

POPULATION RESPONSE OF THE INVASIVE CRAYFISH *ORCONECTES VIRILIS* (HAGEN, 1870) (DECAPODA: ASTACOIDEA: CAMBARIDAE) TO RESTORATION: WHAT ARE THE CONSEQUENCES OF CHANGES IN PREDATORY REGULATION AND PHYSICAL HABITAT IN FOSSIL CREEK, ARIZONA, USA?

Kenneth J. Adams^{1,2,*} and Jane C. Marks^{1,2}

¹ Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86001-5640, USA

² Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011-6077, USA

ABSTRACT

We examined the response of a population of an invading non-indigenous crayfish, *Orconectes virilis* (Hagen, 1870), to a stream restoration project in travertine-forming Fossil Creek, Arizona, USA. Restoration included the re-establishment of the natural flow regime after the decommissioning of a dam and removal of non-native predatory fishes. The goal was to determine if changes in the dominant predatory fishes or changes in physical habitat variables, including substrate modification and base flow influence changes in crayfish abundance. We predicted that increased and unregulated flows and velocities would not generally decrease crayfish abundance, and that the removal of non-native fishes would increase the number of crayfish while local substrate modification by travertine deposition, a form of limestone which fills in interstitial spaces, would decrease the number of crayfish. Consistent with our predictions, there were not generalized decreases in crayfish abundance throughout the river following restoration. More detailed observations of different reaches, however, indicates that fish species and density exert some regulation over crayfish numbers. Crayfish abundance decreased following restoration where exotic fishes remain but slightly increased in numbers where they were removed. Areas in the river with increased travertine deposition had the largest declines following restoration. These observations suggest that crayfish abundance in this system is limited by substrate modification by travertine and to a lesser extent by regulation of fish predation.

KEY WORDS: habitat limitation, population regulation, predation

DOI: 10.1163/1937240X-00002471

INTRODUCTION

We investigated how the spread and abundance of non-native crayfish are influenced by biotic and abiotic factors, in the context of a river restoration project in Arizona. To become established and spread, a nonindigenous species must survive ambient physical and chemical conditions, as well as interspecific interactions with residents of the community (Kolar and Lodge, 2001; Herborg et al., 2007). In turn, the impact of an invading species will be determined by its physiological characteristics and those interactions (Kolar and Lodge, 2001, 2002). For crayfish, biotic factors such as competition and predation are often cited as the determinants for invasion success or failure (Hill and Lodge, 1994; Garvey et al., 2003; Light, 2003). The removal of top predators can reduce predation rates and increase juvenile survival (Momot and Gowing, 1977; Stein, 1977; Seiler and Turner, 2004; Hein, 2006; Reynolds, 2011) leading to increases in crayfish population abundance (Maezono and Miyashita, 2004; Seiler and Turner, 2004). In flowing freshwater systems invasions may also fail due to hydrological factors such as high flow velocities and pulse disturbances (Light, 2003; Kerby et al., 2004). Alternatively, increased flow, by widening the wetted area of the channel, could provide increased shallow riffle and backwater habitat for juveniles (Stein, 1977; En-

glund and Kruppa, 2000). Crayfish abundance, and/or density, is likely determined by an interaction between predatory fishes and abiotic habitat factors, such as substrate size and composition, flow and water velocity, or water chemistry (Hill and Lodge, 1994; Englund, 1999; Englund and Krupa, 2000; Usio and Townsend, 2000; Garvey et al., 2003; Seiler and Turner, 2004; Nystrom et al., 2006; Usio, 2007). It has been suggested that predation may determine the actual abundance of a crayfish population but the physical habitat and substrate sets the upper limits to abundance (Nystrom et al., 2006).

Crayfishes are often considered keystone members of freshwater benthic communities due to their large size, high densities, and omnivore feeding behaviors (Momot, 1995; Nystrom et al., 1996; Gherardi et al., 2011). Although many native species of crayfish are becoming increasingly rare and threatened by environmental degradation (Lodge et al., 2000; Usio, 2007; Taylor et al., 2011), a few North American species have become invasive with worldwide distributions (Hobbs et al., 1989; Lodge et al., 2000; Gherardi et al., 2011). Over the last couple of decades, *Orconectes virilis* (Hagen, 1870) the northern crayfish, has doubled its range in North America, expanding from the upper Midwestern United States and Canada eastward to Maryland, westward to California and Oregon, and south to Mexico. It has also

* Corresponding author; e-mail: kenincreek@gmail.com

been reported in Europe and Africa (Taylor et al., 2011). The impact of invading non-native crayfishes on an ecosystem and its members may be substantial if they reach high densities (Nystrom et al., 1996; Lodge et al., 2000; Gherardi et al., 2011). We examined the population dynamics of non-native *O. virilis* during a river restoration project in Arizona, USA to evaluate how the changes in physical and biological conditions were associated with increases or decreases in crayfish population densities.

Strategies for managing established populations of an invasive crayfish will depend on understanding those factors that potentially limit their spread. Management options and strategies such as ecological and biological restoration may reduce negative impacts and prevent further range expansion (Momot and Gowing, 1977; Light, 2003; Hein et al., 2006; Maezono and Miyashiti, 2006; Gherardi et al., 2011). There are nevertheless not widely accepted and established methods for reducing invading crayfish populations (Gherardi et al., 2011). Some toxicants can eradicate crayfish (Bills and Marking, 1988) but toxicants harm other members of the community including fishes and invertebrates (Gherardi et al., 2011). Predatory fishes may be a viable option for the bio-control of crayfish populations (Rach and Bills, 1989; Hein et al., 2006; Aquiloni et al., 2010; Gherardi et al., 2011) but sustained reductions of a dense crayfish population may require additional resource-intensive remediation, such as manual trapping, which has yet to be effectively demonstrated in flowing systems (Kerby et al., 2004; Hein et al., 2007; Aquiloni et al., 2010). Hydroecological restoration, by increasing flow velocities and the frequency of pulse disturbances, may also be feasible alternatives for the control of crayfish (Light, 2003; Kerby et al., 2004). Water velocities of 0.30 m/s or greater may prevent the upstream movement of crayfish (Kerby et al., 2004). Little is known about the long-term effectiveness of such restoration projects (Palmer et al., 2005; Marks et al., 2010).

This study took place during a stream restoration project in travertine-forming Fossil Creek, AZ, USA, where flow and native fisheries were restored as part of the decommissioning of a dam 100 years old. It was expected that the return of full flows would result in the return of travertine formation in the upper one fourth of the river (Malusa et al., 2003). Travertine is layered calcium carbonate formed by deposition from rapidly flowing mineral-laden spring waters (Malusa et al., 2003). Rapid travertine formation results in the loss of interstitial spaces between substrate particles (Casas and Gessner, 1999). Interstitial spaces are important for juvenile recruitment of crayfish (Brusconi et al., 2008; Olsson and Nystrom, 2009) and protection from predators (Stein, 1977; Hill and Lodge, 1994; Englund, 1999; Englund and Kruppa, 2000). An additional aspect of the restoration included salvaging and reintroducing native fishes in the river, particularly roundtail chub *Gila robusta* (Baird and Girard, 1853) (Marks et al., 2010). Non-native fish assemblages composed primarily of smallmouth bass *Micropterus dolomieu* (Lacépède, 1802) and green sunfish *Lepomis cyanellus* (Rafinesque, 1819) were removed in a 15 km reach with antimycin A in 2004 prior to dam decommissioning (Weedman et al., 2005). Following restoration, native

fishes increased 50 fold in sections of the stream where non-natives were removed (Marks et al., 2010). Managers were nevertheless concerned that the removal of predatory bass would inadvertently cause an increase in *O. virilis* due to release from competition and predation (Zavaleta et al., 2001). Smallmouth bass can consume a large proportion of crayfish production (Rabeni, 1992; Dorn and Mittlebach, 1999). The top native fish predator, *G. robusta*, is a comparatively less aggressive predator of crayfish (Arena et al., 2012; Adams, 2014).

We capitalized on this large restoration project to determine if changes in biotic factors, such as predatory regulation, or abiotic factors would limit or facilitate the spread of this non-native crayfish. This research addressed the following questions: 1) Will a shift in predatory fishes from non-native to native lead to changes in abundance and size distributions? 2) How do modifications to the physical substrate habitat impact crayfish abundance? 3) Will increased water velocities and unregulated flows decrease crayfish abundance?

We tested three predictions: 1) Changes in fish assemblage from non-native to native would increase crayfish abundance. We also predicted that in response to the change in fish predators there would be a change in the mean size of crayfish. 2) Travertine deposition would decrease crayfish abundance in the furthest upstream reach. We hypothesized that crayfish would be habitat limited by rapid and increased travertine deposition on the substrate in the furthest upstream reach. 3) Flow restoration would not generally decrease crayfish abundance in the majority of the river since base-flow velocities likely would not be enough for crayfish displacement or impediment of upstream movements. Alternatively, increased flow velocities could decrease crayfish abundance in some areas of the creek that contain smooth substrate such as travertine and bedrock (Kerby et al., 2004). We hypothesized, however, that crayfish are more influenced by the frequency and size of flood events (Light, 2003; Kerby et al., 2004). The dam operations only altered base flow (run of the river dam) such that peak flows were not changed by restoration (Malusa et al., 2003; Fuller et al., 2011).

To test our predictions we conducted a before and after restoration analysis of crayfish abundance in four reaches. We studied how crayfish abundances varied based on the dominant fish predator by comparing two physically similar reaches separated by a fish barrier. Native fishes were present above the fish barrier whereas non-native fishes were present below the barrier after restoration. We incorporated fish abundance data from a previous study on the fish responses to restoration (Marks et al., 2010). We also tested how changes in substrate by travertine deposition affected crayfish abundance. We compared a reach with high travertine deposition and travertine dam formation after restoration (but had little to no deposition and no travertine dam formation prior to restoration) to a reach that had low deposition (but travertine dam formations prior to restoration) (Malusa et al., 2003; Fuller et al., 2011). Travertine dams are aggregated areas of deposition that grow and rise above the stream bed. We incorporated mean travertine growth data estimates from a previous study on

travertine responses to restoration (Fuller et al., 2011). By comparing changes in crayfish abundance in all four of these reaches we were also able to test the response of crayfish to flow restoration. Since flow was increased in all reaches by 90%, a general response to increased flow velocities should have been detectable in all reaches. In addition to abundance, we also tested for differences in crayfish size in all reaches.

MATERIALS AND METHODS

Study Site

Fossil Creek is a perennial, travertine-depositing, spring-fed stream. From 1909 to 2005 the spring fed base flow of the creek (approximately 1200 l^{-1}) was diverted with a dam for use in two hydroelectric power plants. A restoration program involving the decommissioning of the hydropower operation and restoration of full flows occurred in June 2005. While the hydropower operation was in use, an upstream portion of the river (6.5 km downstream from the diversion dam) contained seepage flow (51 l^{-1}) for that century (Fig. 1; Malusa et al., 2003; Fuller et al., 2011). A portion of flow (151 l^{-1}) was returned to the river through the first power plant (Irvine, river km 6.7). The return of partial flows of the spring water resulted in travertine deposition and travertine terraces in a 1.8 km reach downstream of the power plant prior to restoration (Fig. 1, T2; Malusa et al., 2003; Fuller et al., 2011). After restoration travertine terraces quickly began forming in the first 7.6 km below the original dam site (Fuller et al., 2011; Fig. 1).

Arizona is one of the few areas in the USA without a native species of crayfish. Many freshwater systems in Arizona now contain high densities

of *O. virilis* (Carpenter, 2005). Fossil Creek was likely invaded by crayfish in the late 1980s from the Verde River, where they are abundant (Fig. 1). Prior to restoration of full flows (fall 2004) non-native fishes that were also invading the river from the Verde River were removed from all but the lower 8 km of the river where a fish barrier was installed (Marks et al., 2010; Fig. 1). Patterns of fish distribution and the stable isotope structure of the food web both suggested that native fishes were more strongly reduced before restoration by the presence of non-native fishes than by reduced flow (Marks et al., 2010). Native fishes in Fossil Creek included *Gila robusta*, the Sonoran sucker *Catostomus insignis* (Baird and Girard, 1854), desert sucker *Pantosteus clarki* (S. F. Baird and Girard, 1854), and speckled dace *Rhinichthys osculus* (Girard, 1856). The river was treated with the piscicide antimycin A to remove the non-native fishes from river km 0.8, above which existed populations of native fishes prior to restoration, downstream to the fish barrier (reaches T2 and F1, Fig. 1; Dinger and Marks, 2007; Marks et al., 2010). The piscicide did not harm the crayfish (Adams, 2006; Dinger and Marks, 2007). Native fishes were salvaged prior to chemical treatment and reintroduced into the river. Macroinvertebrate populations were reduced by the chemical treatment but rebounded within the first year following treatment (Dinger and Marks, 2007).

The abundance and size of the crayfish were surveyed for 9 years (two years prior to restoration, one year during, and six years post restoration) at two sites each along four consecutive downstream reaches (Fig. 1). During restoration these four reaches incurred different changes in hydrological regime, travertine deposition (with its associated changes in substrate), and the top fish predator (Table 1). The three upstream reaches had exotic fishes removed to restore native fishes. In the fourth, furthest downstream reach (F2, 15 km downstream from the springs) exotic fishes remained after restoration. The construction of a fish barrier separating the third and fourth

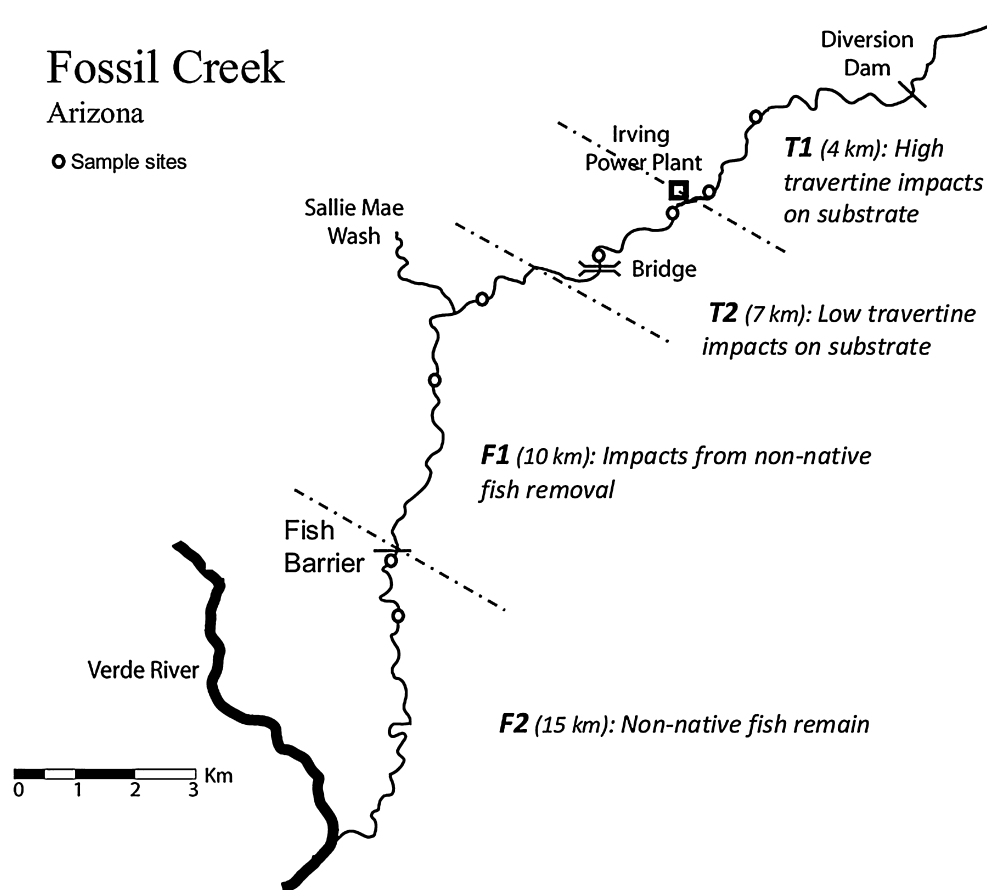


Fig. 1. Eight crayfish-abundance sample sites in Fossil Creek, AZ, USA showing the four reaches that had incurred changes in impacts on substrate by travertine deposition and changes in fish assemblages during removal of non-native fishes after restoration. Reaches T1 and T2 had similar fish assemblages before and after restoration but incurred different travertine deposition both before and after restoration. The reach immediately above the fish barrier (F1) contained native fishes after restoration but was otherwise similar to the downstream reach (F2, where exotic fishes remained) in that it had flows re-established during restoration but no travertine formation.

Table 1. Description of fish community differences and physical habitat variable descriptions, before and after restoration, at each reach (labeled with distance downstream from the spring headwaters). Fish abundance was obtained from data collected from 2003 to 2008 and summarized in Marks et al. (2010).

Reach (km downstream)	Pre-Restoration				Post-Restoration			
	T1 (4 km)	T2 (7 km)	F1 (10 km)	F2 (15 km)	T1 (4 km)	T2 (7 km)	F1 (10 km)	F2 (15 km)
Inst. flow (l/s)	51	151	151	151	546.5	875.6	798.8	482.1
Travertine growth rate (mm/year)	0	2.0	0	0	6.5	2.0	0.25	0
Travertine formation type	Deposits	Terraces	None	None	Terraces	Terraces	Deposits	None
Native fish abundance (fish/100 m)	22.3	10.1	5.8	5.3	281.2	490.7	123.6	1.3
Exotic fish abundance (fish/100 m)	65.8	13.6	4.5	21.9	0	0	0	28.8

reaches is designed to prevent re-invasion of exotic fishes (Fig. 1). The reach immediately above the barrier (F1, 10 km downstream from the springs) contained native fishes after restoration but was otherwise similar to the downstream reach (F2) in that it had flows re-established during restoration and little to no travertine formation. A comparison of changes in crayfish abundance between these two reaches after restoration allowed a test of the influence of changes in the dominant fish predator.

In contrast, the two upstream reaches (T1 and T2) had similar fish assemblages after restoration but incurred different travertine deposition after restoration. (Fig. 1, Table 1). We estimated travertine growth (mm/year) using data from Fuller et al. (2011), who used a micro-topographic surveying technique that measured the magnetic field produced by small magnets embedded within travertine dams. The furthest upstream reach (T1, 4 km downstream of the springs) had minimal travertine deposition prior to restoration because water flows were largely diverted for use in the Irving hydroelectric power generating plant (Table 1). After restoration of flows, travertine deposition was high in this reach (a mean of 6 mm/year, with a maximum over 10 cm/year; Fuller et al., 2011). In contrast, the reach below the Irving power plant (T2, 7 km downstream of the spring) had higher flows and travertine deposition prior to restoration. Comparing reaches T1 and T2 tests for changes in crayfish abundance due to the influence of re-establishing the full flow regime and travertine deposition on the substrate.

We tested for a general influence of increased velocities and flow by comparing changes in crayfish abundance in all four reaches. We used instantaneous flow measurements for each reach after restoration (see below) and pre-restoration estimates of flow from Malusa et al. (2003). A general negative response to increased velocities would be indicated by a decrease in abundance in all four reaches over time. In addition to population characteristics of the crayfish, physical stream characteristics and biological community attributes were compared between reaches in 2009 (three years after restoration) (see below).

Analysis of Relative Abundance

Crayfish were trapped at eight survey areas within four reach segments of Fossil Creek twice during the summer growing season for eight years: two years before restoration (2003–2004), the year during restoration (2005), and six years after restoration (2006–2011). Ten traps were baited and set at each survey area during a night for ten hours. The traps were commercially available g-type cylindrical minnow traps with a galvanized wire mesh and two funnel openings that were modified by enlargement from the production by 2–5 cm (Adams, 2006). These traps tend to be biased toward capturing adult crayfish but not as severe as some trap styles (Adams, 2006). The placement of the traps was segregated and dispersed at ten linearly equidistant locations throughout an approximately 200 m length of the stream survey area. Beyond a certain distance (e.g., 20 m, with catch maximized at a radius of 4 m) the diameter of attraction of a trap is minimized (Acosta and Perry, 2000). The measurement of abundance was the catch per unit of effort (CPUE), which is the number of crayfish caught in one trap per night. Crayfish abundance (CPUE) data during the year of restoration (2005), however, was not included as part of the statistical analysis. We observed very large increases in crayfish abundance at all sites (2× or greater) that might have been attributed to a large amount of nutrients for growth and reproduction from decaying fish. Crayfish

abundance subsequently decreased at all sites the following year after the restoration in 2006.

We conducted three separate statistical analyses for testing the impacts of restoration on crayfish abundance due to travertine increases, exotic fish removal, and flow reestablishment. For each test, the dependent response variable was mean abundance (crayfish CPUE). Surveys taken at 14 different times (four before restoration, ten after restoration) were treated as replicates with reach and time period (pre-restoration and post-restoration) as independent variables.

For the first test, we used a generalized linear model (GLM) with a Poisson distribution to test whether the mean crayfish abundance as a dependent variable could be predicted by reach and whether it could be predicted by the independent reach environmental variables related to flow, fish and travertine. The model included the fixed effects of Reach (T1, T2, F1, and F2), mean instantaneous flow, travertine growth rate, native fish abundance, and exotic fish abundance (Table 1). All factors were regarded as fixed. Statistical analyses were carried out with the general linear model (GLM) procedure in SAS version 11.2 for personal computers (SAS Institute, 2014). In all cases, statistical significance was evaluated at $\alpha = 0.05$. The unbalanced replication of the abundance data (two years of data prior to restoration and five years post restoration) precluded the ability to test time period as a predictor within the generalized linear model. We therefore analyzed the results of the model to determine if reach, as a significant independent variable, could be tested in combination with time period as a second independent variable in a separate statistical analysis.

A second analysis tested for an overall change in abundance throughout the four reaches of the creek due to restoration. We used a mixed model repeated measures ANOVA (rmANOVA) with the method of moments expected means squares (EMS) estimation in JMP version 11.2 (SAS Institute, 2014) to test whether the dependent variable of mean crayfish abundance differed between reaches and between the periods of pre-restoration and post-restoration. The model included the fixed effects of Reach (F1, F2, T1 and T2), Period (pre-restoration and post-restoration) and the Reach × Period interaction. If increased flow had a strong effect on crayfish we would expect to see this manifested at all four reaches and the direction of change would be similar across all sites. If flow was the dominant variable determining crayfish densities and flow caused changes in crayfish abundance (regardless of fish assemblage or travertine deposition) this would be indicated by a significant time effect and insignificant reach effects or interaction effects. In contrast, a significant interaction term would indicate that travertine deposition and/or fish assemblage either interact with flow or have as strong or stronger effects than flow in determining crayfish densities. A Tukey HSD post hoc analysis at an α level of 0.05 was used to test for changes within reaches over time.

Although the design of this analysis was unbalanced in temporal replication, it was intended to overcome some of the confounding problems associated with a proper BACI design (Hurlbert, 1984). In this study, the shorter time period before restoration was in part a consequence of uncertainty in the public policy-making process. The possibility of randomly chosen control sites was confounded by the physical uniqueness of Fossil Creek (as a perennial geothermal, travertine stream in an arid region) and the uniqueness of the action of the restoration of native fish

populations in a region without an intact assemblage of native fishes (Muehlbauer et al., 2009; Marks et al., 2010).

Physical Habitat and Benthic Community Relationships

A third analysis examined the differences in crayfish abundance after restoration due to physical habitat parameters and the benthic community. Physical habitat measurements were conducted at seven transects within a 150 m stretch of riffle/run habitat between two pools at each of the eight sites during July of one year (2009). The measurements (derived from Platts et al., 1983) along each transect included channel measurements (depth and width), velocity, stream bed embeddedness and substrate particle size (using the Wolman pebble count method), the percentage of substrate cemented by travertine, and riparian cover density. Velocity at five equidistant points was taken with a 201D water current meter from Marsh-McBirney along each transect.

Temperature, pH, total dissolved solids, specific conductivity, and salinity were measured along transects at the top and bottom of the reach using a Hydrolab minisonde (Hydrolab-Hach Corporation, Loveland, CO, USA) ($n = 5$ measurements per transect).

We measured the biomass and abundance of benthic macroinvertebrates and their diversity at each site. The macroinvertebrates were sampled with five replicated haphazardly spaced Surber samples (250 μm mesh size, 0.093 m^2) during July of the same year (2009). Samples were preserved in 70% ethanol. All insects of each sample were sorted, counted, measured, and identified to the lowest possible taxonomic level using dissecting microscopes. The lowest possible taxonomic level was genus for most groups, tribes for chironomids, and family for some dipterans, lepidopterans, and coleopterans.

A multiple stepwise regression was used to analyze the relationship between crayfish abundance at each site and the physical habitat and biotic community measurements. Crayfish mean CPUE was the dependent variable and the independent variables were the mean physical habitat measurements and macroinvertebrate community variables. The regression was re-iterated after sequentially removing independent variables with the least correlational significance until finding the last combination of independent variables that produced a significant relationship with crayfish abundance at an α level of 0.05.

The multiple stepwise regression technique was also used to determine if either crayfish abundance and/or physical habitat variables had an influence on the macroinvertebrate community. Mean biomass of the macroinvertebrate community was the dependent variable in the analysis and the independent variables were the mean crayfish CPUE and the physical habitat variables of channel, channel width, velocity, stream bed embeddedness, substrate particle size, and the percentage of substrate cemented by travertine.

Size Distribution Analysis

We analyzed changes in the mean size, measured by the carapace length (CPL), per year for all crayfish in each of the four stream reaches throughout the study period. A second generalized linear model (GLM) with a normal distribution was used to test whether the mean crayfish sizes as dependent variables also differed between reach and whether they could be predicted by the same independent reach environmental variables related to flow, fish, and travertine. The unbalanced replication of the abundance data (two years of data prior to restoration and five years post restoration) precluded the ability to test time period as a predictor within the generalized linear model. We therefore used a second mixed model repeated-measures ANOVA (rmANOVA) with the method of moments expected means squares (EMS) estimation in JMP version 11.2 (SAS Institute, 2014) to test whether the dependent variable of mean crayfish abundance differed between reaches and between the periods of pre-restoration and post-restoration. The model included the fixed effects of Reach (F1, F2, T1 and T2), Period (pre-restoration and post-restoration) and the Reach \times Period time interaction.

RESULTS

Analysis of Relative Abundance

Contrary to initial concerns by managers and scientists, crayfish densities did not show large increases following restoration. Overall mean crayfish abundance declined by -0.09 CPUE after restoration. Decreases were more pronounced in both the travertine impacted reach (T1) and the reach where exotic fish remained after restoration (F2) (Fig. 2). Reach was a significant predictor of mean crayfish abundance (GLM, $\chi^2 = 11.677$, $P = 0.009$). There is also evidence that both travertine growth rate ($\chi^2 = 13.431$, $P = 0.001$) and exotic fish abundance ($\chi^2 = 9.969$, $P = 0.002$) were significant predictors of mean crayfish abundance. Neither mean instantaneous flow ($\chi^2 = 1.972$, $P = 0.160$) nor native fish abundance ($\chi^2 = 3.485$, $P = 0.062$) were predictors of crayfish abundance.

The test for an overall change in abundance throughout the four reaches of the creek due to restoration flow restoration impacts revealed a significant interaction ($F_{1,811.9} = 4.785$, $P = 0.035$), indicating that there was a variable change after restoration among the four reaches ($F_{3,56.9} = 47.796$, $P < 0.001$). Flow therefore appeared not to be the over-

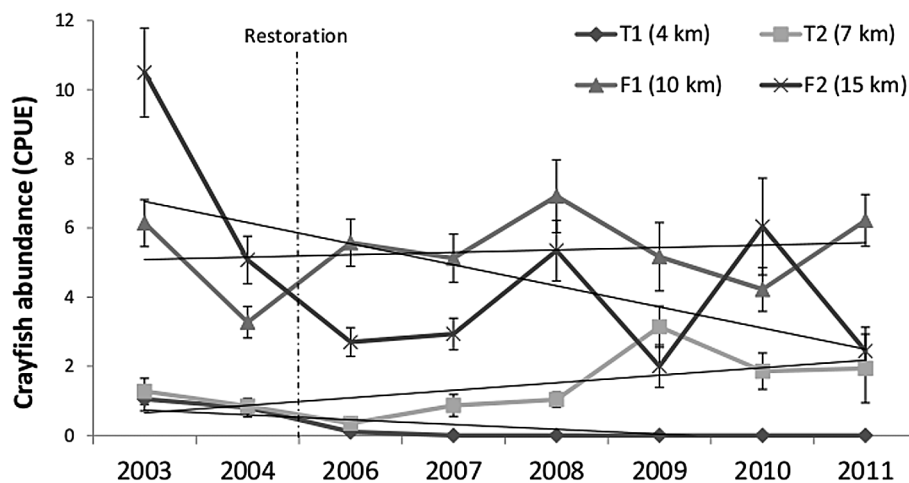


Fig. 2. Crayfish abundances before and after restoration in four reaches of Fossil Creek, AZ, USA show an overall decrease in abundance. Crayfish increased slightly after restoration in the reach above the fish barrier where non-native fishes were removed (F1, 10 km downstream) compared to a substantial decrease in the reach below the fish barrier where invasive crayfish remained (F2, 15 km downstream). There was also a slight increase in crayfish abundance in the reach with travertine dam formation before restoration (T2), whereas crayfish were absent in the upstream reach with rapid travertine deposition after 2006 (T1).

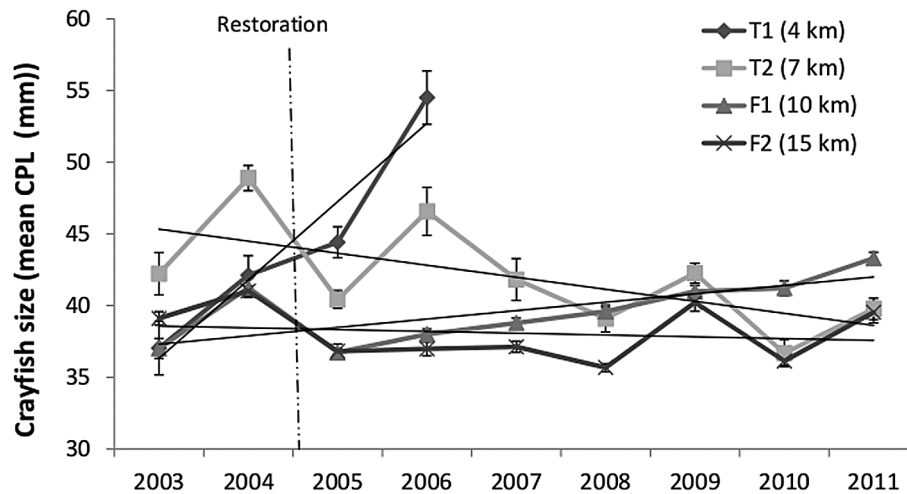


Fig. 3. The size class analysis shows an increase in the mean carapace length of crayfish in the upstream reach (T1) where rapid travertine deposition as well as where non-native fishes were removed (F1). Length data for crayfish is absent after 2006 in the travertine reach (T1) due to crayfish no longer being captured. By comparison, there was a decrease in the mean carapace length of crayfish in the stream reach that contained travertine formation prior to restoration (T2) and a slight decrease where non-native fishes remained (F2).

all predictor of changes in crayfish mean abundance. The significant temporal effect (pre versus post restoration) indicated a slight but significant decrease in crayfish abundance ($F_{3,812.2} = 14.79$, $P < 0.001$), but the declines were not consistent among reaches (Fig. 2). For example, the abundance of crayfish in the reach where exotic fishes were removed (F1) increased by 20% from a mean crayfish CPUE of 4.5 to a mean of 5.69 after restoration (LS Means contrast $F_{1,799} = 5.28$, $P = 0.022$; Fig. 2). In reach F2, where non-native fishes remained, crayfish abundance (CPUE 3.43 ± 0.32) declined by 50% and was significantly reduced compared to the reach where non-native fishes remained (Fig. 3, Tukey's HSD, $\alpha = 0.05$, $Q = 2.578$). After restoration, the mean CPUE of crayfish in the reach where travertine was restored, T1, was significantly decreased (0.02 ± 0.13) compared to the reach with prior travertine formation, T2 (CPUE 1.63 ± 0.23) (Tukey's HSD, $\alpha = 0.05$, $Q = 2.582$; Fig. 3). The mean difference in reach T1 was -0.9 and in reach T2

the mean difference was $+0.53$ (Fig. 3). Together these results indicate that crayfish responses were a function mostly of changes in travertine deposition rate and the fish assemblages. No single factor caused a dramatic response in either direction.

Physical Habitat and Biotic Correlation

In the stepwise regression, crayfish abundance was correlated negatively with a combination of travertine cementation and mean embeddedness ($R^2 = 0.60$, $F_{2,7} = 5.213$, $P = 0.041$; Fig. 4). Only travertine cementation was negatively correlated with abundance by itself. Abundance did not correlate with water chemistry or biotic variables. Although evidence from concurrent and previous studies (Adams, 2006, 2014) suggests that benthic insect abundance and biomass should correlate with crayfish abundance, the benthic samples did not show such pattern in this analysis. The samples were comprised of 97% chironomids and there

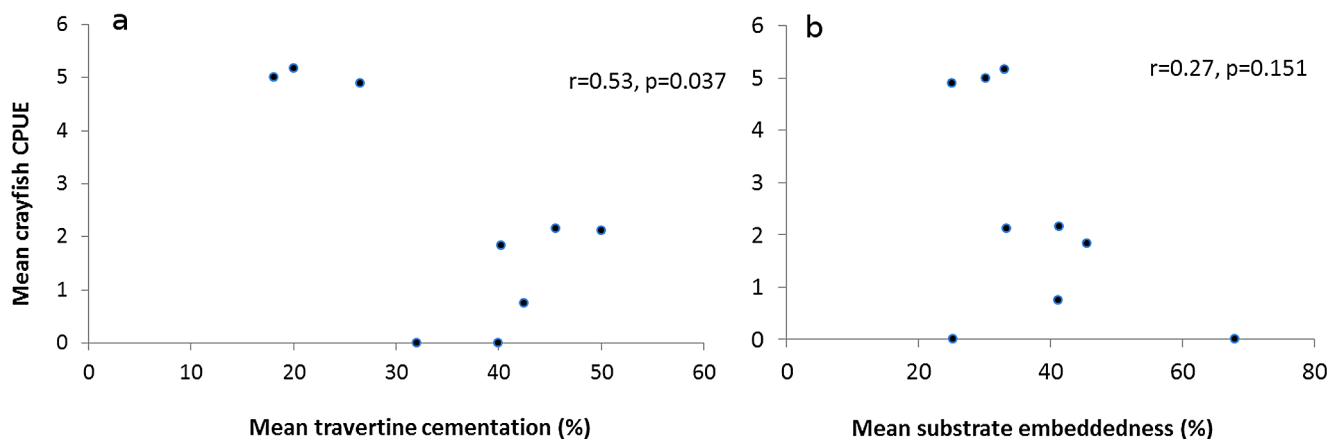


Fig. 4. Crayfish abundance was negatively correlated with the combination of travertine cementation and mean substrate embeddedness (Stepwise regression, $R^2 = 0.60$, $F_{2,7} = 5.213$, $P = 0.041$). Only the percentage of travertine cementation was significantly correlated by itself. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

is evidence that chironomids could not be susceptible to this crayfish population (Adams, 2014).

Size Distribution Analysis

The mean size of the crayfish was also significantly predicted by reach (GLM, $\chi^2 = 7.859$, $P = 0.0482$). There was evidence that both native fish abundance ($\chi^2 = 7.480$, $P = 0.006$) and exotic fish abundance ($\chi^2 = 4.787$, $P = 0.029$) were significant predictors of mean crayfish abundance. Neither mean instantaneous flow ($\chi^2 = 2.173$, $P = 0.141$) nor travertine growth rate ($\chi^2 = 0.944$, $P = 0.319$) were predictors of crayfish abundance.

Crayfish sizes between reaches differed before and after restoration as shown by a significant interaction ($F_{1,404} = 8.971$, $P = 0.003$). However, there was not significant variation in the overall mean size between reaches ($F_{1,404} = 2.375$, $P = 0.124$) or temporal variation before and after restoration ($F_{1,404} = 1.426$, $P = 0.233$). The interaction occurred due to a change in the mean size in the reach with prior travertine formation (T2) where the mean carapace length was significantly decreased from 45.9 ± 1.0 mm CPL to 40.0 ± 0.4 mm CPL after restoration (Tukey's HSD, $\alpha = 0.05$, $Q = 2.580$; Fig. 4). The mean size in the reach impacted by travertine (T1) had a mean size of 39.9 ± 1.1 mm CPL before restoration and a mean of 54.5 ± 1.9 mm CPL after restoration ($n = 6$). There was also a slight but significant increase in crayfish size where non-native fishes were removed (F1), with size increasing from 38.9 ± 0.5 mm CPL to 40.1 ± 0.2 mm CPL. This was coupled with an opposite trend in the reach where non-native fishes remained (F2), where crayfish size decreased from 40.0 ± 0.3 mm CPL to 37.1 ± 0.2 mm CPL (Tukey's HSD, $\alpha = 0.05$, $Q = 2.571$; Fig. 4).

DISCUSSION

Large restoration projects create ecological conditions that allow for studying species responses to large manipulations at relatively large scales, making these studies relevant to scientists and managers (Marks et al., 2010). The experimental design of this study, however, precludes full replication of treatments. Because restoration treatments varied along the river it is difficult to attribute crayfish responses to any single variable (flow, travertine, fish composition) (Underwood, 1992). We nevertheless maintain that these large-scale experiments deepen our understanding of factors that control crayfish abundance and will help predict crayfish responses to other restoration projects.

In this study we observed shifts in the abundance and size distribution of an invasive crayfish after stream restoration that can be attributed to changes in the predatory fish regime and modifications to the physical habitat. The restoration of an unregulated flow regime did not have general negative impacts on crayfish. The upper limit to crayfish abundance in this river likely depends on the influence of the local physical habitat and predatory vulnerability to the dominant fish species. These factors may prevent further upstream invasion by this invasive crayfish.

Changes in predatory fishes (abundance and composition) had an impact on crayfish during this study as evidenced by an interactive response in crayfish abundance during

restoration. Contrary to predictions, crayfish abundance was not substantially increased by restoration. In correlative studies, the predatory control of crayfish by fishes is often supported by reductions in crayfish abundance following the introduction or increase of the density of fish predators (Svardson, 1972; Rach and Bills, 1989; Townsend, 2003; Nystrom et al., 2006; Fortino and Creed, 2007; Hein et al., 2007). Roundtail chub have been found to prey on crayfish when presented the choice, but smallmouth bass are more aggressive predators and are more adept at overcoming defense posturing (Arena et al., 2012; Adams, 2014). The changes in abundance in this study, by replacing one fish predator for another, suggests that there may have been changes in predatory pressure by fish and partially supports the predatory regulation of crayfish abundance in streams (Svardson, 1972; Lodge and Hill, 1994; Dorn and Mittlebach, 1999; Usio and Townsend, 2000; Garvey et al., 2003; Nystrom et al., 2006). The differences in Fossil Creek were nevertheless small.

Predatory regulation in this system may also be influenced by features of the physical habitat as demonstrated by an unexpected decrease in crayfish abundance after restoration in the continued presence of exotic fishes downstream. It was predicted that there would be no change in crayfish abundance due to the continued presence of smallmouth bass. The decrease could have been the result of habitat modifications after flow restoration that increased the vulnerability of juvenile crayfish to the smallmouth bass (Stein, 1977; Blake and Hart, 1993; Englund, 1999). Instead of an increase in channel width in non-travertine areas there were increases in the depth of the channel and an increase in flow velocity (Compton et al., 2009). The initial distribution of juvenile crayfish is dependent on the habitat preferences of gravid females and is a function of survival from predation in those areas (Stein, 1977; Blake and Hart, 1993). Deeper water after restoration could have allowed better access to the breeding areas of gravid females by fish predators resulting in decreased juvenile survival and recruitment.

Trends in crayfish size distributions after restoration appeared to be an interactive response to changes in fish predation and physical factors. The mean size of a crayfish population should increase over time under more intense and continuous predatory pressure on juvenile crayfish (Momot and Gowing, 1977; Stein, 1977; Englund and Kruppa, 2000; Seiler and Turner, 2004). We saw evidence of this pattern in the furthest upstream travertine reach where native fish abundance and travertine deposition increased. Crayfish size also increased above the fish barrier where exotic fishes were removed; however, this pattern was not evident in between those two reaches where native fishes also increased. The reach with travertine deposition before restoration did have some isolated side channels without travertine that could have been breeding areas for crayfish, but these areas were also exposed to the fish. In contrast, there was a decrease in size below the barrier after restoration where smallmouth bass abundance remained similar. Predation is not the only factor that can regulate the mean size of a population and crayfish growth is often correlated with productivity and food availability (Momot, 1984; Rabeni, 1992; Nystrom et al., 2006; Olsson and Nystrom, 2009). We

did not measure productivity and food availability directly, but indirect predatory effects on juvenile crayfish include restriction to foraging for resources (Stein, 1977; Momot, 1984; Olsson and Nystrom, 2009). The decrease in the overall mean size of the crayfish below the barrier, with decreases in crayfish abundance, may have been influenced by decreased growth in response to indirect effects from the smallmouth bass (Nystrom, 2005).

Further evidence that physical habitat factors can impact crayfish abundance was demonstrated by the reduction in crayfish by travertine deposition. Rapidly forming travertine reach in the upstream halted the migration of crayfish. During the two years after restoration until their disappearance, the mean size distribution of the remaining crayfish also increased, indicating decreases in juvenile survival (Momot and Gowing, 1977; Stein, 1977; Englund and Kruppa, 2000). The only abiotic factors measured in our study that showed a negative correlation to crayfish abundance were related to substrate and were the percentage of travertine and particle embeddedness. Travertine deposition does not appear to directly impact the health of crayfish (Adams, 2006), but it does cover the substrate and impact the habitat. In some upstream sections, travertine growth averaged more than 10 mm/year following restoration (Fuller et al., 2011). We observed substantial covering and filling of interstitial spaces between gravel and cobbles which likely decreased the available shelter from predation for juvenile crayfish (Englund, 1999; Usio and Townsend, 2000; Usio, 2007; Olsson and Nystrom, 2009). An alternate hypothesis could be that crayfish are vulnerable to travertine deposition on their carapaces. Although we have observed travertine coated crayfish surviving in the reach, further tests would be needed to test this hypothesis.

This research highlights considerations for strategies for managing and preventing the spread of invasive crayfish populations. Fish predation is a potential control agent (Svardson, 1972; Hein et al., 2007; Aquiloni et al., 2010; Gherardi et al., 2011; Tetzlaff et al., 2011) but the effectiveness of the control is not always supported (Gowing and Momot, 1979; Hill and Lodge, 1994; Hein et al., 2007; Roell and DiStefano, 2010; Gerardi et al., 2011). This study suggests that considerations for the use of fish as a control agent in streams includes the effectiveness of the proposed predatory species and the vulnerability of the crayfish in the targeted environment. A strategy based on predatory fish alone, however, does not address the persistence of adult crayfish in the system (Hein et al., 2006). The manual removal of crayfish, which is biased toward adult crayfish (Bills and Markings, 1988; Kerby et al., 2004; Adams, 2006; Hein et al., 2006) can supplement and increase the effectiveness of predation (Hein et al., 2007) and is an advocated strategy for short segments of streams (Kerby et al., 2004; Aquiloni et al., 2010).

It has also been suggested that manual removal of invasive crayfish in lotic systems may be more effective after high flow events especially in conjunction with downstream barriers (Rach and Bills, 1989; Kerby et al., 2004). Kerby et al. (2004) suggested that barriers with water velocities of 0.30 m/s or greater can prevent upstream movement of crayfish. Barriers (in the form of waterfalls approaching

5 m in height) did not prevent establishment of crayfish in the upper reaches of Fossil Creek before restoration. Large floods are not uncommon in Fossil Creek due to its high gradient (Malusa et al., 2003) and a couple of larger floods have occurred in Fossil Creek after restoration (Fuller et al., 2011; Adams, 2014). Fluctuations in crayfish abundance were observed, but there were not sustained decreases except upstream. Such a strategy should therefore include careful consideration of the role of the substrate in protection during high flow events (Parkyn and Collier, 2004). It may be worthwhile to test if re-establishment by an invading crayfish population may be deterred after high flow events if manual removal is coupled with the sustained use of predatory pressure by fish.

In conclusion, crayfish abundance was influenced by both changes in the dominant fish species and changes in the physical environment by travertine deposition during restoration. Contrary to initial concerns by managers and scientists, we did not find a substantial predatory release but there were significant differences in abundance. Modifications in the physical habitat by travertine deposition also likely interacted with changes in predation. These factors may help prevent further upstream invasion of this system. The upper limit of crayfish abundance has been found in other research to be imposed by the carrying capacity of the substrate with predation determining the actual abundance (Nystrom et al., 2006). These observations may be useful for predicting factors that determine the impact and regulation of crayfish abundance during establishment and spread in lotic systems.

ACKNOWLEDGEMENTS

We thank T. Theimer, A. Gibb, and D. Ward whose wise guidance and constructive criticism helped shape and strengthen this work. The Marks Laboratory of Aquatic Ecology and the Merriam-Powell Center for Environmental Research provided intellectual discussions, constructive critique, and collaborative thoughtfulness. We also like to thank two anonymous reviewers for their thoughtful and helpful review and critique of the manuscript. We thank a talented and caring cast of student workers, field helpers, and collaborators, including Z. Compson, M. James, T. Adams-Clark, L. Clark, B. Harrop, J. Maestas, K. Maldonado, C. Sawyer and J. Edwards.

REFERENCES

- Acosta, C. A., and S. A. Perry. 2000. Effective sampling area: a quantitative method for sampling crayfish in freshwater marshes. *Crustaceana* 73: 4225-4231.
- Adams, K. J. 2006. The potential consequences of stream restoration on an exotic crayfish population. M.S. Thesis, Northern Arizona University, Flagstaff, AZ, USA.
- . 2014. Conditions influencing the spread of invasive crayfish during restoration and its consequences. Ph.D. Thesis, Northern Arizona University, Flagstaff, AZ, USA.
- Aquiloni, L., S. Brusconi, E. Cecchinelli, E. Tricarico, G. Mazza, A. Paglianti, and F. Gherardi. 2010. Biological control of invasive populations of crayfish: the European eel (*Anguilla anguilla*) as a predator of *Procambarus clarkia*. *Biological Invasions* 12: 3817-3824.
- Arena, A., L. A. Ferry, and A. C. Gibb. 2012. Prey capture behavior of native vs. nonnative fishes: a case study from the Colorado River drainage basin (USA). *Journal of Experimental Zoology* 31: 103-116.
- Bills, T. D., and L. L. Marking. 1988. Control of nuisance populations of crayfish with traps and toxicants. *Progressive Fish-Culturist* 50: 103-106.
- Blake, M. A., and P. J. B. Hart. 1993. Habitat preferences and survival of juvenile signal crayfish, *Pacifastacus leniusculus* – the influence of water depth, substratum, predatory fish, and gravid female crayfish. *Freshwater Crayfish* 9: 318-328.

- Brusconi, B., S. Bertocchi, B. Renai, M. Scalici, C. Souty-Grosset, and F. Gherardi. 2008. Conserving indigenous crayfish: stock assessment and habitat requirements in the threatened *Austropotamobius italicus*. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 1227-1239.
- Carpenter, J. 2005. Competition for food between an introduced crayfish and two fishes endemic to the Colorado River basin. *Environmental Biology of Fishes* 72: 335-342.
- Casas, J. J., and M. O. Gessner. 1999. Leaf litter breakdown in a Mediterranean stream characterized by travertine precipitation. *Freshwater Biology* 41: 781-793.
- Compton, Z. G., M. Z. Mier, and J. C. Marks. 2009. Effects of travertine and flow on leaf retention in Fossil Creek, Arizona. *Hydrobiologia* 630: 187-197.
- 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.
- Dorn, N. J., and G. G. Mittelbach. 1999. More than predator and prey: a review of interactions between fish and crayfish. *Vie et Milieu* 49: 229-237.
- Englund, G. 1999. Effects of fish on the local abundance of crayfish in stream pools. *Oikos* 87: 48-56.
- , and J. J. Krupa. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshwater Biology* 43: 75-83.
- Fortino, K., and R. F. Creed. 2007. Abiotic factors, competition, or predation: what determines the distribution of young crayfish in a watershed? *Hydrobiologia* 575: 301-314.
- Fuller, B. M., L. S. Sklar, Z. G. Compton, K. J. Adams, J. C. Marks, and A. C. Wilcox. 2011. Ecogeomorphic feedbacks in regrowth of travertine step-pool morphology after dam decommissioning, Fossil Creek, Arizona. *Geomorphology* 126: 314-332.
- Garvey, J. E., J. E. Rettig, R. A. Stein, D. M. Lodge, and S. P. Klosiewski. 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. *Ecology* 84: 3339-3348.
- Gherardi, F., L. Aquiloni, J. Dieguez-Urbeondo, and E. Tricarico. 2011. Managing invasive crayfish: is there a hope? *Aquatic Sciences* 73: 185-200.
- Gowing, H., and W. T. Momot. 1979. Impact of brook trout (*Salvelinus fontinalis*) predation on the crayfish *Orconectes virilis* in three Michigan lakes. *Journal of the Fisheries Research Board of Canada* 36: 1191-1196.
- Hagen, H. A. 1870. Monograph of the North American Astacidae. Illustrated Catalog of the Museum of Comparative Zoology at Harvard College 3: i-viii, 1-19.
- Hein, C. L., B. M. Roth, A. R. Ives, and M. J. Vander Zanden. 2006. Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 383-393.
- , M. J. Vander Zanden, and J. J. Magnuson. 2007. Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biology* 52: 1134-1146.
- Herborg, L. M., C. L. Jerde, D. M. Lodge, G. M. Ruiz, and H. J. MacIsaac. 2007. Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications* 17: 663-674.
- Hill, A. M., and D. M. Lodge. 1999. Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. *Ecological Applications* 9: 678-690.
- Hobbs III, H. H., J. P. Jass, and J. V. Huner. 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). *Crustaceana* 56: 299-316.
- Kerby, J. L., S. P. D. Riley, L. B. Kats, and P. Wilson. 2004. Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams. *Biological Conservation* 126: 402-409.
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199-204.
- , and ———. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* 298: 1233-1236.
- Light, T. 2003. Success and failure in a lotic crayfish invasion: the roles of hydrologic variability and habitat alteration. *Freshwater Biology* 48: 1886-1897.
- Lodge, D. M., and A. H. Hill. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nordic Journal of Freshwater Research* 69: 111-136.
- , C. A. Taylor, D. M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries* 7: 7-20.
- Maazono, 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 Jr., and S. Overby. 2003. Processes influencing travertine precipitation and aquatic habitat formation, Fossil Creek, Arizona. *Applied Geochemistry* 18: 1081-1094.
- Marks, J. C., M. E. Power, and M. S. Parker. 2000. Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos* 90: 20-27.
- , G. A. Haden, M. O'Neill, and C. Pace. 2010. Effects of flow restoration and exotic species removal on recovery of native fish: lessons from a dam decommissioning. *Restoration Ecology* 18: 934-943.
- McCarthy, J. M., C. L. Hein, J. D. Olden, and M. J. Vander Zanden. 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology* 51: 224-235.
- Momot, W. T. 1984. Crayfish production: a reflection of community energetics. *Journal of Crustacean Biology* 4: 35-54.
- . 1995. Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science* 3: 33-63.
- , and H. Gowing. 1977. Results of an experimental fishery on the crayfish *Orconectes virilis*. *Journal of the Fisheries Research Board of Canada* 34: 2056-2066.
- Muehlbauer, J. D., C. J. LeRoy, J. M. Lovett, K. K. Flaccus, J. K. Vlieg, and J. C. Marks. 2009. Short-term responses of decomposers to flow restoration in Fossil Creek, Arizona, USA. *Hydrobiologia* 618: 35-45.
- Nystrom, P. 2005. Non-lethal predator effects on the performance of a native and an exotic crayfish species. *Freshwater Biology* 50: 938-1949.
- , C. Bronmark, and W. Graneli. 1996. Patterns in benthic food webs: a role for omnivorous crayfish? *Freshwater Biology* 36: 631-646.
- , P. Stenroth, N. Holmqvist, O. Berglund, and P. Larsson. 2006. Crayfish in lakes and streams: individual and population responses to predation, productivity and substratum availability. *Freshwater Biology* 51: 2096-2113.
- Olsson, K., and P. Nystrom. 2009. Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*). *Freshwater Biology* 54: 35-46.
- Palmer, M. A., E. S. Bernhardt, J. D. Allen, P. S. Lake, G. Alexander, S. Brooks, J. Carr, S. Clayton, C. N. Dahm, J. Follstad Shah, D. L. Galat, S. G. Loss, P. Goodwin, D. D. Hart, B. Hassett, R. Jenkinson, G. M. Kondolf, R. Lave, J. L. Myer, T. K. O'Donnell, L. Pagano, and E. Suddath. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* 42: 208-217.
- Parkyn, S. M., and K. J. Collier. 2004. Interaction of press and pulse disturbance on crayfish populations: flood impacts in pasture and forest streams. *Hydrobiologia* 527: 113-124.
- Platts, W., W. Megahan, and G. Minshall. 1983. Methods for Evaluating Stream, Riparian and Biotic Conditions. U.S.D.A. Forest Service, General Technical Report INT-138. Intermountain Forest and Range Experiment Station, Ogden, UT.
- Rabeni, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1714-1721.
- Rach, J. J., and T. D. Bills. 1989. Crayfish control with traps and largemouth bass. *Progressive Fish-Culturist* 51: 157-160.
- Reynolds, J. D. 2011. A review of ecological interactions between crayfish and fish, indigenous and introduced. *Knowledge and Management of Aquatic Ecosystems* 401: 10, 1-21.
- Roell, M. J., and R. J. DiStefano. 2010. Effects of a conservative rock bass length limit on angler participation, sport fish populations, and crayfish prey in a Missouri Ozark stream. *North American Journal of Fisheries Management* 30: 552-564.
- Seiler, S. M., and A. M. Turner. 2004. Growth and population size of crayfish in headwater streams: individual- and higher-level consequences of acidification. *Freshwater Biology* 49: 870-881.
- Stein, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58: 1237-1253.
- Svardson, G. 1972. The predatory impact of eel (*Anguilla anguilla* L.) on populations of crayfish (*Astacus astacus* L.). Report of the Institute of Freshwater Research, Drottningholm 52: 149-191.
- Taylor, C. A., G. A. Schuster, J. E. Cooper, R. J. DiStefano, A. G. Eversole, P. Hamr, H. H. Hobbs III, H. W. Robison, C. E. Skelton, and R. F.

- Thomas. 2011. A reassessment of the conservation status of crayfishes of the United States and Canada after 10+ years of increased awareness. *Fisheries* 32: 372-389.
- Tetzlaff, J. C., B. M. Roth, B. C. Weidel, and J. F. Kitchell. 2011. Predation by native sunfishes (Centrarchidae) on the invasive crayfish *Orconectes rusticus* in four northern Wisconsin lakes. *Ecology of Freshwater Fish* 20: 133-143.
- Townsend, C. R. 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology* 17: 38-47.
- Underwood, A. J. 1992. Beyond BACI: the detections of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology* 161: 145-178.
- Usio, N. 2007. Endangered crayfish in northern Japan: distribution, abundance and microhabitat specificity in relation to stream and riparian environment. *Biological Conservation* 134: 517-526.
- , and C. R. Townsend. 2000. Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physico-chemistry, predatory fish, and invertebrate prey. *New Zealand Journal of Marine and Freshwater Research* 34: 557-567.
- Weedman, D. A., P. Sponholtz, and S. Hedwall. 2005. Fossil Creek Native Fish Restoration Project. Arizona Game and Fish Department, Phoenix, AZ.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16: 454-459.

RECEIVED: 5 April 2016.

ACCEPTED: 2 July 2016.

AVAILABLE ONLINE: 22 July 2016.