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ERADICATION OF INVASIVE *TAMARIX RAMOSISSIMA* ALONG A DESERT STREAM INCREASES NATIVE FISH DENSITY

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Abstract. Spring ecosystems of the western United States have high conservation value, particularly because of the highly endemic, and often endangered, fauna that they support. Refuges now protect these habitats from many of the human impacts that once threatened them, but invasive species often persist. Invasive saltcedar is ubiquitous along streams, rivers, and spring ecosystems of the western United States, yet the impact of saltcedar invasion on these ecosystems, or ecosystem response to its removal, have rarely been quantified. Along Jackrabbit Spring, a springbrook in Nevada that supports populations of two endangered fish (Ash Meadows pupfish and Ash Meadows speckled dace) as well as several exotic aquatic consumers, we quantified the response of aquatic consumers to large-scale saltcedar removal and identified the mechanism underlying consumer response to the removal. Clearing saltcedar from the riparian zone increased densities of native pupfish and exotic screw snails, but decreased the density of exotic crayfish. Positive effects of saltcedar removal on pupfish and snails occurred because saltcedar heavily shades the stream, greatly reducing the availability of algae for herbivores. This was confirmed by analyses of potential organic matter sources and consumer ^{13}C: pupfish and snails, along with native dace and exotic mosquitofish, relied heavily on algae-derived carbon and not saltcedar-derived carbon. By contrast, crayfish $\delta^{13}C$ values mirrored algae $\delta^{13}C$ during summer, but in winter indicated reliance on allochthonous saltcedar litter that dominated organic inputs in saltcedar reaches and on algae-derived carbon where saltcedar was absent. The seasonal use of saltcedar by crayfish likely explains its negative response to saltcedar removal. Clearing saltcedar effectively restored the springbrook of Jackrabbit Spring to the conditions characteristic of native vegetation sites. Given the high conservation value of spring ecosystems and the potential conservation benefits of saltcedar removal that this research highlights, eradicating saltcedar from spring ecosystems of the western United States should clearly be a management priority.

Key words: biological invasion; crayfish; desert springbrook; ecosystem restoration; food web; mosquitofish; pupfish; screw snail; speckled dace; stable isotope; Tamarix.

INTRODUCTION

Springs and associated habitats (e.g., springbrooks, marshes, etc.) of the arid western United States support a highly endemic fauna that includes fish, aquatic insects, and mollusks and contribute dramatically to local and regional biodiversity (Williams et al. 1985, Abell et al. 2000). Human activities such as water diversion and groundwater pumping, habitat destruction, and species introductions have dramatically altered or, in the case of water diversion, totally eliminated many of the spring ecosystems in the western United States (Williams et al. 1985, Minckley et al. 1991). Although 16 species and subspecies of fish from western U.S. spring ecosystems are already extinct because of human activities (Meffe 1989), the prospects for many of the extant species of aquatic spring fauna have been improved with the creation of refuges that protect the springs that support these species (Williams 1991). While the creation of protected refuges has lessened or eliminated the threats that human activities such as water diversion or habitat destruction posed to spring ecosystems, introduced species persist in these systems because they are often difficult or impossible to remove without also eliminating native species (Williams 1991).

Anthropogenic biological invasions are one of the most pervasive features of global change (Lodge 1993, Vitousek et al. 1996). Multiple invaders in a habitat are commonplace and research efforts need to address this reality if they are to be relevant to land managers. Effective management and/or eradication of invasive species require knowledge of individual invader impacts so that management actions can be prioritized. Further, when multiple invaders are present, knowledge of interactions between invasive and native species is critical to determine whether potential management actions might lead to unwanted secondary impacts (Zavaleta et al. 2001). For example, eradication of an ex-

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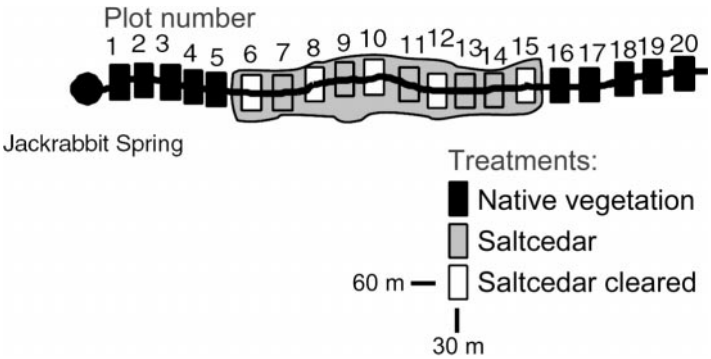

FIG. 1. Schematic of the study site at Jackrabbit Spring, Ash Meadows National Wildlife Refuge, Nevada, USA. The five native vegetation sites immediately downstream of Jackrabbit Spring are in warm water (native upstream sites), while the five native vegetation sites downstream of the saltcedar stand are in cooler water (native downstream sites). The schematic is not to scale: the minimum distance between cleared and saltcedar plots is 20 m, while the minimum distance between native vegetation plots is 30 m (modified from Kennedy and Hobbie [2004]).

otic predator could lead to huge increases in an exotic prey species because of predator release; such knowledge of species interactions is very often lacking. Exotic species threaten the persistence of >50% of the endangered species in North America (Wilcove et al. 1998), so documenting the cascading effects of invasive species is especially critical in habitats that support endangered species.

Saltcedar (*Tamarix ramosissima* (Ledeb)), a tree native to Eurasia, was intentionally introduced to arid regions of the western United States in the mid-1800s as an ornamental tree and to prevent soil erosion (Everitt 1980). Though the spread of saltcedar was initially slow, its range rapidly expanded during the 1930s, perhaps because of widespread drought, clearing of native riparian forests, and water diversions and the installation of dams that altered stream and river flow regimes (Everitt 1980). It is currently the dominant tree of riparian forests along streams and rivers throughout the western United States, covering over 600 000 ha of this habitat (DiTomaso 1998), and it is also common along springs and springbrooks throughout this region (Sada et al. 2001).

Jackrabbit Spring (JRS; see Plate 1), in the Ash Meadows National Wildlife Refuge (hereafter Ash Meadows), is a model system to examine how the removal of a dominant invasive species (saltcedar) affects native and nonnative consumer abundance in spring ecosystems of the western United States. Ash Meadows is a desert wetland complex fed by >30 springs and seeps in the Mojave Desert of southwestern Nevada (Soltz and Naiman 1978). Five fish and at least 11 invertebrates are endemic to the aquatic habitats of Ash Meadows (Williams et al. 1985). Jackrabbit Spring supports populations of two of these endemic fish, the federally endangered Ash Meadows speckled dace (*Rhinichthys osculus nevadensis* (Girard)) and the Ash Meadows pupfish (*Cyprinodon nevadensis mionectes* (Miller)) (Anonymous 1999). The purpose of this research was to determine (1) what impact saltcedar removal has on native and nonnative consumers, (2) whether removal of saltcedar is an effective restoration tool, (3) the food web structure and trophic interactions of consumers in JRS, and (4) whether potential shifts in consumer abundance arise from the effect of saltcedar removal on resource availability.

METHODS

Experimental design and site description

Twenty 30 × 60 m research plots were established in June 1998 along a 3-km reach of JRS (Fig. 1). Native vegetation dominated the riparian zone of the five furthest upstream and the five furthest downstream plots. Saltcedar dominated the riparian zone of the 10 middle plots. Plots were roughly evenly spaced and the minimum distance between plots was 20 m. Saltcedar was removed from five of the 10 plots dominated by saltcedar in February and April 1999 using the cut-stump method (Sudbrock 1993); saltcedar trees were cut at their base using a chainsaw, the stumps were sprayed with Garlon 4 herbicide (Dow Agrosciences, Indianapolis, Indiana, USA) to prevent resprouting, and the downed trees were dragged out of the plot. To account for the effects of a downstream temperature gradient, we used a blocked design to determine which plots would be cleared of saltcedar.

Sampling prior to clearing saltcedar revealed no differences in consumer abundance in the stream reaches where saltcedar was left intact relative to sites that were eventually cleared of saltcedar (Kennedy 2002). Thus, differences in consumer abundance between removal and non-removal plots are assumed to be due to treatment effects. This study design yielded four riparian vegetation types (native vegetation upstream, native vegetation downstream, saltcedar, cleared) with five replicates of each vegetation type.

Native vegetation plots had only scattered ash (*Fraxinus velutina* (Torrey)) and mesquite (*Prosopis pubescens* (Benth.)) trees leading to an open canopy above the stream. High densities of the emergent macrophyte bulrush (*Scirpus americanus* (Pers.)) lined the stream banks in native vegetation reaches and also quickly colonized cleared reaches (Kennedy and Hobbie 2004). In contrast, the canopy was closed at saltcedar sites because of dense saltcedar trees, and bulrush were rare (see photographs in the Appendix). During this study, algae productivity was more than twofold greater in

PLATE 1. Jackrabbit Spring, Ash Meadows National Wildlife Refuge, Nevada. The pool measures ~10 m across and ~3 m deep and has a discharge of ~47 liters per second. The location of the outflow is to the right of the photograph. Photo Credit: T. A. Kennedy.

cleared and native upstream sites relative to saltcedar and native downstream sites, and allochthonous litter inputs were tenfold greater at saltcedar sites relative to all other sites (Kennedy and Hobbie 2004). Native downstream reaches lie in the transition zone between the spring runs that are upstream (wider and more open *thalweg,* vertical walled channel, unsaturated soils adjacent to stream, high algae productivity, and low benthic organic matter) and the large ciénega that is downstream (riparian marshland with narrower and closed *thalweg* and/or braided channel, sloping channel walls, permanently saturated soils adjacent to stream, low algae productivity and high benthic organic matter; T. A. Kennedy, *personal observations*).

Jackrabbit Spring has an average depth of 0.25 m and width of 1.01 m. Stream substrate consists of very fine inorganic and organic particles (i.e., <0.1 mm), and bulrush provide virtually the only stable substrate (T. A. Kennedy, *personal observations*). There is a strong downstream decline in water temperature during the winter months (mean daily water temperature at the springhead is 28°C and ~12–14°C at the furthest downstream site), but water temperature is relatively constant across sites during the summer (27°–29°C; Kennedy 2002). The limestone geology of the Ash Meadows groundwater basin results in relatively high carbonate alkalinity (total dissolved inorganic carbon ~4.4 mmol/L), pH (~7.5–8.3), and specific conductance (~800 μS/cm) (Kennedy 2002).

Consumer species

Ash Meadows pupfish (hereafter pupfish) are most abundant in the warmer water of the spring pools at Ash Meadows, while Ash Meadows speckled dace (hereafter dace) are common throughout the length of the outflow streams, from the warm water near the spring pool to the cool water of the ciénagas downstream (Soltz and Naiman 1978). Pupfish consume filamentous algae almost exclusively (Naiman 1975), but the relative contribution of invertebrates and microbes associated with algae, vs. the algae itself, to pupfish production is unclear. Dace are water-column and benthos-feeding omnivores, and in other systems they have been shown to preferentially consume invertebrates (Angradi et al. 1991).

The red swamp crayfish (*Procambarus clarkii*) is native to the southeastern United States but has been introduced for use as a human food source to 14 additional states (Benson 2000). Crayfish are opportunistic omnivores and will consume anything from detritus to algae to invertebrates (Gutierrez-Yurrita et al. 1998). Introduced crayfish have been linked to declines in native fish abundance through predation of fish eggs (Soltz and Naiman 1978).

Mosquitofish (*Gambusia affinis*) are native to southern Texas and northern Mexico, but have been introduced to 34 additional U.S. states and 21 countries, ostensibly for mosquito control (Benson 2000). Mosquitofish prey on invertebrates and the eggs and fry of native fish and have been linked to the extinction and decline of native fish due to predation and competition (Schoenherr 1981, Courtenay and Meffe 1989).

The screw snail (*Melanoides tuberculata*) is native to tropical Africa, Asia, and parts of Oceania, but is now distributed worldwide due to transport and introductions associated with the aquarium trade (Contreras-Arquieta and Contreras-Balderas 2000). Screw snails are grazers of benthic algae. The impacts of screw snail invasion are largely undocumented, although declines and local extinctions of native mollusks have been reported for some springs in Mexico following screw snail invasion (Contreras-Arquieta and Contreras-Balderas 2000). We collected several other types of macroinvertebrates from JRS (e.g., Zygoptera, chironomids, Trichoptera), but their densities were too low to quantify or analyze for isotopic composition.

Consumer abundance

Screw snail abundance was quantified on 10 December 1999 and 22 June 2000 using a Hess sampler with a sampling area of 95 cm^2 (Benke 1996). Four samples, two from each of two permanently marked transects within a plot, were collected, and all snails greater than 1 mm in width were counted to determine snail density.

Crayfish and fish abundance was quantified using standardized minnow trapping on 10–13 December 1999 and 29 June to 2 July 2000. Trapping was conducted with a government biologist (David St. George, Ash Meadows National Wildlife Refuge) and handling of pupfish and dace was done in accordance with federal and state endangered species research regulations. Plots were sampled from upstream to downstream with five plots sampled each day. The weather was comparable across all four days of each sampling effort. Four minnow traps, baited with dry dog food, were placed within each reach around sunrise. Traps were evenly spaced within the middle 20 m of each reach and were thus never closer than 5 m to the edge of a reach. Minnow traps have an effective trapping radius of at least 2 m for fish (Bryant 2000). This sampling protocol ensured that fish, and presumably crayfish, in the middle of any given reach were never far from a trap (~2.5 m) and also minimized the chance of capturing individuals from outside of the plot. Traps were checked after 4–6 h. Fish were marked with a small caudal fin clip and crayfish were marked by removing a posterior leg. All animals were released immediately after marking, and then the traps were reset and later rechecked after a second 4–6 h trapping period.

It was not possible to estimate species density using mark-recapture methods because the number of individuals, particularly marked ones, captured during the second trapping was generally low. Data presented are the total number of unmarked fish or crayfish captured within each 30-m reach during the two trapping periods, after standardizing for differences in trapping effort and habitat area among plots.

Because there were only five replicates of each vegetation type and variances were unequal, we used the Dwass nonparametric multiple comparisons method based on pairwise rankings to make statistical comparisons of consumer abundance among vegetation treatments (Hollander and Wolfe 1999). We compared consumer density in saltcedar vs. cleared plots to determine whether consumer populations responded to saltcedar removal. We then compared consumer density at cleared plots with native vegetation plots to determine whether saltcedar removal is an effective restoration tool and results in consumer densities typical of pre-saltcedar conditions. We chose to evaluate the impact of saltcedar removal and its effectiveness as a restoration tool from a population level rather than a community level because the main goal for restoration in a system like this is not to exactly replicate community structure at native vegetation sites where undesirable exotic consumers may be abundant. Rather, the goal for restoration is to increase the density of native fish and, if possible, reduce the density of exotic consumers, particularly ones that have the potential to adversely affect native species in JRS (i.e., mosquitofish and crayfish).

Isotope methods

We used stable isotope analysis to identify trophic relationships among consumers and determine whether saltcedar removal affects consumer density via shifts in resource availability. Carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, respectively) are powerful tools for tracking energy flow through food webs (DeNiro and Epstein 1978, Fry and Sherr 1984) and have also recently been used to study the consequences of species invasions (Vander Zanden et al. 1999). Because terrestrial (leaf litter) and aquatic (algae and emergent vegetation) organic matter sources often have distinct $\delta^{13}C$ signatures (Fry and Sherr 1984), and these signatures are largely conserved up the food chain, they can provide information about the carbon basis of secondary production (Peterson and Fry 1987, Peterson et al. 1993, Finlay 2001). In contrast, $\delta^{15}N$ values become enriched by an average of 3.4‰ with each trophic transfer and therefore provide an indication of trophic

TABLE 1. Consumer abundance (means, with SE in parentheses) by vegetation type and time of year.

Species	Native upstream	Cleared	Saltcedar	Native downstream
December 1999				
Speckled dace	12.4[a] (1.8)	8.5[ab] (1.6)	7.3[b] (2.0)	18.2[c] (2.2)
Pupfish	19.1[a] (10.5)	3.7[a] (2.1)	0.3[b] (0.3)	0[b] (0)
Crayfish	25.3[ab] (11.5)	5.9[a] (1.3)	12.0[b] (3.2)	17.1[b] (5.1)
Mosquitofish	26.8[a] (13.3)	11.8[a] (3.6)	17.9[a] (7.9)	3.0[a] (2.3)
Screw snail	2058[a] (910)	3500[a] (1068)	422[b] (137)	143[b] (143)
June 2000				
Speckled dace	23.8[a] (3.4)	13.1[abc] (5.0)	4.8[b] (0.9)	14.8[c] (2.7)
Pupfish	33.7[a] (18.4)	5.2[a] (2.1)	0.1[b] (0.1)	0[b] (0)
Crayfish	64.9[ab] (25.4)	16.4[ab] (3.2)	29.0[a] (10.4)	90.0[b] (18.6)
Mosquitofish	46.5[ab] (20.4)	35.3[a] (7.2)	48.6[ab] (12.8)	19.2[b] (6.3)
Screw snail	5872[a] (2100)	3684[a] (1558)	615[b] (141)	47[c] (47)

Notes: Values for fish and crayfish represent the mean number of each that were caught within a 30-m reach, after standardizing for trapping effort and the width of the reach. Screw snail data presented are the number of individuals per square meter. Different letters across a row indicate a significant difference in consumer abundance among vegetation treatments (nonparametric all-treatments multiple comparisons based on pairwise rankings, $P < 0.05$). The study was conducted at Jackrabbit Spring, Ash Meadows National Wildlife Refuge, Nevada, USA.

position (Minagawa and Wada 1984). Finally, stable isotope analyses provide time-integrated measures of the carbon basis of production and trophic position (Fry and Arnold 1982, Hesslein et al. 1993).

Samples of the most common organic matter sources and macroconsumers were collected from each of the 20 research plots in which they were present in December 1999 and June 2000 and analyzed for carbon and nitrogen stable isotope ratios at the University of California Berkeley Center for Stable Isotope Biogeochemistry (Berkeley, California, USA). For consumers, tissues from 5–10 individuals collected at each plot were pooled and subsequently analyzed, providing an estimate of the mean isotopic ratio for the population at each site (Hershey and Peterson 1996, Lancaster and Waldron 2001). We assumed that stable isotope ratios of fish fin and muscle tissues were similar (Rounick and Hicks 1985). Individual animals (snails, mosquitofish, crayfish) were frozen whole within 2 h of collection and later dissected using a microscope to remove gut contents, bones, and shell fragments (snails, mosquitofish, and crayfish). Fin clips (pupfish and dace) were air-dried immediately after collection. Sample processing for animal, plant, and detritus included an initial rinse with deionized water, followed by acidification with 1 mol/L HCl for 1 h to remove carbonates in shell fragments, bones, and exogenous inorganic carbon. Samples were then thoroughly rinsed with deionized water, oven-dried at 55°C, and pulverized using a steel rod (animal and algae and organic matter) or grinding mill (leaves).

Several ramets, clumps, or leaves from bulrush, filamentous algae, or saltcedar, respectively, were collected from each plot and aggregated for isotopic analysis. *Spirogyra* sp., the dominant filamentous alga in JRS, was cleaned of detritus under a dissecting scope before processing. We only analyzed samples of filamentous algae because it was not possible to collect microalgae forms in sufficient quantity for analysis. Detritus that accumulated on artificial substrates and saltcedar roots that grew into the stream were also analyzed from the limited sites where they were present. The chitinous peduncle of mature screw snails and immature snails that are retained within their shells were removed as part of sample preparation. Crayfish tail muscle and muscle tissue from frozen mosquitofish were used for analysis.

We used regression analysis to test for consumer dependence on autochthonous- vs. allochthonous-derived carbon. Carbon and nitrogen stable isotope values for organic matter, particularly lotic algae, are often spatially variable (Finlay et al. 1999). While this variability can complicate the interpretation of data, it may also provide a ''signal'' of consumer dependence on a specific type of organic matter, for example, if a population of consumers' $\delta^{13}C$ values closely track the spatially variable $\delta^{13}C$ value of a specific organic matter type. To this end, we used the $\delta^{13}C$ values of the dominant autochthonous (algae, bulrush) and allochthonous (saltcedar litter) organic matter sources as predictors of consumer $\delta^{13}C$ at each site. If there was a significant and positive relationship between the $\delta^{13}C$ of an organic matter source and consumer $\delta^{13}C$ across all sites, we concluded the consumer was dependent on that organic matter source.

We analyzed samples of algae collected during both sampling periods but other organic matter types (i.e., saltcedar and bulrush) were only analyzed from samples collected in December 1999, when they were actually available to the food web (Kennedy and Hobbie 2004). It was only possible to conduct bivariate regression, using a single organic matter type as predictor, because filamentous algae were never present in the heavily shaded saltcedar sites. We also evaluated

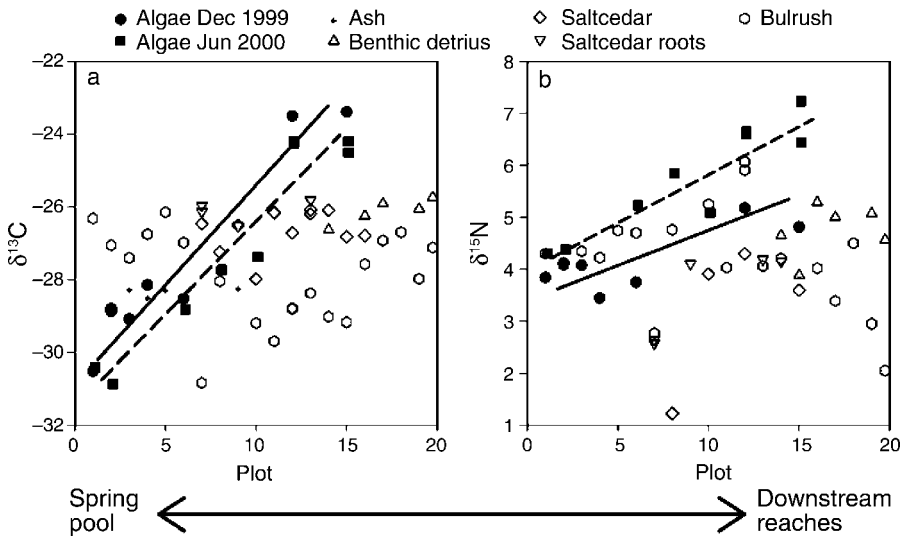

FIG. 2. Carbon and nitrogen stable isotope ratios for the dominant organic matter inputs in Jackrabbit Spring. All samples were collected in early December 1999, and algae samples were also collected in June 2000. Regression lines were added to the algae plots to highlight their downstream pattern of enrichment for both carbon and nitrogen stable isotope ratios.

the relative dependence of consumers on algae-derived carbon using hypothetical data modeled after algae and bulrush isotopic values and a simple two-source mixing model.

RESULTS

Saltcedar removal and consumer abundance

Saltcedar removal led to significant increases in the density of pupfish and exotic screw snails across both sampling periods (Table 1). Crayfish density declined in response to saltcedar removal, although the difference was statistically significant only during the winter sampling period. Although not statistically significant, the density of speckled dace increased, while mosquitofish density decreased, following saltcedar removal.

Consumer density among cleared and native upstream sites was statistically indistinguishable across all sampling periods (Table 1). The density of pupfish, screw snails, and mosquitofish was almost always significantly higher at cleared sites than native downstream sites, while speckled dace and crayfish density was generally higher at native downstream sites relative to cleared sites. In fact, pupfish were never found in native downstream sites and screw snails were found in only the most upstream of the native downstream plots (i.e., plot 16). Consumer density at saltcedar and native downstream sites was comparable, except that speckled dace were always more abundant at native downstream sites.

Stable isotope ratios of organic matter

There was considerable variability and overlap in the $\delta^{13}C$ of organic matter sources among plots but algae $\delta^{13}C$ alone exhibited a linear downstream ^{13}C enrichment that provided a unique tracer of algae-derived carbon (Fig. 2a, Table 2). Bulrush and saltcedar $\delta^{13}C$ values displayed no consistent downstream pattern. Ash litter and saltcedar roots were present in only five or fewer plots and their $\delta^{13}C$ values showed no consistent downstream pattern and spanned a range of <1‰. The $\delta^{13}C$ of benthic detritus displayed a slight downstream enrichment of <1‰ from plots 14–20, the locations where it was present in sufficient quantity for analysis. In contrast, filamentous algae $\delta^{13}C$ values displayed a linear downstream enrichment of 7‰ from the spring pool to plot 15, the furthest downstream plot where it was present, during both December and June (Fig. 2a, Table 2).

Algae $\delta^{15}N$ values also displayed a linear downstream enrichment in both December and June (Fig. 2b). Bulrush $\delta^{15}N$ varied by over 4‰ across the study site. The nitrogen content and size of some saltcedar and all ash litter samples was too low for analysis of $\delta^{15}N$ values. The $\delta^{15}N$ values of saltcedar roots and detritus displayed no consistent downstream trend.

Stable isotope ratios and trophic positions of consumers

The $\delta^{13}C$ for all consumers became ^{13}C enriched along the downstream gradient (Fig. 3, Table 2). Screw snails, mosquitofish, dace, and pupfish $\delta^{13}C$ all increased 4–6‰ from plot 1 to the furthest downstream reach, in both December and June. There was no consistent difference in consumer $\delta^{13}C$ values between saltcedar and adjacent cleared plots.

While crayfish $\delta^{13}C$ exhibited overall enrichment along the downstream gradient, the pattern of enrichment varied between summer and winter (Fig. 3), indicating some seasonal consumption of saltcedar litter. In December, crayfish $\delta^{13}C$ followed the trend observed

TABLE 2. Patterns of downstream enrichment for filamentous algae and consumer carbon stable isotope values and the percentage of algae-derived carbon in consumer diets.

Species	Intercept		Slope		Algae-derived carbon in diet (%)	
	December	June	December	June	December	June
Algae	−30.3	−31.5	(0.50)***	(0.51)***		
Crayfish	−25.2	−25.8	(0.12)***	(0.16)**	24	31
Dace	−25.8	−24.7	(0.28)***	(0.14)***	56	27
Mosquitofish	−25.5	−25.0	(0.22)***	(0.21)***	44	41
Pupfish	−32.3	−29.7	(0.56)*	(0.34)**	112	67
Screw snail	−27.6	−27.4	(0.32)***	(0.27)***	64	53

Notes: Downstream patterns of enrichment were quantified using linear regression analysis with the location along the downstream gradient (i.e., plot number) as the predictor of the raw isotopic data. Data presented are the predicted intercept (i.e., plot 0 = value at springhead) and the slope of downstream enrichment. All regressions were significant (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The percentage of algae-derived carbon in consumer diets was determined by dividing consumer slope by the algae slope for each date (see *Results* for justification).

for other consumers only in native vegetation plots upstream and downstream of the saltcedar reach. Within the saltcedar-dominated section of the stream, crayfish $\delta^{13}C$ showed only a weak downstream trend. In contrast, crayfish $\delta^{13}C$ values increased linearly in June across the entire study site with no discernable breaks in this pattern on either side of the saltcedar reach.

Consumer $\delta^{15}N$ values were highly variable across the study site with considerable overlap among consumers (Table 3). All of the organic matter sources available in JRS had $\delta^{15}N$ values that were on average between 4‰ and 5‰ (Fig. 2b). We estimated trophic positions for consumers using each of the organic matter resources as a baseline and the following equation (Post 2002):

$$\tau_{con} = \tau_{base} + (\delta^{15}N_{con} - \delta^{15}N_{base})/\Delta_N,$$

where τ_{con} is the trophic poition of the consumer of interest, τ_{base} is the trophic position of the organism used to estimate $\delta^{15}N_{base}$ (i.e., $\tau_{base} = 1$ for organic mat-

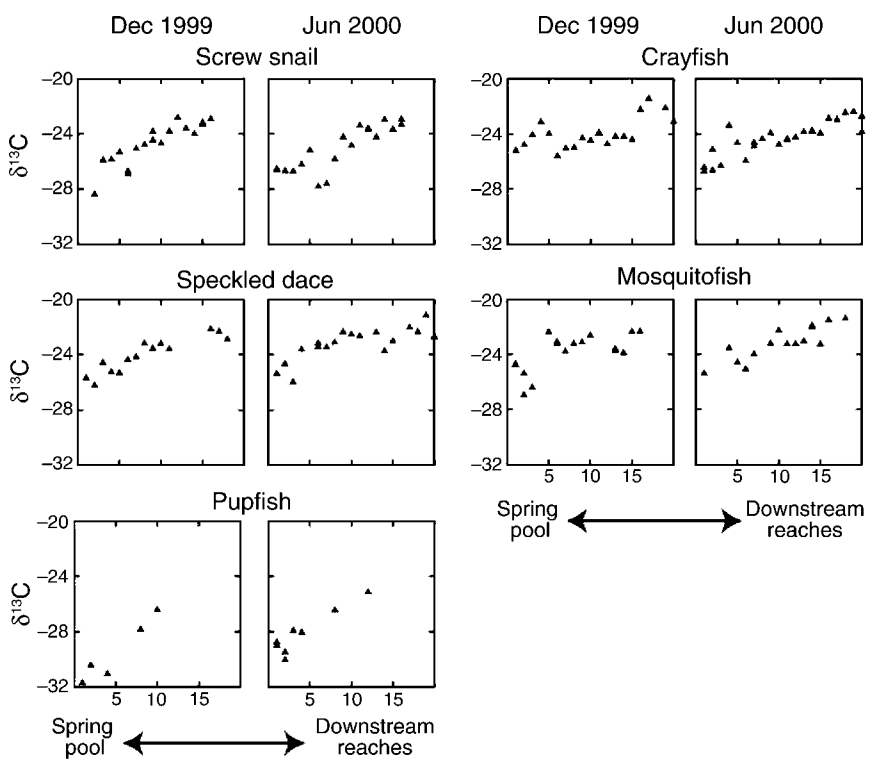

FIG. 3. Carbon stable isotope ratios for the most abundant consumers in Jackrabbit Spring. At least five individuals of each species from each plot were aggregated for analysis. The saltcedar reach begins just upstream of plot 6 and ends downstream of plot 15.

TABLE 3. Trophic position of consumers in Jackrabbit Spring.

	$\delta^{15}N$		Trophic position			
			Algae baseline		Bulrush baseline	Saltcedar baseline
Species	December	June	December	June	December	December
Crayfish	8.1 (0.2)	7.5 (0.1)	2.2[a]	1.6[a]	2.2[a]	2.5[a]
Dace	11.0 (0.1)	10.7 (0.2)	3.0[b]	2.5[b]	3.0[b]	3.7[b]
Mosquitofish	11.3 (0.2)	11.5 (0.2)	3.0[b]	2.7[b]	3.2[b]	3.8[b]
Pupfish	9.0 (0.4)	9.5 (0.3)	2.4[a]	2.2[c]	2.3[a]	
Screw snail	8.2 (0.2)	8.1 (0.2)	2.1[a]	1.6[a]	2.1[a]	2.9[a]

Notes: Data presented are the mean trophic position for each consumer based on estimated trophic position from each study plot where both that consumer and organic matter sources (i.e., algae, bulrush, or saltcedar) were present. Trophic position was estimated using an algae baseline during both December and June, but bulrush and saltcedar were used as a baseline for trophic position estimated only during the December sampling period, when these organic matter resources were actually available to consumers in Jackrabbit Spring. Pupfish were generally absent from saltcedar sites, so we were not able to estimate their trophic position using saltcedar as a baseline. Values in parentheses are standard errors. Standard error for all estimates of trophic position was 0.1. Different letters within a column indicate significant differences in trophic position among consumers (ANOVA, $P < 0.05$).

ter), $\delta^{15}N_{con}$ and $\delta^{15}N_{base}$ were measured directly, and Δ_N is the mean enrichment in $\delta^{15}N$ per trophic level (3.4‰). $\delta^{15}N$ of basal resources were variable but on average similar, so estimates of trophic position relative to algae, saltcedar, and bulrush were in agreement. These analyses show that crayfish, screw snails, and pupfish are primary consumers, while mosquitofish and dace are secondary consumers, in JRS (Table 3).

The relative contribution of algae-derived carbon to consumer diets

The 2–3‰ enrichment of $\delta^{13}C$ values for consumers at each site relative to the algae that we contend is supporting much of their growth is greater than the slight enrichment (~0.4‰) in $\delta^{13}C$ expected per trophic transfer of C (Vander Zanden and Rasmussen 2001). This relatively large enrichment likely arises because most consumers are relying on microalgae (i.e., epiphytic and benthic forms), rather than the filamentous algae that we used for isotopic analysis. In lotic ecosystems, microalgae $\delta^{13}C$ are consistently enriched relative to filamentous forms because of larger boundary layer constraints on CO_2 uptake and hence less discrimination for microalgae in benthic biofilms (Whitledge and Rabeni 1997, Finlay et al. 1999, Trudeau and Rasmussen 2003). In JRS, the linear downstream enrichment of filamentous algae $\delta^{13}C$ is due to a decline in CO_2 concentration (Kennedy 2002), and both filamentous and microalgae forms should respond similarly to this gradient. Another mechanism that could contribute to downstream enrichment of algal $\delta^{13}C$ values is ^{13}C enrichment of dissolved CO_2 via losses of isotopically light CO_2 and addition of ^{13}C-enriched atmospheric CO_2. However, there was no downstream change in the $\delta^{13}C$ of dissolved CO_2 (Kennedy 2002) because the isotopic equilibration of dissolved inorganic carbon, dominated by HCO_3^-, occurs at a much slower rate than the concentration equilibration of CO_2, which represents a very small part of the total dissolved inorganic carbon in the system.

The 2–3‰ enrichment of consumer $\delta^{13}C$ values relative to all organic matter sources and the high spatial variability of organic matter $\delta^{15}N$ values prevent the use of mixing models to quantify the relative contribution of algae, bulrush, and saltcedar to secondary production. However, the linear downstream enrichment of consumer $\delta^{13}C$ points strongly to consumer reliance on algal-derived carbon. We therefore assumed that consumers were in fact relying on microalgae and that microalgae $\delta^{13}C$ values exhibited a downstream pattern of enrichment similar to that observed for filamentous algae. We then compared the slope of downstream algal and consumer $\delta^{13}C$ enrichment to quantify consumer dependence on algal-derived carbon (sensu Peterson et al. 1993).

As an example, if we assume that algae in an idealized stream have $\delta^{13}C$ values of −30‰ at the springhead (plot 0) and linear enrichment to a value of −20‰ at a downstream reach (plot 20), using plot number as a predictor of algae $\delta^{13}C$ yields a *y*-intercept of −30‰ and a slope of 0.5. Further, we assume that a second carbon source (e.g., bulrush) has a constant value of −26‰ throughout the system. Using a two-source mixing model we can evaluate the sensitivity of a hypothetical consumer's $\delta^{13}C$ along the downstream gradient to different ''diets'' of these food sources. This analysis indicates that as the relative contribution of algae to consumer diets goes down, the slope of downstream enrichment in consumer $\delta^{13}C$ becomes shallower and the intercept becomes less negative (e.g., 100% algae diet leads to a consumer slope of 0.5 and *y*-intercept of −30‰, 50% algae leads to a consumer slope of 0.25 and a *y*-intercept of −28‰, etc.).

Comparison of algae and actual consumer slopes indicates that pupfish (67% to ~100% algae-derived carbon) and screw snails (53–64% algae-derived carbon)

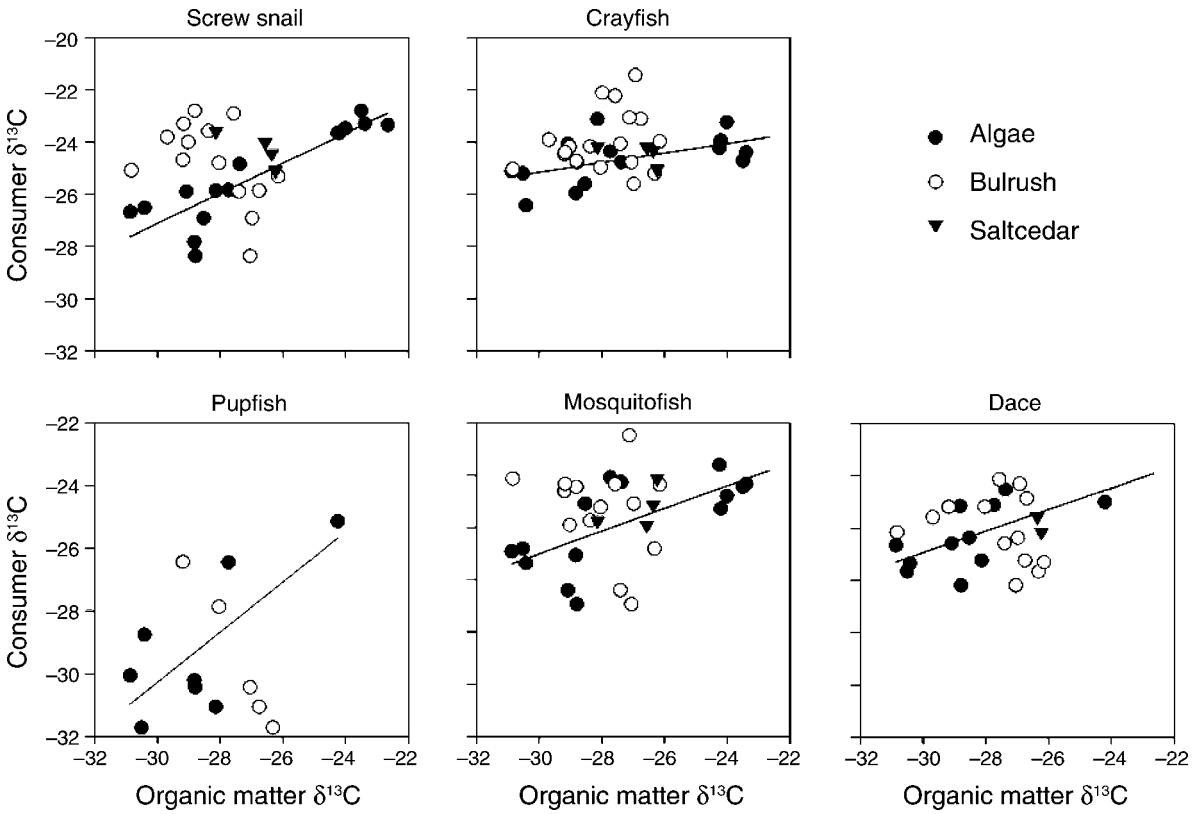

FIG. 4. Simple linear regression results using organic matter (algae, bulrush, or saltcedar) $\delta^{13}C$ values from a given plot as a predictor of the consumer $\delta^{13}C$ values at that plot. Only significant positive regression lines that demonstrate a feeding relationship are plotted (linear regression, $P < 0.05$). Algae isotopic values were analyzed in both December and June, and consumer $\delta^{13}C$ values from these respective sampling periods were used in regression analysis that averaged across both sampling periods. Bulrush and saltcedar isotopic values were analyzed only when these organic matter sources were actually present as detritus in Jackrabbit Spring, in December. Thus, consumer isotopic values from only the December sampling were used in these regression analyses. Pupfish were generally absent from saltcedar plots, so it was not possible to plot the relationship between pupfish and saltcedar ^{13}C.

are both relying heavily on algae-derived carbon (Table 2). Other consumers appear to be less dependent on algae-derived carbon, from a low of 24% algae-carbon for crayfish in winter to a high of 56% algae-carbon for dace in winter.

Consistent with downstream $\delta^{13}C$ enrichment for algae and all consumers, algae $\delta^{13}C$ values were a highly significant and positive predictor of $\delta^{13}C$ values for all consumers (Fig. 4). Bulrush $\delta^{13}C$ was unrelated to consumer $\delta^{13}C$ except that bulrush values were negatively correlated with pupfish $\delta^{13}C$ values, driven by increasing pupfish $\delta^{13}C$ downstream and decreasing bulrush $\delta^{13}C$ along the limited section of JRS where pupfish were present (Fig. 4). Saltcedar $\delta^{13}C$ was not a significant predictor of the $\delta^{13}C$ for any consumers.

DISCUSSION

Saltcedar removal as a restoration tool

Saltcedar removal was a highly effective restoration tool because it led to significant increases in pupfish abundance and significant decreases in crayfish abundance. Further, the response of speckled dace (increase) and mosquitofish (decrease), though not statistically significant, was also consistent with the restoration goal of increasing native fish abundance and decreasing exotic consumer abundance. Algal productivity increased significantly following saltcedar removal (Kennedy and Hobbie 2004), and stable isotope analysis provides conclusive evidence that this drove significant increases in pupfish and screw snail density, both of which are strongly dependent on algae-derived carbon. Saltcedar removal had a significant negative impact on crayfish density during the winter sampling period because crayfish consume saltcedar leaf litter and are not strongly dependent on algae-derived carbon.

Clearing saltcedar restores stream reaches to the ''pre-saltcedar'' conditions characteristic of native upstream sites; both native upstream and cleared sites had high rates of algae and bulrush productivity (Kennedy and Hobbie 2004) and comparable densities of native and exotic consumers. Pupfish and screw snails are virtually absent from native downstream reaches be-

cause these habitats represent the transition between spring runs that are driven by algae production and ciénagas that are detritus dominated (Williams et al. 1985, Meffe 1989). Saltcedar abruptly shifts a long segment of JRS to a detritus-dominated system, but saltcedar sites are fundamentally different from native downstream sites and ciénagas because bulrush and the cover they provide are absent and the dominant organic input is allochthonous material that is strongly seasonally pulsed (Kennedy and Hobbie 2004). The reason for the lower density of speckled dace at saltcedar sites relative to native downstream sites is unclear but may arise from the negative impact of saltcedar on bulrush (Kennedy and Hobbie 2004); speckled dace abundance in JRS is positively correlated with macrophyte density (T. A. Kennedy, *unpublished data*).

Trophic position of consumers

Crayfish, screw snails, and pupfish are primary consumers in Jackrabbit Spring. This trophic placement is in agreement with published diet studies for these species from other systems (Naiman 1975, Dundee and Paine 1977, Gutierrez-Yurrita et al. 1998). However, these results contrast numerous studies that have reported that crayfish, though they are omnivores, preferentially consume invertebrates and their growth can be disproportionately supported by these invertebrates (Momot 1995, Charlebois and Lamberti 1996, Whitledge and Rabeni 1997). Our $\delta^{15}N$ data indicate that red swamp crayfish do not consume screw snails in significant quantity in JRS, as has been reported elsewhere (Hofkin et al. 1992). Both dace and mosquitofish are secondary consumers in JRS, consistent with published diet studies for these species from other systems (Meffe 1985, Angradi et al. 1991).

Our $\delta^{15}N$ data indicate that exotic consumers probably compete with native fish. High densities of snails can lead to reductions in periphyton standing crop via grazing and reductions in macroinvertebrates density via interference competition (Harvey and Hill 1991). Introduced crayfish have led to reductions in periphyton standing crop and macroinvertebrate density and biomass via grazing/predation (Creed 1994, Momot 1995, Charlebois and Lamberti 1996), can compete with benthic fish for space (Guan and Wiles 1997), and have been linked to native fish declines due to predation on fish eggs (Soltz and Naiman 1978). Crayfish and snails are all extremely abundant in JRS, so it seems likely that they are having a negative impact on native fish, particularly via indirect pathways including competition for limited algae. Mosquitofish may be impacting native fish populations indirectly due to competition for macroinvertebrates and directly due to predation on native pupfish (Meffe 1984, Lydeard and Belk 1993). However, our isotope data are insufficient to resolve whether mosquitofish are actually preying on pupfish or simply eating macroinvertebrates that are also primary consumers.

Restoration of spring ecosystems in the western United States

Exotic species can facilitate the subsequent invasion and/or establishment of other exotic species (Simberloff and Von Holle 1999). Saltcedar invasion along JRS almost certainly did not facilitate the invasion or establishment of the exotic consumers that are present there (the density of exotic consumers was generally greatest in native sites). However, saltcedar fundamentally alters resource availability and habitat complexity in ways that favor exotic consumers over native fish of high conservation value.

Removal of exotic species can result in undesirable changes to other ecosystem components, particularly when an ecosystem supports several interacting exotics (Zavaleta et al. 2001). Although removal of saltcedar from JRS did benefit exotic screw snails, both native fish responded positively to saltcedar removal while exotic mosquitofish and crayfish, both of which have been linked to declines of native fish due to predation of eggs and fry, responded negatively. It seems unlikely that high densities of screw snails are having any direct negative impacts on the native fish in JRS, but countless spring ecosystems in the western United States support endemic mollusks (Abell et al. 2000) that might be adversely impacted by an increase in exotic mollusk abundance. Therefore, land managers planning to eradicate saltcedar from spring ecosystems would be well served to follow the recommendations of Zavaleta et al. (2001) by developing an understanding of the aquatic food web and the functional role of native and exotic consumers, so their restoration plan takes into account the possibility of unwanted secondary impacts. Eradication of saltcedar from spring ecosystems throughout the western United States should clearly be a management priority given the high conservation value of these systems and the potential conservation benefits of saltcedar removal that this research highlights.

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APPENDIX

Photographs showing Jackrabbit Spring pool and representative native vegetation reaches, saltcedar reaches, and cleared reaches during and after removal of saltcedar are available in ESA's Electronic Data Archive: *Ecological Archives* A015-062-A1.