosia chrysogaster)*. Fish trapping and salvage data showed that longfin dace were extremely rare, suggesting that the majority of dace observed were speckled dace (Table 1, Marks et al. 2005). The data used for each site are the means of the three independent snorkel passes for each survey period. We used snorkel surveys rather than capturing fish because snorkeling is non-invasive, causing no incidental mortalities, and because managers specifically requested that researchers minimize handling of fish for the first few years following recovery efforts. Prior to restoration, we conducted more invasive sampling by capturing fish with hoop nets, minnow traps, and electroshocking to test the efficacy of snorkel surveys. We and others found that snorkel surveys in Fossil Creek, where water clarity is very high, yield similar relative abundance patterns to other methods (Marks et al. 2005; Marsh et al. 2006). Sampling was consistent across times and sites, and should represent an unbiased estimate of the relative differences in fish populations before and after restoration. Sample sites were not equally distributed across treatments due to different sized treatment reaches (1–15 km) and because monitoring began before managers decided in which areas of the stream to remove exotic fish. Specifically, there are a disproportionate number of sites where exotic fish were removed because the fish barrier was built further downstream than was suggested in the initial management plans.

Fish densities among treatment reaches prior to restoration were analyzed using a one-way ANOVA where sites within treatment reaches were used as replicates. This pseudo-replicated design described whether treatment reaches differed prior to restoration, but did not allow for statistical inference to test whether reaches differed due to their environmental condition (flow diversion, presence of exotics). Nevertheless, this analysis provided a rational basis for evaluating threats and predicting responses to restoration. Fish responses to restoration were analyzed using a BACI ANOVA as described earlier. Here, sites were nested or averaged within treatments for each sampling period. Samples taken at different dates were treated as replicates in a two-way ANOVA with restoration treatment and time as main effects. The independent variable, restoration treatment, had four treatment categories (above dam control, water restored no exotic fish, water restored exotic fish removed, water restored exotic fish remain). The independent variable time had two categories (before and after restoration). A significant interaction term (treatment × time) indicated that the relative differences among treatments changed following restoration. Because this modified BACI design has multiple impact treatments, the following two post hoc hypotheses were tested to evaluate how treatment reaches differed post-restoration: (1) native fish populations at the control site would not change significantly following restoration but would increase in the restored sites; and (2) increases in native fish populations would be significantly higher where exotic fish were removed than where they remain.

Table 1. Number of native fish salvaged prior to chemical renovation.

	Above Irving Power Plant	*Below Irving Power Plant*	*Total*
Gila nigra and *G. robusta* (headwater and roundtail chub)	174	103	277
Pantosteous clarki (desert sucker)	344	49	393
Catostomus insignis (Sonora sucker)	44	204	248
Rhinichthys osculus (speckled dace)	986	0	986
Agosia chrysogaster (longfin dace)	13	0	13

Salvaged fish were maintained in stock tanks at the Irving Power Plant for up to two weeks while the river was treated with antimycin A to remove exotic fish. Fish were returned to the river once the chemical had degraded. For complete description of exotic fish removal, see Weedman et al. (2005).

Stable Isotope Collections. Fish fin clips and whole invertebrates were collected for isotope analysis from three treatments: full flows with non-natives absent, dewatered flows with non-natives absent, and partially dewatered flows with non-natives present. Fin clips were used to avoid sacrificing individuals of listed fish species. Samples were collected in August 2002. The third reach was re-sampled in November 2003 because there were inadequate replicates of smallmouth bass captured during the first sampling. All fish and invertebrates were re-sampled in November 2003 and used in mixing models. Invertebrate samples were identified and categorized into functional feeding groups using Merritt and Cummins (1996). Samples were oven-dried at 60°C and sub-samples were weighed into 4×6 mm tin boats. Samples weighed approximately 0.4 mg. Samples were analyzed for $\delta^{13}C$, $\delta^{15}N$,

%C and %N using a CE Elantech elemental analyzer (NC 2100) coupled to a ThermoFinnigan Delta^{PLUS}-XL isotope-ratio mass spectrometer. Samples were run against internal laboratory and NIST standard materials. For both $\delta^{13}C$ and $\delta^{15}N$, the standard error from five repeated analyses of the same standard reference material was always less than 0.2 per mil. Stable Isotope data were analyzed using the dual isotope, multi-source mixing models in the ISOSOURCE computer program (Phillips & Gregg 2001, 2003). Mixing models assumed a 3.4‰ enrichment of ^{15}N for each trophic level (Minagawa & Wada 1984). Mixing models generate diet estimates by calculating mean and confidence intervals for different diet items. Mixing models provide quantitative estimates of the likelihood that a given food is part of a consumer's diet as long as the isotopic signals of food sources and consumers are measured.

Results

Pre-Restoration

Prior to flow restoration and exotic fish extirpation, the patterns of fish distribution and the stable isotope structure of the food web both suggested that native fish were more strongly reduced by the presence of exotic fish than by reduced flow. Native fish densities were more than 20-fold lower in treatments with non-native fish than treatments without them ($F = 14.6$, $p < 0.0001$), but did not differ significantly between full flow and dewatered treatments that contained only native fish (Fig. 2A). Native fish densities were more than two times higher in the control reach than the dewatered area, but this difference was not significant ($p > 0.05$). Native fish densities were 40-fold lower in the reach with both reduced flow and exotic fish relative to the control site (Fig. 2A). Native fish species were distributed differently across treatments (Fig. 2B). Chub was the only species that appeared to be sensitive to reduced flow, whereas both dace and chub declined significantly in the presence of exotic fish (Figs. 2B & 3A). In contrast, neither desert nor Sonoran suckers were negatively affected by exotics (Fig. 3B).

Stable isotope analysis of food web structure suggested that non-natives had a greater effect on the feeding ecology of native fish than flow diversion (Fig. 4). At the reference reach with full flows and no non-natives, native fish were at the top of the food chain, feeding mainly on aquatic invertebrates (Fig. 4). In the reference reach, the $\delta^{15}N$ values of native fish, were 3.9‰ higher than the average value for aquatic invertebrates, indicating that native fish under pristine conditions are a full trophic level above invertebrates (Peterson et al. 1986; Peterson & Fry 1987). Downstream, in the reach with exotic fish, the mean $\delta^{15}N$ difference between native fish and aquatic invertebrates was only 2.2‰, indicating that exotic fish had reduced the trophic position of natives. In this same downstream reach, exotic smallmouth bass and green sunfish appeared to displace native fish as top predators, having $\delta^{15}N$ values indicating a full trophic position (3.5‰) between these exotic fish and their aquatic insect prey (Fig. 4). It is possible

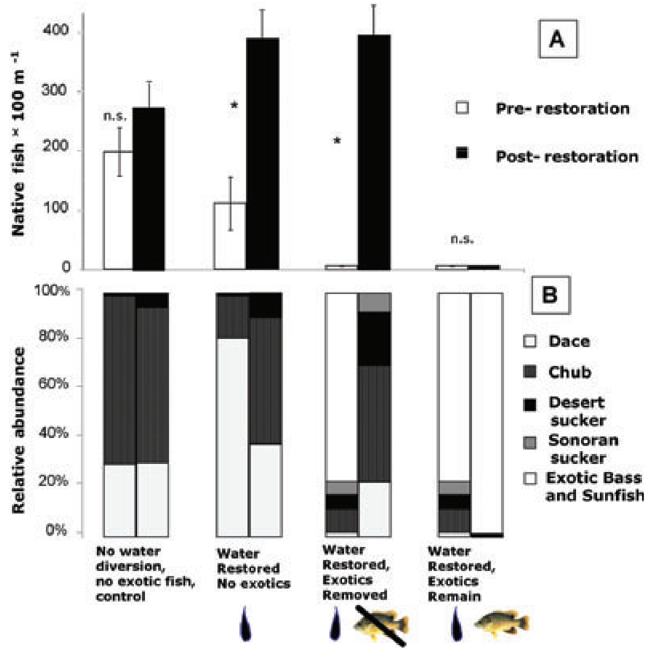

Figure 2. (A) Native fish densities before and after restoration across restoration treatments. Native fish increased significantly after flow restoration where exotics were either removed or never present. Fish did not increase after flow restoration in either the control site where no restoration activities took place or where exotic fish were not removed. Significant responses to restoration are denoted by an *. (B) The relative abundance of native and exotic fish species across treatment reaches before (left bar) and after (right bar) restoration.

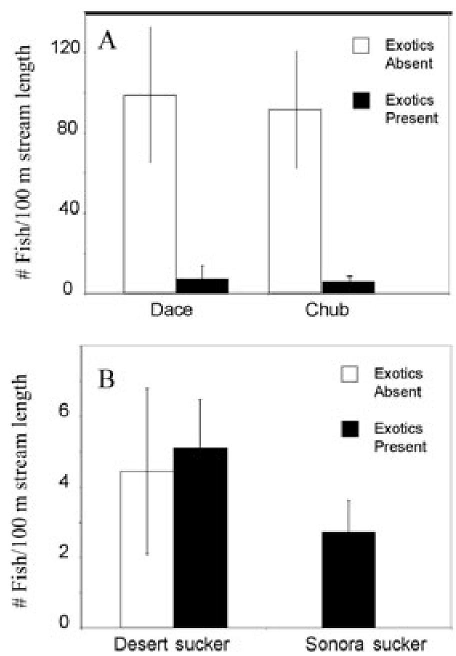

Figure 3. The distribution of four native fish species in the presence and absence of exotic fish, prior to restoration. Dace and chub populations were significantly lower in the presence of non-native fish (A) whereas densities of both sucker species were either similar or higher in the presence of non-native fish (B).

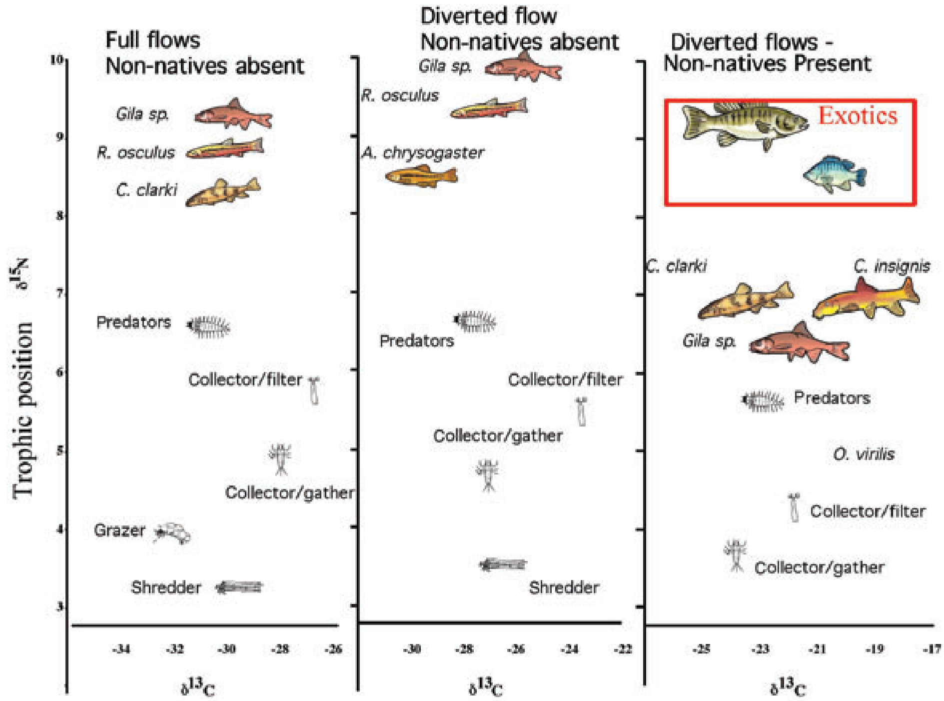

Figure 4. Stable isotope diagrams depicting food web structure prior to restoration at a control site with full flows and no exotic fish, a site with reduced flows and no exotic fish and a site with reduced flows and exotic *Micropterus dolemie* (smallmouth bass) and *Loepomis cyanellus* (green sunfish).

that exotic fish also feed on juvenile native fish. The similarity in δ^{15}N values of native fish between the reach with reduced flow and the control reach, both without exotic fish, suggests little effect of flow diversion on the trophic position of native fish.

Multiple source mixing models using stable isotopes of carbon and nitrogen revealed that reduced flow alone was associated with no major changes in the relative proportions of invertebrate guilds in the diets of native fish (Table 2). In contrast, the diets of native chub, the dominant native fish, changed significantly in the presence of exotic fish (Table 2). In the absence of non-natives, chub diet included large bodied invertebrate predators (44% relative abundance) and shredders (44% relative abundance) but was dominated by small filter feeders (82%) where exotic fish were present (Table 2). As with fish densities, observed differences in stable isotope values between treatment reaches could be due to other aspects of intersite variation rather than to exotic fish. The treatment with exotic fish is further downstream than the other treatments and has minor differences in physical and chemical variables (Marks et al. 2006; Carter & Marks 2007). Nevertheless, this analysis can be used as observational evidence for evaluating threats and generating hypothesis about how fish densities and diets will change with restoration. Although stable isotope

Table 2. Percent contribution to diet for items included in ISOSOURCE multi-source mixing models for Gila nigra and G. robusta (Gila sp.), Pantosteous clarki (desert sucker), green sunfish and smallmouth bass at sites in Fossil Creek.

	Full Flows/Native		*Dewatered Flows/Native*	*Restored Flows/Non-native*				
	Gila sp.	*Desert sucker*	*Gila sp.*	*Gila sp.*	*Desert sucker*	*Green sunfish*	*Smallmouth <150 mm*	*Smallmouth >150 mm*
Filterer	0, **2**, 11	0, **12**, 44	0, **44**, 78	74, **82**, 100	0, **20**, 74	0, **20**, 66	0, **16**, 68	0, **26**, 74
Grazer	0, **1**, 8	0, **8**, 34	*	0, **0**, 2	0, **16**, 72	0, **12**, 50	0, **18**, 68	0, **6**, 32
Predator	35, **44**, 64	0, **26**, 76	0, **24**, 66	0, **0**, 2	0, **8**, 20	0, **12**, 60	0, **10**, 46	0, **8**, 42
Col/gath	0, **5**, 23	0, **18**, 78	0, **2**, 8	0, **0**, 2	0, **20**, 76	0, **10**, 46	0, **18**, 68	0, **6**, 30
Shredder	32, **44**, 53	0, **24**, 56	18, **30**, 36	*	*	*	*	*
Crayfish	*	*	*	0, **16**, 24	0, **20**, 72	0, **20**, 66	0, **12**, 64	0, **32**, 74
Fish	*	*	*	0, **0**, 2	*	0, **12**, 44	0, **6**, 26	0, **8**, 44

Mixing models include both δ15N and δ13C isotope values. Data given are distribution (1st percentile, **50th percentile**, 99th percentile) of percent contribution. An * indicates item not considered as diet item because of availability or isotopic signal which indicated that item was outside the realm of possible diet contributors

Table 3. Results from analysis of variance for fish densities across time and treatment.

	Sum of Squares	*Df*	*F-Ratio*	*p*
Source				
Treatment	215389.270	3	36.8	<0.001
Time	188404.487	1	97.7	<0.001
Treatment × time	138239.974	3	23.6	<0.001
Error	31187.962	16		

The independent variable "time" had two levels: before and after restoration. The independent variable treatment had four levels: (1) control—full flow, no exotic fish; (2) flow restored, no exotic fish; (3) flow restored exotic fish removed; and (4) flow restored exotic fish remain. The significant interaction term indicated that fish in different treatments responded differently to restoration

data do not directly verify fish diets, they provide indirect evidence of differences in diets and are particularly useful when researchers and managers do not want to conduct invasive gut analysis studies on threatened species.

The shifts in δ13C values of native fish concurrent with water diversion suggested that fish living in the pristine reach above the dam relied more on algal productivity whereas fish living in the disturbed reach was dominated by leaf litter inputs. Carbon isotopes, however, are of limited utility for distinguishing between algae and leaf litter because their isotopic values are too similar. Stable isotopes of hydrogen should help resolve this problem (Doucett et al. 2007).

Based on this threats analysis, we predicted that native fish densities would increase only slightly with flow restoration alone but would increase up to 40-fold where exotic fish were removed. We predicted that dace and chub, whose densities were depressed and diets altered in the presence of exotic fish, would show larger increases to exotic fish removal than either desert or Sonoran suckers.

Response to Restoration

Both flow restoration and exotic fish removal increased native fish populations; however, the response to flow required the absence of exotic fish (Fig. 2A; Table 3). All terms in the BACI ANOVA were strongly significant; the significant interaction term indicated that treatments responded differently to restoration (Table 3). Native fish increased 3-fold where flow was restored in the absence of exotic fish but showed no response where exotic fish remained (Fig. 2A). As predicted, recovery was most pronounced where flow was restored and exotic fish were removed, with an almost 50-fold increase in native fish (Fig. 2A). Fish densities were higher at the restored sites than in the reference reach due to high densities of small, young fish at restored sites. In addition, some of the sites where exotic fish were removed had travertine terraces and pools, ideal habitat for native fish (Marks et al. 2006). We expect that the observed relative differences between the control and the restored sites will decline as fish in restored areas reach a stable age distribution. Native fish did not increase below the fish barrier where exotic fish remain (Fig. 2A). Below the fish barrier, the fish community comprises mostly exotic fish (Fig. 2B). A BACI ANOVA comparing fish responses in only the control treatment and where exotic fish remain indicated no significant response of native fish to restoration within either of these two treatments.

As predicted, dace and chub showed the strongest responses to restoration (Fig. 5). To compare differences in responses of

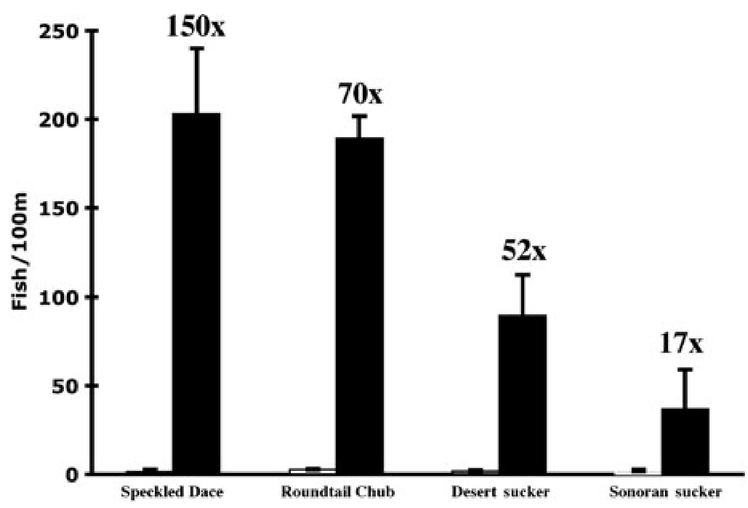

Figure 5. Increases in four species of native fish in response to removal of exotic fish. Data used in this figure show changes in fish densities in sites where each native fish coexisted with exotic bass and sunfish prior to restoration.

native species to exotic fish removal, we compared densities of fish before and after restoration within the treatment reach where exotic fish were removed at sites where each native species overlapped with bass or sunfish before restoration. For example, dace, which were only present in the 5 km below the dam prior to restoration, increased 150-fold at these sites and have not yet dispersed downstream. It is not clear what is limiting their dispersal. Chub cosed with exotic fish throughout the reach and increased 70-fold (Fig. 5). The two suckers also increased significantly, but their responses were less dramatic (Fig. 5). Desert suckers increased 52-fold and Sonoran suckers, which were only found below the Irving Power plant before restoration, increased 17-fold at these sites (Fig. 5). Despite this modest increase, Sonoran suckers are dispersing upstream and are now found at sites where they were not observed prior to restoration. More dace were repatriated than the other species (Table 1), which may account in part for their large populations after restoration. Although dace showed the largest proportional increase where they were repatriated, chub now dominate the native assemblage (Fig. 2B). Dace remained concentrated above the Irving Power Plant with only a few individuals observed downstream. In contrast, chub and suckers were repatriated below the Irving Power Plant (Fig. 1), and have been observed throughout the river.

Cost-Benefit Analysis

The exotic fish removal added significant value to the restoration effort because exotic fish posed a bigger threat than reduced flow and cost considerably less to remove than decommissioning the hydropower facility. We estimated that in the last 2 years, restoration actions led to a total increase of approximately 49,710 native fish. We assumed that flow restoration alone in the presence of exotic fish caused no change in native fish. We further assumed that observed changes in fish density in the treatment reaches were dominated by effects of restoration treatments and far less by natural variation. The first assumption is supported by the lack of response of native fish below the fish barrier where exotic fish remain, and the second by the low level of interannual variation observed at the reference site. Although there was no treatment where exotics were removed and flow remained diverted, it is possible to estimate what the effects of exotic fish removal might have been given the pre-restoration survey data and the assumption that the effects of flow restoration and exotic removal are additive. We attribute recovery of 1,022 native fish to the effects of flow restoration, and the recovery of 48,697 fish to the effects of removing exotics. Flow restoration alone yielded 0.08 fish per $1,000; with exotic fish removal, the yield increased to 3.6 fish per $1,000. Thus, the 10% increase in cost of the exotic fish removal increased native fish recovery substantially. Although our analysis indicates greater benefit to native fish from removing exotics, flow restoration will almost certainly promote ecosystem recovery in other ways, such as extensive recovery of Fossil Creek's namesake geomorphic feature, travertine dams and pools (Malusa et al. 2003; Marks et al. 2006; Marks 2007).

Discussion

This study shows that although both flow restoration and exotic fish removal increased native fish, the effect of exotic fish removal far outweighed the effect of flow restoration. Flow restoration likely facilitated the dramatic response of native fish to the removal of exotic fish by increasing carrying capacity and spawning rates of the small existing populations of native fish. Although there have been hundreds of articles implicating exotic fish in the demise of native fish, there are few studies documenting how natives respond to exotic removal (Lintermans 2000; Maezona & Miyashito 2004; Lepak et al. 2006; Bunnell et al. 2006) and no studies comparing the efficacy of flow restoration and exotic removal. In Fossil Creek, if exotic fish had not been removed, flow restoration may have facilitated upstream migration of exotic bass and sunfish, ultimately causing native fish to decline. This study indicated that in the southwestern United States, and other regions where exotic fish have largely displaced natives, habitat restoration alone may do little to promote recovery of native fish and could unintentionally harm natives where disturbances prevent dispersal of exotics or favor natives over exotics. For example, in the Great Lakes region, artificial barriers such as dams can limit dispersal of exotic lampreys so here removing barriers could harm native fish (Harford & McLaughlin 2007). Similarly, in New Zealand streams that have been invaded by brown trout, native species find refuge in highly disturbed reaches where flow has been diverted (Leprieur et al. 2006). In an Australian stream, however, removal of exotic rainbow trout resulted in the recovery of the native fish (*Galaxis olidus*) without other habitat alterations (Lintermans 2000).

The pre-restoration threats analysis yielded surprisingly accurate predictions about fish recovery, illustrating how correlative studies can be powerful tools for generating hypotheses in an adaptive management cycle despite problems with pseudo-replication and statistical inference. Not only did the threats analysis predict that recovery would be most pronounced where exotics were removed, but it also predicted which species would respond the strongest. In contrast to our findings, other studies implicate flow as the major factor causing the demise of native fish populations (Marchetti & Moyle 2001; Sada & Vinyard 2002). In Fossil Creek, all native fish species were able to persist under reduced flow, although their densities were reduced by 30%. The stable isotope results suggested that exotic fish had displaced natives as top predators. Because the stable isotope study was not replicated at the treatment level (replicate samples were taken within treatment sites), it is possible that the lower δ^{15}N values of native fish were not caused by exotic fish but are due to different food availability at the site where natives and exotics coexisted. Research in progress by our team will test how fish isotope values change with restoration. If δ^{15}N values of native fish increase where exotic fish were removed, this would support the hypothesis that exotic fish caused natives to feed lower on the food chain. Shifts in the trophic position of exotic fish in the presence of natives have been detected using stable isotopes in other ecosystems (e.g, Vander Zanden et al. 1999), suggesting a general mechanism of exotic fish forcing native fish to eat lower quality food resources. Rapid shifts in diet in response to the removal of exotic bass were observed, using stable isotopes, in native lake trout indicating rapid recovery of food web linkages following the extirpation of exotics (Lepak et al. 2006).

Many stream restoration projects are poorly monitored, making it difficult to learn from prior actions. Although projects on federal lands, such as this one, require environmental assessments under the National Environmental Protection Act (NEPA), monitoring is rarely conducted when the intent of the project is to improve conditions for listed species. Neither of the two initial environmental impact assessments (for dam decommissioning and exotic removal) recommended monitoring native fish and invertebrates even though enhancement of native fish and their habitat was a primary goal for both projects. Monitoring programs are usually only required where management actions are expected to have negative effects on listed species.

Despite the positive intent of restoration projects for native species, it is possible that interventions reverse one disturbance but create or exacerbate others pointing to the need for viewing interventions from an ecosystem perspective (Zavaleta et al. 2001). For example, studies from other dam decommissioning projects showed that sediments released from behind the dam can reduce densities of native filter feeders such as mussels (Sethi et al. 2004), and drained reservoirs can be vulnerable to the invasion of exotic plants (Stanley & Doyle 2003; Orr & Stanley 2006). Removal of exotic fish can facilitate invasions of other exotic species such as crayfish, which increased in ponds when exotic bass and bluegill were removed (Maezona & Miyashita 2004). In Fossil Creek, exotic crayfish are increasing more rapidly in areas where exotic bass were removed relative to sites where they remain (Adams 2006). Crayfish, however, do not appear to be affecting recruitment of native fish based on results presented herein. Chemical treatment to remove exotic fish can kill non-target vertebrates and invertebrates. In Fossil Creek, antimycin A increased macroinvertebrate mortality and decreased macroinvertebrate densities, but these effects were relatively short lived. Within 6 months after treatment, invertebrate densities rebounded to pre-treatment levels at most sites and did not appear to limit fish recovery (Dinger & Marks 2007).

This analysis shows how additional investments to large restoration projects can insure that specific objectives are met. Many restoration programs will benefit from this approach because most ecosystems face multiple threats where minimal additional investments could yield large ecological benefits. Although habitat improvements can enhance many other attributes of ecosystem health, such as improving water quality, increasing habitat for plants and animals and improving the aesthetic and recreation value of a stream, exotic fish removal programs may need to accompany projects where native fish recovery is a major goal and exotic fish are prevalent.

Implications for Practice

- Flow restoration and exotic fish removal are both powerful tools for increasing native fish populations.
- In some southwestern U.S. streams exotic fish likely pose bigger threats than habitat deterioration to native fish.
- Habitat improvements alone may do little for native fish recovery where exotic fish dominate the fish assemblage.

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LITERATURE CITED

Adams, K. J. 2006. The potential consequences of stream restoration on an exotic crayfish population. Master's Thesis. Northern Arizona University, Flagstaff.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters: identifying the major factors that threaten destruction of riverine species and ecosystems. BioScience **43:**32–43.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, et al. 2005. Synthesizing US river restoration efforts. Science **308:**636–637.

Bunnell, D. B., C. P. Madenjian, and R. M. Claramunt. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences **63:**2434–2446.

Carter, C., and J. C. Marks. 2007. Influences of travertine dam formation on leaf litter decomposition and algal accrual. Hydrobiologia **575:**329–341.

Dinger, E. C., and J. C. Marks. 2007. Effects of high levels of Antimycin A on aquatic invertebrates in a warmwater Arizona stream. North American Journal of Fisheries Management **27:**1243–1256.

Doucett, R. R., J. C. Marks, D. W. Blinn, M. Caron, and B. A. Hungate. 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. Ecology **88:**1587–1592.

Dynesius, M., and C. Nilsson. 1993. The status of northern river systems: a basis for conservation management of watersheds. World Wildlife Fund, Sweden, 24.

Harford, W. J., and R. L. McLaughlin. 2007. Understanding uncertainty in the effect of low-head dams on fishes of Great Lakes tributaries. Ecological Applications **17:**1783–1796.

Hart, D. D., T. E. Johnson, K. L. Horwitz, R. J. Bushaw-Newton, A. T. Bednarek, D. F. Charles, D. A. Kreeger, and D. J. Velinsky. 2002. Dam removal: challenges and opportunities for ecological research and river restoration. Bioscience **52:**669–682.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecological Systems **4:**1–23.

Keough, M. J., and G. P. Quinn. 2000. Legislative vs. practical protection of an intertidal shoreline in southeastern Australia. Ecological Applications **10:**871–881.

Lepak, J. M., C. E. Kraft, and B. C. Weidel. 2006. Rapid food web recovery in response to removal of an introduced apex predator. Canadian Journal of Fisheries and Aquatic Science **63:**569–575.

Leprieur, F., M. A. Hickey, C. J. Arbuckle, G. P. Closs, S. Brosse, and C. R. Townsend. 2006. Hydrological disturbance benefits a native fish at the expense of an exotic fish. Journal of Applied Ecology **43:**930–939.

LeRoy, C. J., and J. C. Marks. 2006. Litter quality, stream condition, and litter diversity influence decomposition rates and macroinvertebrate communities. Freshwater Biology **51:**606–617.

Lintermans, M. 2000. Recolinization by the mountain galaxies *Galaxis olidius* of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. Marine and Freshwater Research **51:**799–804.

MacMahon, J. A., and K. D. Holl. 2001. Ecological restoration: a key to conservation biology's future. Pages 245–269 in M. E. Soule and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C.

Maezono, Y., and T. Miyashita. 2004. Impact of exotic fish removal on native communities in farm ponds. Ecological Research **19:**263–267.

Malusa, J., R. A. Parnell, and S. T. Overby. 2003. Processes influencing travertine precipitation and aquatic habitat formation, Fossil Creek, Arizona. Applied Geochemistry **18:**1081–1094.

Marchetti, M. P., and P. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications **11:**530–539.

Marks, J. C. 2007. Down go the dams. Scientific American **296:**66–71.

Marks, J. C., E. C. Dinger, and G. A. Haden. 2003. Biological assessment of restoration options for Fossil Creek, Arizona. Final Report to Arizona Public Service (available from http://www.aps.com/images/CI/ITEM6A.pdf) accessed on 18 December 2007.

Marks, J. C., G. A. Haden, E. C. Dinger, and K. J. Adams. 2005. A survey of the aquatic community at Fossil Creek, Arizona. Heritage Grant I03003. Arizona Game and Fish Department, Phoenix, Arizona, (available from http://www.watershed.nau.edu/FossilCreekProject/research.htm) accessed on 14 November 2007.

Marks, J. C., R. Parnell, C. Carter, E. C. Dinger, and G. A. Haden. 2006. Interactions between geomorphology and ecosystem processes in travertine streams—implications for dam decommissioning in Fossil Creek, Arizona. Geomorphology **77:**299–307.

Marsh P. C., J. A. Stefferud, and S. E. Stefferud. 2006. Fossil Creek Fish Monitoring Annual Report. United States Bureau of Reclamation, Phoenix Arizona (available from http://www.watershed.nau.edu/FossilCreekProject/research.htm) accessed on 21 September 2007.

Merritt, R. W., and K. W. Cummins, editors. 1996. An Introduction to the Aquatic Insects of North America. 3rd edition. Kendall, Hunt, Iowa.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries **14:**22–38.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of 15 N along food chains: further evidence and the relation between 15 N and animal age. Geochimica et Cosmochimica Acta **48:**1135–1140.

Minckley, W. L., and J. E. Deacon. 1991. Battle against extinction: native fish management in the American west. University of Arizona Press, Tucson.

Monroe, S. A. 2002. Travertine and concrete: a geomorphological and historical study of a damsite at Fossil Creek, Arizona. Masters Thesis. Northern Arizona University, Flagstaff.

Moyle, P. B. 1995. Conservation of native freshwater fishes in the Mediterranean-type climate of California, USA: a review. Biological Conservation **72:**271–279.

Olden, J. D., and N. R. Poff. 2005. Long-term trends of native and non-native fish faunas in the American Southwest. Animal Biodiversity and Conservation **28:**75–89.

Orr, C. H., and E. H. Stanley. 2006. Vegetation development and restoration potential of drained reservoirs following dam removal in Wisconsin. River Research and Applications **22:**281–295.

Palmer, M. A., E. S. Bernhardt, J. D. Allen, P. S. Lake, G. Alexander, S. Brooks, et al. 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology **42:**208–217.

Peterson, B. J., R. W. Howarth, and R. H. Garritt. 1986. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science **227:**1361–1363.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics **18:**293–320.

Phillips, D. L., and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia **127:**171–179.

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia **136:**261–269.

Poff, N. L., J. D. Allan, M. A. Palmer, D. D. Hart, B. D. Richter, A. H. Arthington, K. H. Rogers, J. L. Meyer, and J. A. Stanford. 2003. River flows and water wars: emerging science for environmental decision making. Frontiers in Ecology and the Environment **1:**298–306.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology **11:**1081–1093.

Sada, D. W., and G. L. Vinyard. 2002. Anthropogenic changes in biogeography of Great Basin aquatic biota. Smithsonian Contributions to the Earth Sciences **33:**277–294.

Schlinger, C., J. Janecek, J. Ramsey, P. Trotta, and S. Welch. 2002. Hydrologic, hydraulic and sediment transport evaluation for fossil springs dam site management scenario options. Northern Arizona Project # EGR39DV prepared for Arizona Public Service, USA (available from http://www.aps.com.images/CI/ITEM2B.pdf) accessed on 3 August 2007.

Schmitt, R. J., and C. W. Osenberg. 1996. Detecting ecological impacts. Academic Press, Oxford, United Kingdom.

Sethi, S. A., A. R. Selle, M. W. Doyle, E. H. Stanley, and H. E. Kitchel. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA). Hydrobiologia **525:**157–165.

Stanley, E. H., and M. W. Doyle. 2003. Trading off: the ecological effects of dam removal. Frontiers in Ecology and the Environment **1:**15–22.

Stewart-Oaten, A., W. M. Murdoch, and K. Parker. 1986. Environmental impact assessment: pseudoreplication in time? Ecology **67:**929–940.

Underwood, A. J. 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Australian Journal of Marine and Freshwater Research **42:**569–587.

Underwood, A. J. 1994. On Beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications **4:**3–15.

Vander Zanden, M. F., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature **401:**464–467.

Weedman, D. A., P. Sponholtz, and S. Hedwall. 2005. Fossil Creek native fish restoration project. Arizona Game and Fish Department, Phoenix (available from www.azgfd.gov/pdfs/w_c/tech_reports/Fossil%20Creek%20Restoration.pdf) accessed on 16 October 2007.

Williams, J. E., and R. R. Miller. 1990. Conservation status of the North American fish fauna in freshwater. Journal of Fish Biology **37:**79–85.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution **16:**454–459.