ECOLOGICAL EFFECTS OF AN INVASIVE

FISH IN AN ARID-LAND STREAM

Final Report

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ABSTRACT

Arid and semi-arid lands are globally prevalent ecosystems, and they possess many
intermittent streams. Persistent habitats in these streams can harbor native species during
environmental disturbance, but their capacity to function as refugia is threatened by
invasive species. Competition of non-native detritivorous longfin dace (*Agosia
chrysogaster*) with native algivorous Rio Grande sucker (*Catostomus plebeius*) and
invertivorous Rio Grande chub (*Gila pandora*), and its effect on multiple trophic levels,
was investigated in two experiments using enclosures in isolated pools of Las Animas
Creek in New Mexico. In each experiment, control enclosures contained one fish species
only, whereas treatment enclosures combined the invasive fish with either native fish
species. Results suggested that the invasive fish species impacted fitness of both native
fishes. Dace gained more weight in treatment enclosures with either native fish species
than in controls. Conversely, both native fishes grew less in treatments with dace than in
controls. Additionally, dace mortality was less in treatments than in controls, whereas
more sucker and chub died in treatments than in controls. Organization of the
invertebrate assemblage and utilization of periphyton and detritus were affected
asymmetrically by competition in the three fish species. Effects of longfin dace were
greatest on detritus biomass and abundance of invertebrate collectors and shredders. Rio
Grande sucker had larger effects on periphyton biomass and invertebrate grazer
abundance. Rio Grande chub strongly affected invertebrate predator abundance but
weakly affected biomass of periphyton and detritus and abundance of non-predatory
invertebrates. Competition of longfin dace with Rio Grande sucker may have been
mediated directly through reductions in biomass of periphyton and detritus by longfin
dace, whereas competition between longfin dace and Rio Grande chub may have been
mediated indirectly through bottom-up effects of reduced periphyton and detritus biomass
by longfin dace that caused decreases in abundance of invertebrates. Invasive longfin
dace appeared to severely impact the capacity of isolated pools in Las Animas Creek to
serve as refugia for native Rio Grande sucker and Rio Grande chub. This impact

emphasizes a potential problem for species management in river systems if climate change causes more extensive intermittency of streams.

INTRODUCTION

Invasive species constitute a threat to biological diversity and ecosystem health, with lakes and streams predicted to be the ecosystems most impacted globally by species invasions in the near future (Carpenter et al. 1992; Sala et al. 2000; Moyle and Marchetti 2006). Mack et al. (2000) define biotic invaders as "species that establish a new range in which they proliferate, spread, and persist to the detriment of the environment". The consequences of species invasions extend from the homogenization of species assemblages (Gido and Brown 1999; Rahel 2000) to modifications of the structure and function of invaded ecosystems (Flecker and Townsend 1994; Simon and Townsend 2003). Studies of biological invasions have typically been skewed toward predation by prominent non-native species, such as game fishes, that have had obvious effects on invaded ecosystems (Moyle 1986; Moyle et al. 1986; Townsend 2003). Information is generally deficient for less familiar invasive species and for the more ambiguous effects of competition in biological invasions (Allan and Flecker 1993; Moyle and Light 1996a).

Biological invasions follow three phases—arrival, establishment and integration (Vermeij 1991). An invasive species at the latter two stages encounters environmental and biotic resistance from the recipient ecosystem and biological constraints from its own life history and ecology (Moyle and Light 1996a; Sakai et al. 2001). Environmental resistance derives from the physical and chemical qualities of the invaded ecosystem (Moyle and Light 1996b; Gido and Brown 1999). Biotic resistance depends on the suite of resident species that may be predators of or potential competitors with the invading species (Marchetti et al. 2004; Olden et al. 2006). Biological constraints of the invasive species that can influence invasion success include food habits, feeding habits, growth rate, reproductive strategy and life span (Sakai et al. 2001; Kolar and Lodge 2002).

All levels of ecological organization in invaded ecosystems can be impacted by biotic invaders (Simon and Townsend 2003; Townsend 2003), but it can be difficult to establish the effects of biological invasions on community structure and ecosystem function because they are regularly confounded with concomitant land use changes (Flecker and Townsend 1994; Moyle and Light 1996b). Ecosystems that have experienced few anthropogenic changes are thus desirable for studying biotic mechanisms of species invasions, such as predation and competition (Ross 1991; Lodge 1993), versus environmental mechanisms, such as alteration of flow regimes (Gido and Brown 1999; Bunn and Arthington 2002). A more thorough understanding of the biotic mechanisms that can contribute to successful species invasions will enhance efforts to manage invasive species and to conserve indigenous biota.

Most species invasions do not appear to generate prevalent changes to the receiving ecosystems (Moyle and Light 1996a, 1996b), but the more ambiguous effects of an invasive species at multiple trophic levels in an invaded ecosystem have not been thoroughly studied (Flecker and Townsend 1994; McIntosh and Townsend 1996). Additionally, predation of native species by invaders has been understood to considerably affect invaded ecosystems (Moyle 1986; Moyle et al. 1986), but the structural and functional effects of competition of invasive species with residents have been less recognized (Charlebois and Lamberti 1996; Byers 2000; Bohn and Amundsen 2001; Gido and Franssen 2007). Even though competition may not be as responsible as predation in the extinction of species (Davis 2003), it can have considerable effects on the population dynamics of species and on community structure and ecosystem function (see reviews by Connell 1983; Schoener 1983; Gurevitch et al. 1992). These impacts can be especially acute in headwater streams (Grimm and Fisher 1992; Davies et al. 1994; Labbe and Fausch 2000; Magoulick and Kobza 2003; Meyer et al. 2007).

Headwater streams, which include intermittent and perennial streams, can be important for maintaining biological diversity in river systems (Meyer et al. 2007). Native species may use headwater streams as refuges from extreme environmental conditions or harmful

biotic interactions with non-native species (Meyer et al. 2007). This capacity to function as refuges for native species has driven efforts to conserve headwater streams (Saunders et al. 2002). Lancaster and Belyea (1997) define refugia as "places (or times) where the negative effects of disturbance are lower than in the surrounding area (or time)". Because tributary streams can experience environmental disturbance, such as drought (Resh et al. 1988; Lake 2000), the persistence of species assemblages in a river system is contingent on the existence of refugia for native species (Sedell et al. 1990; Magoulick and Kobza 2003).

Isolated pools in intermittent streams can serve as refugia for many fish (e.g., Fausch and Bramblett 1991; Labbe and Fausch 2000; Magoulick and Kobza 2003) and invertebrate species (e.g., Stanley et al. 1994; Miller and Golladay 1996) during seasonal drought. The capacity of refugia to sustain native species through disturbance, however, may be impacted by invasive species (Magoulick and Kobza 2003) and climate change (Davies et al. 1994). With climate change anticipated to introduce ecosystem contraction to perennial streams (Carpenter et al. 1992; Grimm and Fisher 1992), intermittent streams in arid and semi-arid lands, which constitute greater than 65% of the world's land surface (Stanley et al. 1997), may serve as appropriate model systems for predicting the ecological effects of invasive species in perennial streams experiencing climate change.

The present study investigated the effects of an invasive species in Las Animas Creek, an intermittent stream in New Mexico. This stream has been targeted for restoration of the native fish community, which comprises Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*), Rio Grande sucker (*Catostomus plebeius*) and Rio Grande chub (*Gila pandora*). The creek presently contains a hybridized population of cutthroat trout (Pritchard et al. 2007) and an invasive population of longfin dace (*Agosia chrysogaster*). It is unknown if interactions of invasive longfin dace with the native fishes will cause restoration of the native fish community to ultimately fail, but it may be necessary to completely remove longfin dace before proceeding. The objective of this study was to examine effects of competitive interactions between non-native longfin dace and native

Rio Grande sucker and Rio Grande chub. Competition was expected to affect (1) fitness of the native fishes, (2) organization of the invertebrate assemblage and (3) utilization of periphyton and detritus. It was predicted that invasive longfin dace would have effects on multiple trophic levels in Las Animas Creek.

METHODS

Surveys on Habitat and the Fishes

Nine pools, isolated by dry streambed during stream intermittency, were selected in three groups of three pools from the upper, middle and lower sections of the intermittent mid-reach of Las Animas Creek (Figure 1). These nine pools were used to investigate variation in habitat characteristics related to the abundance and biomass of native and non-native fishes. The three pools from the lower section (approximately 33°02′15″ N, 107°35′00″ W), at an elevation of about 1675 m, were also used for conducting two experiments that examined the competitive interactions of native and non-native fishes in isolated pools during seasonal drought. These three pools were chosen due to the expectation that they would not dry for the duration of both experiments.

Habitat surveys were conducted in the nine isolated pools (Figure 1) on 29 May and 28 August 2005. The location of each pool was determined as its distance from the headwater (approximately 32°58′15″ N, 107°48′30″ W) using ArcGIS® software (ESRI 2005) to measure river distance. Length, width and depth of each pool were measured to the nearest 0.1 m. Surface area and volume of each pool were calculated from one length measurement and two to four width measurements (surface area) and six to twelve depth measurements (volume). Subsurface current velocity was measured with a soft rubber ball as a neutrally buoyant float (Overton et al. 1997), recording the time elapsed for the float to traverse a 5-m distance down the center of each pool. Water temperature and dissolved oxygen were measured with a handheld meter and probe (YSI® model 55) in the afternoon at mid-depth in the middle of each pool. Canopy cover was measured with
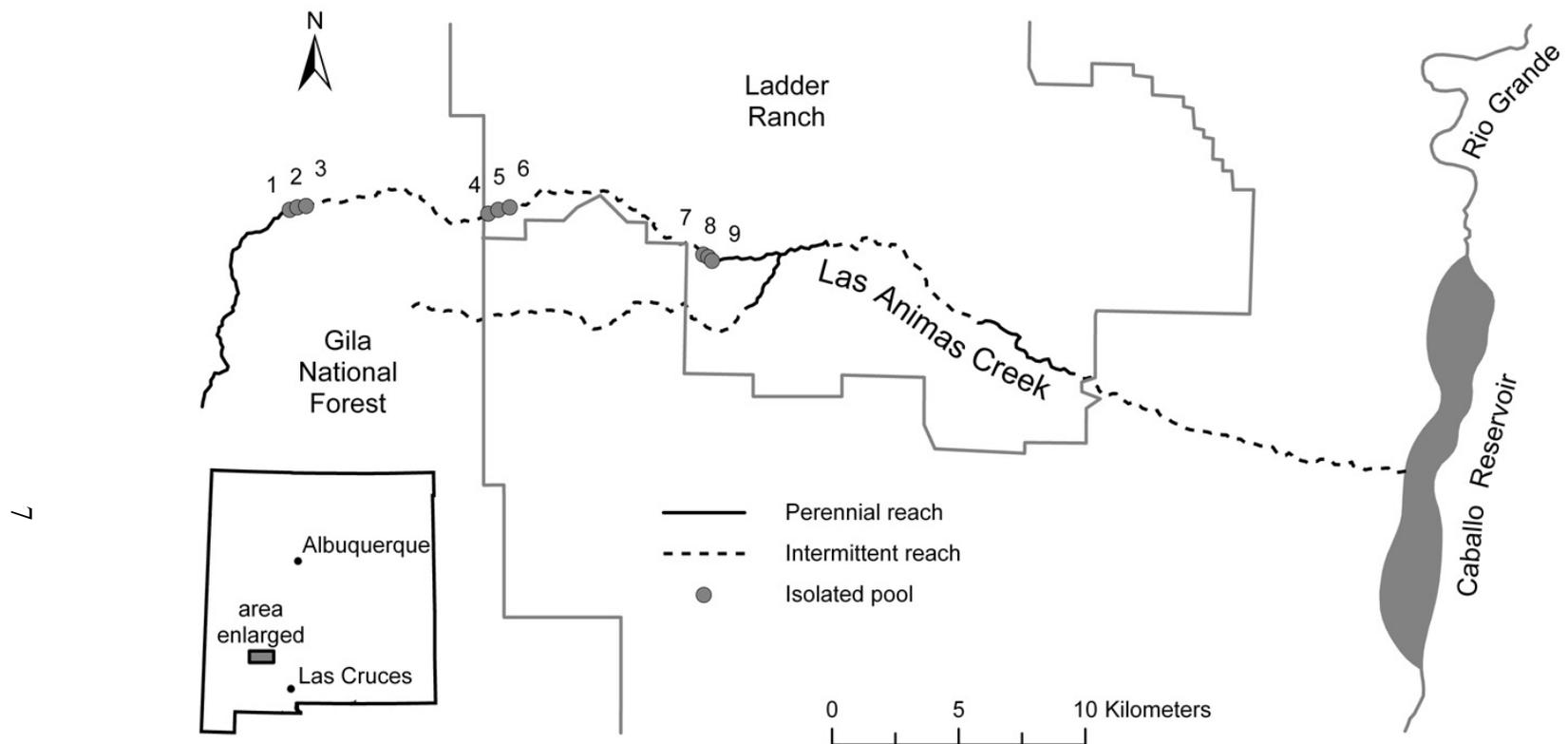
Figure 1. Location of the study area on Las Animas Creek, New Mexico. The headwater and limited sections of the middle elevation reach are perennially flowing, but most of the mid-reach has intermittent flow with many isolated pools that persist during seasonal drought and function as refugia for fish and invertebrates. Numbers identify the position of nine isolated pools chosen for study along the intermittent mid-reach. Pools 7, 8 and 9 were used for conducting two experiments that examined competitive interactions of non-native longfin dace with native Rio Grande sucker or Rio Grande chub.

a concave spherical crown densitometer (Forestry Suppliers® model A) in the center of each pool. Substrate composition was assessed by a visual estimate of each pool as a whole (Overton et al. 1997). Substrate particle sizes included fines (< 2 mm), gravel (2 to 64 mm), cobble (> 64 to 256 mm) and boulder (> 256 mm).

Fish surveys of the nine isolated pools (Figure 1) were performed on 28 May and 27 August 2005, two weeks before conducting each experiment, and standing crop of fish was estimated. Fish were sampled using a backpack electroshocker (Smith-Root® model LR-24). Three depletion passes were conducted in each pool, and ten fish of each species collected from each pool were weighed to the nearest 0.1 g. To estimate total fish abundance, the number of fish per pool by species was calculated using the removal method in Seber (1982, p. 309). The estimated total abundance of each fish species was multiplied by its average weight in each pool to estimate total fish biomass, which was divided by pool surface area to estimate standing crop as g m^{-2}. The standing crop of each fish species was summed to estimate total standing crop across all fish species per pool. Total standing crop of fish averaged across all pools was used as the target biomass of fish to be stocked into enclosures in the two experiments.

Experiments on Fish Competition

The two experiments in Las Animas Creek were conducted in 2005, each for 28 days: Experiment 1 from 12 June to 10 July and Experiment 2 from 11 September to 9 October. The fish species tested in the first experiment were native Rio Grande sucker (or 'sucker' hereafter) and non-native longfin dace (or 'dace'); in the second, they were longfin dace and native Rio Grande chub (or 'chub'). Competitive interactions were examined using enclosures that differed by combination of fishes (one species only or both species combined), with a reference enclosure (fish exclusion) used to assess effects on lower trophic levels (invertebrates, periphyton and detritus) caused by the different fish combinations. A randomized complete block design was used to assign fish combinations and the fish exclusion to separate enclosures: (a) 'dace' only control,

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'sucker' only control, 'sucker + dace' combined treatment and 'fishless' in Experiment 1 ('Sucker-Dace'); (b) 'dace' only control, 'chub' only control, 'chub + dace' combined treatment and 'fishless' in Experiment 2 ('Chub-Dace'). A block comprised four enclosures (three fish combinations and the fish exclusion) in a pool, with each block replicated in three pools.

Enclosures were constructed from expanded sheet metal panels attached to posts anchored in the substrate. They were diamond-shaped, with axes of 4.4 m by 1.6 m, enclosing an area of approximately 3.5 m^2. Due to the risk of flash flooding in the study area, enclosures were shaped like diamonds to present a narrower profile against any potential spate, with their long axis oriented parallel to stream flow. Their tops were not covered because their sides were much taller than pools were deep. They were constructed without bottoms to use the natural, pre-existing substrate during the experiments. The substrate in enclosures was minimally disturbed during their construction, so invertebrates, periphyton and detritus were already established before the experiments were conducted. The sides of enclosures were 9.5-mm diamond mesh, which permitted the passage of invertebrates but not fish. Fiberglass screen was fastened to the outside of enclosures along the bottom and covered with sediment to prevent the movement of fish through the substrate.

Individual fish stocked into each fish combination enclosure were marked by clipping a different combination of fins, which allowed each fish to be followed over the course of an experiment. Each fish was weighed to the nearest 0.1 g at the beginning and end of an experiment. Deaths of individual fish were tallied during recapture at the end of an experiment. Fish were stocked into the fish combination enclosures using a substitutive design (Fausch 1998). Total biomass of fish in control enclosures with one species only was equal to that in treatment enclosures with both species combined (i.e., biomass of each fish species in treatment enclosures was equal to half its biomass in control enclosures).

A substitutive design is useful for determining the relative strength of intraspecific competition (control enclosures with one species only) versus interspecific competition (treatment enclosures with both species combined). This design can furthermore be used to assess the comparative effect of intraspecific versus interspecific competition on other trophic levels (Sokol-Hessner and Schmitz 2002). The rationale is that the expected effect in the treatment enclosure should equal the mean of observed effects in both control enclosures if interspecific competition has not occurred. If the observed effect in the treatment enclosure does not equal the expected effect, then interspecific competition has likely occurred, with one species having a greater effect than the other species.

Samples of periphyton, detritus and invertebrates were collected from each fish combination and fishless enclosure immediately before and after each experiment to assess effects of competitive interactions on lower trophic levels. Three 37.5-cm^2 samples of periphyton were collected from different cobbles in each enclosure by placing a plastic cap onto a stone, discarding the periphyton around the cap and retaining the periphyton left behind. Detritus and invertebrates were collected concurrently with a vacuum sampler, which was constructed following the design of Brown et al. (1987). Three 325-cm^2 samples of invertebrates and detritus were collected from the substrate into separate filter bags (250-μm mesh size). All samples of periphyton, detritus and invertebrates were preserved in 95% ethanol in the field.

In the laboratory, invertebrates were separated from detritus in the collective samples. Detritus was partitioned with a sieve into fine benthic organic matter (FBOM; ≤ 1 mm) and coarse benthic organic matter (CBOM; > 1 mm) and deposited into ceramic crucibles. Periphyton was strained onto pre-dried glass-fiber filters (GF/C; 1.2 μm pore size) using a hand vacuum pump. Periphyton and detritus (FBOM and CBOM) were quantified by drying samples in an oven at 60°C for 24 hours and weighing them to the nearest 0.1 mg. Invertebrates were identified to the lowest taxon possible and classified by functional feeding group using the keys of Merritt and Cummins (1996) and Thorp and Covich (2001). Functional feeding groups are categories of invertebrate taxa based

on food habits and feeding habits: 'predators' consume other fauna, 'grazers' consume periphyton, 'collectors' consume FBOM and 'shredders' consume CBOM (Merritt and Cummins 1996).

Statistical Analysis of Data

Distribution of the three fish species in the nine isolated pools in the intermittent mid-reach of Las Animas Creek were compared using product-moment correlation coefficients (Sokal and Rohlf 1995, p. 559). Analyses of data from the two experiments were performed separately using the same statistical models. Growth, the response variable measured for fish, served as a direct measure of competition. Growth of each fish was calculated as its change in weight over the duration of an experiment (i.e., end value minus beginning value). A separate analysis for each species within an experiment was conducted to test growth of each species in treatment versus control enclosures. These analyses used a one-way analysis of variance (ANOVA) with pools as a fixed block effect. An ANOVA was also used to test if initial biomass of fish stocked into enclosures differed among control or treatment enclosures or across blocks within an experiment and to test if growth of longfin dace in control enclosures differed between the two experiments.

The abundance of invertebrates (taxa and functional feeding groups) and the biomass of periphyton and detritus (FBOM and CBOM) served as indirect measures of competition in the three fish species. These data enabled the evaluation of ways that competition was mediated by the native and non-native fish species. Each response variable was calculated as its change over the duration of an experiment in abundance for invertebrate taxa and groups or biomass for periphyton and detritus (i.e., end value minus beginning value). These data were standardized as densities, with the abundance of invertebrates analyzed as number m^{-2} and the biomass of periphyton and detritus analyzed as g m^{-2}. A separate analysis was performed for each response variable using an ANOVA with pools as a fixed block effect. To determine if the three fish species effected dissimilar changes

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in diversity of the invertebrate assemblage, invertebrate taxa richness and indices of diversity (Shannon H') and evenness (Shannon J') (Magurran 2004, p. 106) were calculated for each enclosure at the start and conclusion of an experiment.

All correlations and analyses of variance were performed using the correlation and general linear models procedures of SAS® software (version 9.1; SAS Institute 2003). Shapiro-Wilk's test for normality and a modified Levene's test for homogeneity of variances were performed to ensure that the assumptions of ANOVA were satisfied. The level of significance was set at $P < 0.1$ for all tests. Type III sums of squares from ANOVA were used in hypothesis tests for differences in growth of fish, change in abundance of invertebrate taxa and groups and change in biomass of periphyton and detritus. Least squares means from ANOVA (Goodnight and Harvey 1978) were used in Tukey posthoc pairwise comparisons of changes in the abundance of invertebrate taxa and groups and the biomass of periphyton and detritus (FBOM and CBOM) among fish combination and fishless enclosures.

RESULTS

Measurement of Habitat Variables and Fish Distribution

The nine isolated pools along the intermittent mid-reach of Las Animas Creek possessed similar habitat characteristics (Table 1). Minimum and maximum pool surface areas differed by 20 m^2 and volumes by 5 m^3. Pool depths ranged from 0.25 to 0.45 m, widths from 3.8 to 5.6 m and lengths from 10.4 to 18.5 m. Pools had mostly coarse substrate. Cobble was the most abundant particle size, constituting greater than 35% of the substrate, whereas fine particles composed approximately 10%. None of the pools had surface inflow or outflow, but current velocities averaged approximately 0.03 m s^{-1}. Pools were moderately shaded, with canopy cover ranging from 56 to 73%. Despite cool water temperatures, which averaged approximately 19°C, dissolved oxygen was below saturation, ranging from 3.9 to 5.0 mg l^{-1}. For the three pools used to conduct the two

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Table 1. River distance and habitat characteristics of nine isolated pools along the intermittent segment of Las Animas Creek, New Mexico. Except for river distance, each number is the average of two measurements recorded from habitat surveys conducted before each experiment.

Pool	River distance (km)	Surface Area (m^2)	Volume (m^3)	Flow (m s^{-1})	Temperature (°C)	Dissolved oxygen (mg l^{-1})	Canopy cover (%)	Substrate composition (%)			
								Fines	Gravel	Cobble	Boulder
1	10.3	67.5	21.8	0.02	18.9	4.2	59.8	7.5	12.5	30.0	50.0
2	10.6	64.4	22.7	0.03	18.0	4.8	62.9	7.5	25.0	30.0	37.5
3	11.1	52.8	21.0	0.02	17.4	5.0	73.2	12.5	25.0	32.5	30.0
4	19.5	71.1	20.6	0.03	19.6	4.0	56.3	5.0	27.5	35.0	32.5
5	19.9	58.2	21.5	0.03	17.7	4.7	65.2	12.5	35.0	32.5	20.0
6	20.5	73.4	24.4	0.03	18.4	4.2	60.9	12.5	30.0	32.5	25.0
7	30.3	64.3	19.3	0.03	20.1	3.9	59.2	5.0	30.0	50.0	15.0
8	30.7	57.5	22.1	0.02	18.4	4.2	72.4	17.5	45.0	32.5	5.0
9	30.9	71.1	24.7	0.03	18.9	4.4	65.5	12.5	32.5	42.5	12.5
Average	—	64.5	22.0	0.03	18.6	4.4	63.9	10.3	29.2	35.3	25.3

experiments, temperatures were slightly higher and dimensions slightly larger during the second experiment, but no habitat variable differed significantly between the two experiments (all $P > 0.1$).

Longfin dace, Rio Grande sucker and Rio Grande chub were the only fish species collected during surveys of the nine isolated pools (Table 2). Standing crop of all fishes averaged 34.9 g m^{-2}, and density averaged 6.8 individuals m^{-2} (Table 2). Longfin dace was prevalent in the isolated pools throughout the seasonally dry mid-reach, comprising greater than 75% of the abundance and greater than 55% of the biomass of all fishes. The two native fishes displayed some longitudinal variation in abundance along the intermittent segment; Rio Grande sucker had greater numbers upstream, whereas Rio Grande chub was more numerous downstream (Table 2; Figure 2). No habitat variables were correlated with the abundance of any fish species (all $P > 0.1$). The abundance of longfin dace was not correlated with Rio Grande sucker or Rio Grande chub abundance (both $P > 0.2$), but the abundance of the two native fishes was significantly negatively correlated ($P < 0.05$) (Figure 2).

The average individual weight of Rio Grande sucker and Rio Grande chub was approximately three times greater than for longfin dace (Table 3). Individual weights of longfin dace, Rio Grande sucker and Rio Grande chub averaged approximately 3.6, 10.6 and 10.7 g, respectively, so three times as many dace as sucker or chub were stocked into fish combination enclosures in the two experiments. Control enclosures, with one species only, included 36 longfin dace or 12 Rio Grande sucker in Experiment 1 and 36 longfin dace or 12 Rio Grande chub in Experiment 2. Treatment enclosures, with both species combined, included 6 Rio Grande sucker and 18 longfin dace in Experiment 1 or 6 Rio Grande chub and 18 longfin dace in Experiment 2 (Table 3).

Table 2. Mean (± SD) abundance and biomass of three fish species in nine isolated pools along the intermittent segment of Las Animas Creek, New Mexico. Column headings denote non-native longfin dace (Dace), native Rio Grande sucker (Sucker) and native Rio Grande chub (Chub). Each mean is the average of two estimates calculated from fish surveys conducted before each experiment.

Pool	Dace	Sucker	Chub	Total
		Abundance (number m^{-2})		
1	5.4 ± 0.3	0.4 ± 0.1	0.9 ± 0.1	6.6 ± 0.4
2	5.3 ± 0.7	0.3 ± 0.1	0.7 ± 0.1	6.3 ± 0.8
3	5.4 ± 0.7	0.4 ± 0.1	1.1 ± 0.2	6.8 ± 0.8
4	5.8 ± 0.2	0.2 ± 0.1	1.2 ± 0.1	7.2 ± 0.2
5	5.9 ± 0.3	0.2 ± 0.1	1.3 ± 0.1	7.4 ± 0.3
6	6.1 ± 0.1	0.2 ± 0.1	1.0 ± 0.1	7.2 ± 0.1
7	4.7 ± 0.2	0.1 ± 0.1	1.5 ± 0.1	6.3 ± 0.2
8	5.1 ± 0.1	0.1 ± 0.1	1.5 ± 0.1	6.8 ± 0.1
9	4.9 ± 0.7	0.1 ± 0.1	1.5 ± 0.1	6.5 ± 0.6
Average	5.4	0.2	1.2	6.8
		Biomass (g m^{-2})		
1	20.5 ± 0.1	3.8 ± 1.0	9.1 ± 1.0	33.4 ± 0.1
2	20.0 ± 1.3	3.3 ± 0.4	7.4 ± 0.9	30.7 ± 1.8
3	20.3 ± 1.5	3.8 ± 1.1	10.9 ± 1.3	34.9 ± 1.8
4	21.6 ± 1.5	2.6 ± 0.6	12.3 ± 0.8	36.5 ± 2.9
5	21.9 ± 0.3	2.4 ± 0.4	13.3 ± 0.3	37.6 ± 0.4
6	22.5 ± 0.7	1.6 ± 0.3	10.4 ± 0.1	34.6 ± 0.9
7	17.6 ± 0.2	1.0 ± 0.4	16.1 ± 1.2	34.6 ± 1.0
8	19.0 ± 1.4	1.3 ± 1.0	16.4 ± 1.3	36.9 ± 1.8
9	18.3 ± 1.7	1.1 ± 0.3	15.7 ± 1.7	35.0 ± 0.3
Average	20.2	2.3	12.4	34.9
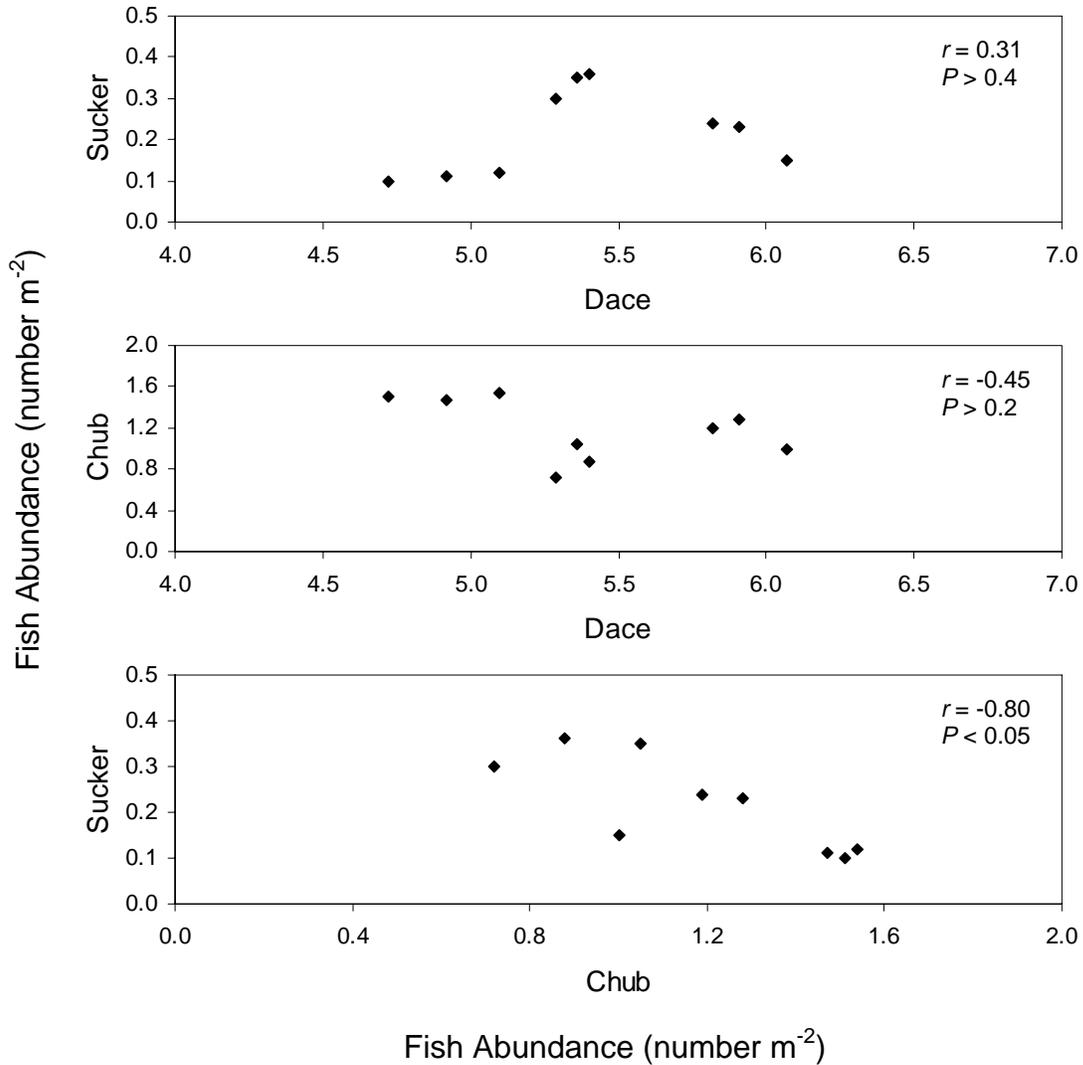
Figure 2. Relationship of abundance among three fish species in nine isolated pools along the intermittent segment of Las Animas Creek, New Mexico. Axis titles denote native Rio Grande sucker (Sucker), native Rio Grande chub (Chub) or non-native longfin dace (Dace). Pairwise comparisons are between Rio Grande sucker and longfin dace (top panel), Rio Grande chub and longfin dace (middle) and Rio Grande sucker and Rio Grande chub (bottom).

Table 3. Mean (± SD) individual weight (g) of fish, number of fish and total biomass (g) of fish in each control and treatment enclosure at the beginning of each experiment. Longfin dace (Dace) and Rio Grande sucker (Sucker) were tested in the Sucker-Dace experiment, and longfin dace and Rio Grande chub (Chub) were tested in the Chub-Dace experiment. Intraspecific control enclosures contained fish of one species, and interspecific treatment enclosures combined fish from both species.

Pool	Control	Treatment		Control
	Sucker-Dace Experiment			
	Dace	Dace	Sucker	Sucker
7	3.6 ± 0.4	3.6 ± 0.4	10.4 ± 0.8	10.6 ± 0.9
	36	18	6	12
	128.1	64.7	62.2	126.7
8	3.6 ± 0.4	3.7 ± 0.4	10.5 ± 1.0	10.4 ± 1.1
	36	18	6	12
	131.0	65.9	63.1	124.5
9	3.6 ± 0.4	3.6 ± 0.4	10.8 ± 0.8	10.7 ± 1.0
	36	18	6	12
	129.4	64.0	64.7	128.1
	Chub-Dace Experiment			
	Dace	Dace	Chub	Chub
7	3.6 ± 0.5	3.6 ± 0.4	10.8 ± 0.9	10.6 ± 1.1
	36	18	6	12
	131.2	65.1	64.5	126.8
8	3.6 ± 0.5	3.6 ± 0.4	10.4 ± 1.0	11.0 ± 1.1
	36	18	6	12
	129.5	65.6	62.6	131.5
9	3.7 ± 0.5	3.7 ± 0.4	11.0 ± 0.9	10.7 ± 0.9
	36	18	6	12
	132.7	66.3	65.8	127.9

Growth and Mortality of the Fishes

None of the control or treatment enclosures between or within pools (blocks) differed significantly in total biomass of fish stocked at the start of each experiment (Sucker-Dace: $F_{4,4} = 1.78$, $P = 0.295$; Chub-Dace: $F_{4,4} = 0.64$, $P = 0.660$). Longfin dace ranged, in individual weight, from 2.9 to 4.4 g in each experiment. Individual weights of Rio Grande sucker ranged from 9.2 to 12.1 g and Rio Grande chub from 9.0 to 12.4 g. Deaths of 5 of 36 control and 4 of 18 treatment Rio Grande sucker and 14 of 108 control and 5 of 54 treatment longfin dace were documented by the end of the Sucker-Dace experiment. At the end of the Chub-Dace experiment, mortality had been documented for 7 of 36 control and 5 of 18 treatment Rio Grande chub and 17 of 108 control and 6 of 54 treatment longfin dace. The only unmarked fish recovered in enclosures were some young-of-year longfin dace, all measuring less than 25 mm; a maximum of five such individuals were recovered from any enclosure, which negligibly affected the total biomass of fish stocked.

In both experiments, longfin dace exhibited positive growth in control and treatment enclosures, but individuals gained significantly more weight in treatments with Rio Grande sucker ($P = 0.022$) or Rio Grande chub ($P = 0.019$) than in controls (Figure 3). Growth of Rio Grande sucker in control enclosures differed significantly from treatments with longfin dace ($P < 0.001$), with individuals gaining weight in controls but losing weight in treatments. This difference was also significant for growth of Rio Grande chub in control enclosures and in treatments with longfin dace ($P < 0.001$), as individuals showed weight gain in controls but weight loss in treatments. There was no significant difference between dace controls from the two experiments ($F_{1,2} = 2.18$; $P = 0.278$). For the three fish species in control enclosures, comparisons of growth of individuals relative to their initial weight revealed that per capita growth was 6.2% for longfin dace, 4.0% for Rio Grande sucker and 2.2% for Rio Grande chub.
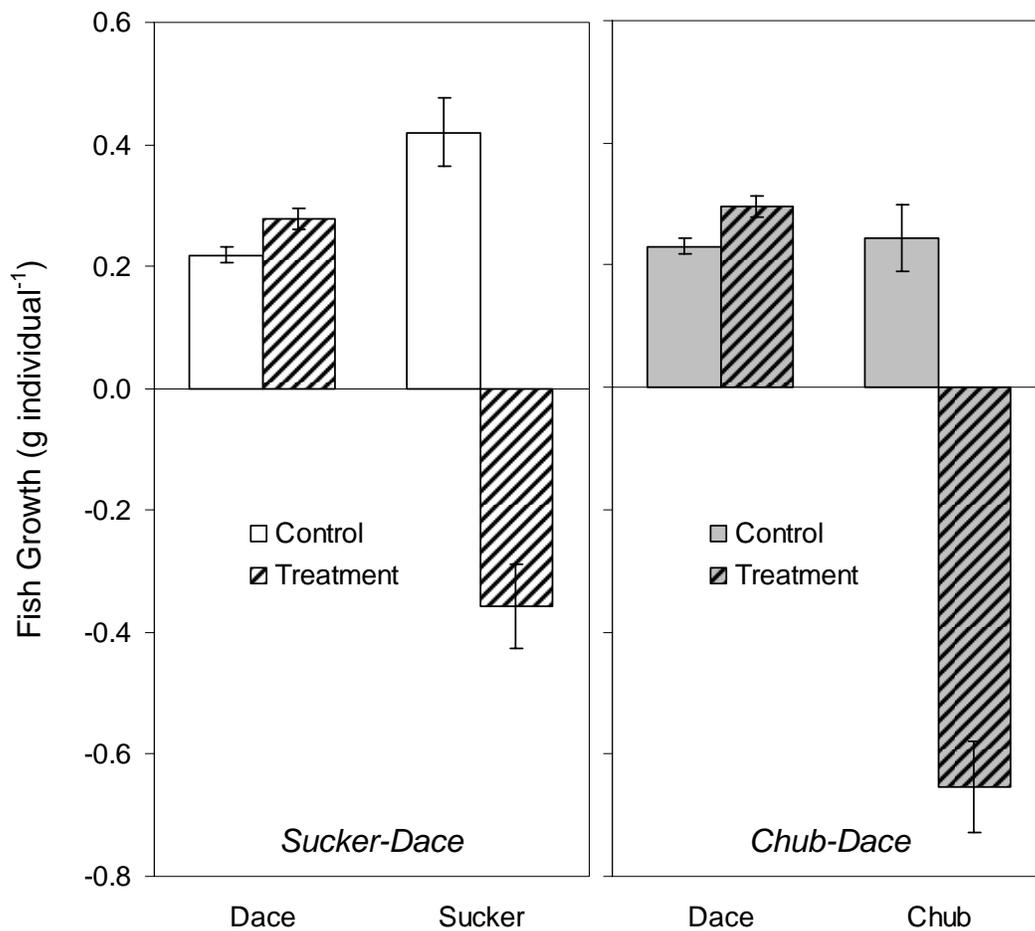
Figure 3. Mean (± SE) individual growth of fish in control and treatment enclosures over the duration of the two experiments. Longfin dace (Dace) and Rio Grande sucker were tested in the Sucker-Dace experiment, and longfin dace and Rio Grande chub (Chub) were tested in the Chub-Dace experiment. Intraspecific control enclosures contained fish of one species, and interspecific treatment enclosures combined fish from both species.

Abundance and Diversity of the Invertebrate Assemblage

Invertebrates were abundant in the experiments, averaging greater than 6000 individuals m^{-2}. All functional feeding groups were well-represented. Predators were primarily water bugs (Hemiptera) and dragonflies and damselflies (Odonata) with some hellgrammites (Megaloptera) and diving beetles (Coleoptera). The mayflies *Ameletus sp.* and *Nixe sp.* (Ephemeroptera) were the most common grazers. Midges (Diptera: Chironomidae) and aquatic worms (Oligochaeta) were the most abundant collectors. The principal shredders were the caddisflies *Lepidostoma sp.*, *Phylloicus sp.* and *Hesperophylax sp.* (Trichoptera) and the stonefly *Taeniopteryx sp.* (Plecoptera). The most abundant invertebrate taxa in the experiments included Diptera (25%), Ephemeroptera (25%), Trichoptera (21%) and Oligochaeta (12%), which collectively averaged approximately 83% of the relative abundance of all invertebrates.

Fish combination enclosures had significant effects on the total abundance of invertebrates in each experiment (Sucker-Dace: $P = 0.016$; Chub-Dace: $P = 0.002$) (Figure 4). Total invertebrate abundance in sucker controls was reduced significantly less than in dace controls ($P = 0.015$) and sucker-dace treatments ($P = 0.046$). Total invertebrate abundance was likewise decreased significantly less in chub controls than in dace controls ($P = 0.002$) and chub-dace treatments ($P = 0.009$). In both experiments, changes in the total abundance of invertebrates in treatments and dace controls were not significantly different (both $P > 0.2$). Total invertebrate abundance was reduced equivalently in fishless enclosures and in chub controls, but it was much less decreased in fishless enclosures than in sucker or dace controls (Figure 4).

The most abundant invertebrate taxa in the experiments were the most affected in the enclosures (Table 4). Fish combination enclosures in the Sucker-Dace experiment had significant effects on the abundance of Diptera ($P = 0.022$), Ephemeroptera ($P = 0.032$), Odonata ($P = 0.040$) and Trichoptera ($P = 0.025$) (Table 4). In the Chub-Dace experiment, fish combination enclosures had significant effects on the abundance of

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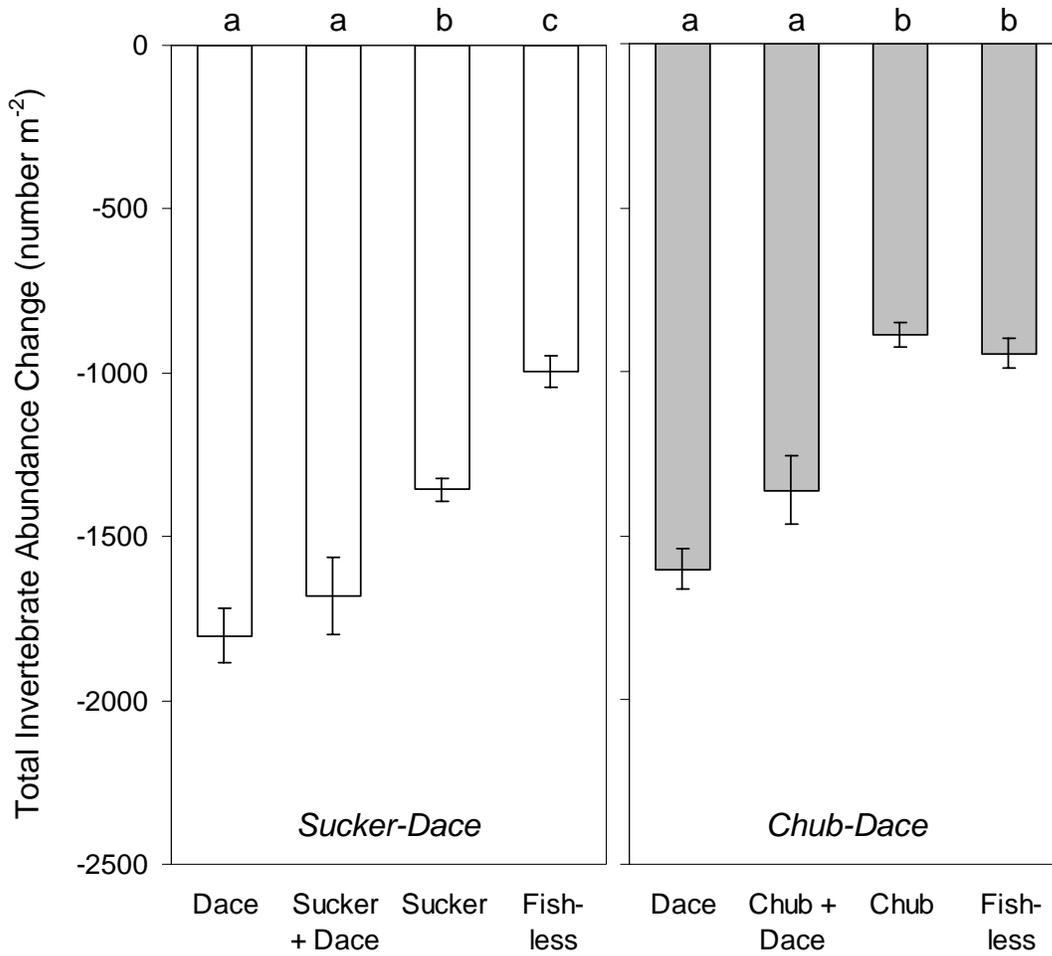
Figure 4. Change in mean (± SE) total abundance of invertebrates from three fish combination enclosures and a fishless enclosure in each experiment. Change was calculated as the end value minus the beginning value in each enclosure. Each mean is the average of nine values: three invertebrate samples from each of three replicate enclosures per fish combination or fish exclusion. Significant differences ($P < 0.1$) for Tukey posthoc pairwise comparisons are designated with letters above columns; enclosures with the same letter are not significantly different.

Table 4. Change in mean (± SE) abundance (number m^{-2}) of invertebrate taxa from three fish combination enclosures and a fishless enclosure in each experiment. Change was calculated as the end value minus the beginning value in each enclosure. Each mean is the average of nine values: three invertebrate samples from each of three replicate enclosures per fish combination or fish exclusion. Significant differences ($P < 0.1$) for Tukey posthoc pairwise comparisons are designated with letters after columns; enclosures with the same letter are not significantly different.

Taxon	Enclosure							
	Sucker-Dace Experiment							
	Dace		Sucker **+** Dace		Sucker		Fishless	
Bivalvia	0 ± 6	a	-14 ± 7	a	-10 ± 6	a	-17 ± 9	a
Coleoptera	-3 ± 12	a	-3 ± 9	a	-7 ± 12	a	14 ± 3	a
Diptera	-602 ± 88	a	-462 ± 21	ab	-263 ± 46	b	-280 ± 7	b
Ephemeroptera	-294 ± 12	a	-352 ± 29	ab	-492 ± 62	b	-304 ± 33	a
Gastropoda	-10 ± 10	a	-3 ± 3	a	-7 ± 3	a	3 ± 3	a
Hemiptera	17 ± 3	a	10 ± 6	a	3 ± 3	a	62 ± 16	b
Megaloptera	0 ± 0	a	3 ± 3	a	0 ± 0	a	3 ± 3	a
Odonata	27 ± 3	a	7 ± 7	b	7 ± 3	b	48 ± 7	c
Oligochaeta	-318 ± 47	a	-304 ± 59	ab	-174 ± 16	b	-188 ± 18	b
Plecoptera	-123 ± 16	a	-85 ± 24	ab	-65 ± 16	ab	-51 ± 6	b
Trichoptera	-496 ± 7	a	-475 ± 42	a	-349 ± 27	b	-287 ± 47	b
	Chub-Dace Experiment							
	Dace		Chub **+** Dace		Chub		Fishless	
Bivalvia	-3 ± 3	a	-7 ± 9	a	-3 ± 3	a	3 ± 7	a
Coleoptera	-21 ± 10	a	-17 ± 9	a	-7 ± 7	a	7 ± 9	a
Diptera	-438 ± 24	a	-380 ± 56	a	-236 ± 21	b	-198 ± 30	b
Ephemeroptera	-362 ± 35	a	-284 ± 40	ab	-205 ± 6	b	-356 ± 24	a
Gastropoda	-21 ± 6	a	-17 ± 3	a	-10 ± 6	a	-21 ± 6	a
Hemiptera	38 ± 3	a	-17 ± 7	b	-75 ± 9	c	106 ± 7	d
Megaloptera	0 ± 0	a	-3 ± 3	a	0 ± 0	a	3 ± 3	a
Odonata	7 ± 3	a	-17 ± 3	ab	-34 ± 12	b	24 ± 3	c
Oligochaeta	-222 ± 28	a	-219 ± 12	a	-92 ± 26	b	-140 ± 28	ab
Plecoptera	-62 ± 18	a	-38 ± 3	ab	-10 ± 10	b	-34 ± 9	ab
Trichoptera	-516 ± 33	a	-362 ± 56	ab	-212 ± 28	b	-338 ± 52	ab

seven taxa (all $P < 0.05$; Table 4). Longfin dace in control enclosures decreased the abundance of Diptera, Trichoptera and Oligochaeta more than Rio Grande sucker in controls did, but sucker had a greater effect on Ephemeroptera abundance (Figure 5; Table 4). Longfin dace in control enclosures also had a greater effect on these four invertebrate taxa than Rio Grande chub in controls did, but chub had a greater effect on predaceous Hemiptera and Odonata (Figure 5; Table 4). In fishless enclosures, changes in the abundance of Diptera, Oligochaeta and Trichoptera were similar to those in sucker or chub control enclosures, and change in the abundance of Ephemeroptera was similar to that in dace controls. The abundance of Hemiptera and Odonata, however, increased much more in fishless enclosures than in any of the fish combination enclosures (Table 4).

Separating the effects of fish combination enclosures on some invertebrate taxa (e.g., Hemiptera and Odonata) was complicated by the relatively low abundance of many taxa, which produced high variability in enclosures. To counter some of this variability, invertebrate taxa were classified into functional feeding groups. Fish combination enclosures in the Sucker-Dace experiment had significant effects on the abundance of predators ($P = 0.049$), grazers ($P = 0.060$), collectors ($P < 0.001$) and shredders ($P = 0.057$) (Figure 6). In the Chub-Dace experiment, fish combination enclosures also had significant effects on all functional feeding group abundances (all $P < 0.05$) (Figure 6). Predators were the only group that increased in abundance in any fish combination enclosure, increasing in dace and sucker controls and sucker-dace treatments. The greatest reduction in grazers occurred in sucker controls. Reductions in collectors and shredders were similar across all fish combination enclosures, decreasing most in dace controls and least in chub controls. Except for predators, all functional feeding group abundances were reduced least in chub controls. The three non-predatory invertebrate groups in fishless enclosures had reductions equivalent to those in sucker control enclosures but greater than in chub controls and less than in dace controls. Invertebrate predator abundance was greatly increased in fishless enclosures (Figure 6).
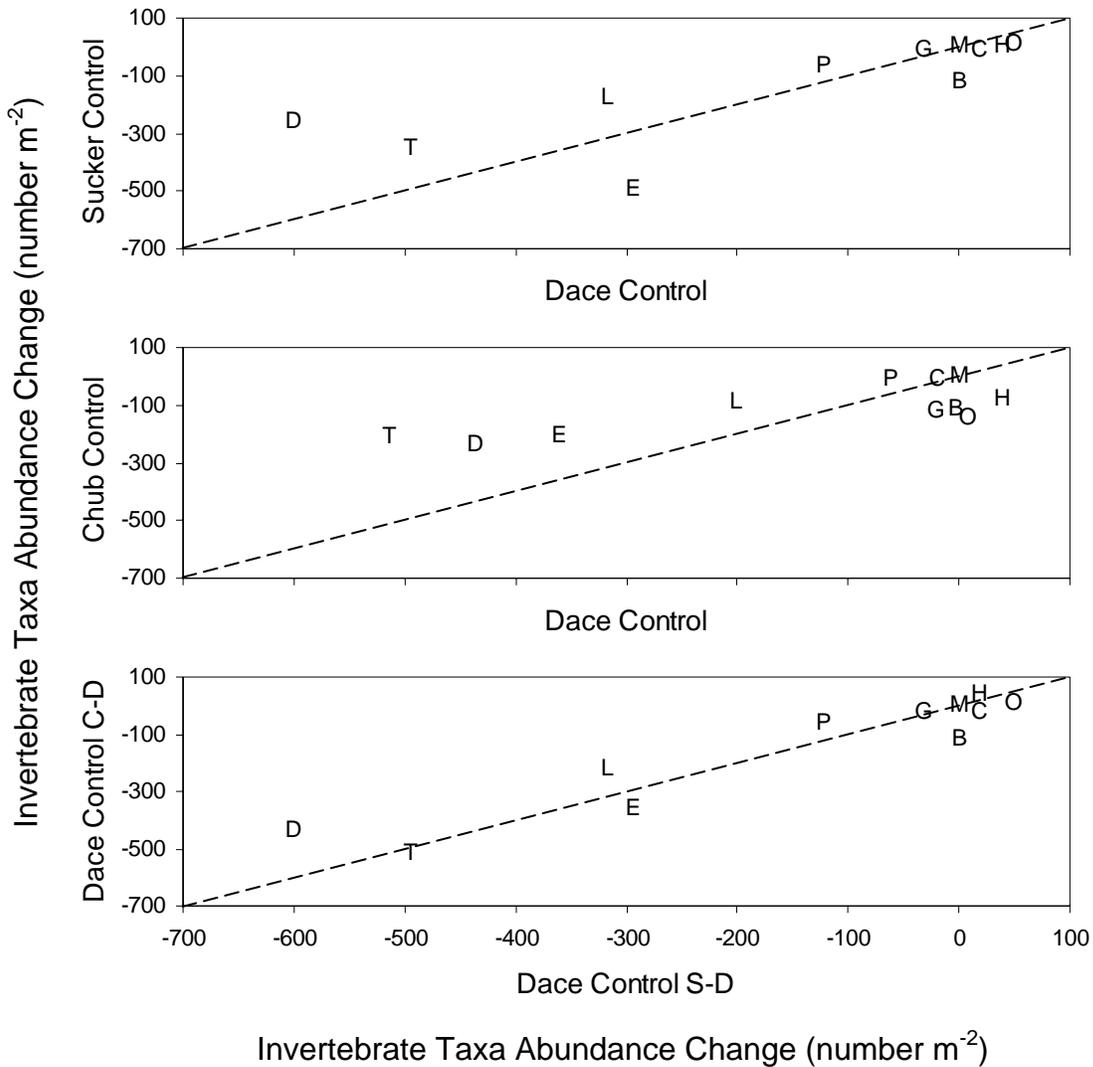
Figure 5. Relationship of change in abundance of invertebrate taxa among fish control enclosures in each experiment. Pairwise comparisons are between Rio Grande sucker and longfin dace controls (top panel), Rio Grande chub and longfin dace controls (middle) and longfin dace controls in the Sucker-Dace (S-D) and Chub-Dace (C-D) experiments (bottom). The dashed line represents a 1:1 relationship between enclosures. In the top and middle panels, invertebrate taxa lying above the dashed line were more affected by longfin dace, with taxa below the line more affected by Rio Grande sucker or Rio Grande chub. Invertebrate taxa include Bivalvia (B), Coleoptera (C), Diptera (D), Ephemeroptera (E), Gastropoda (G), Hemiptera (H), Megaloptera (M), Odonata (O), Oligochaeta (L), Plecoptera (P) and Trichoptera (T).
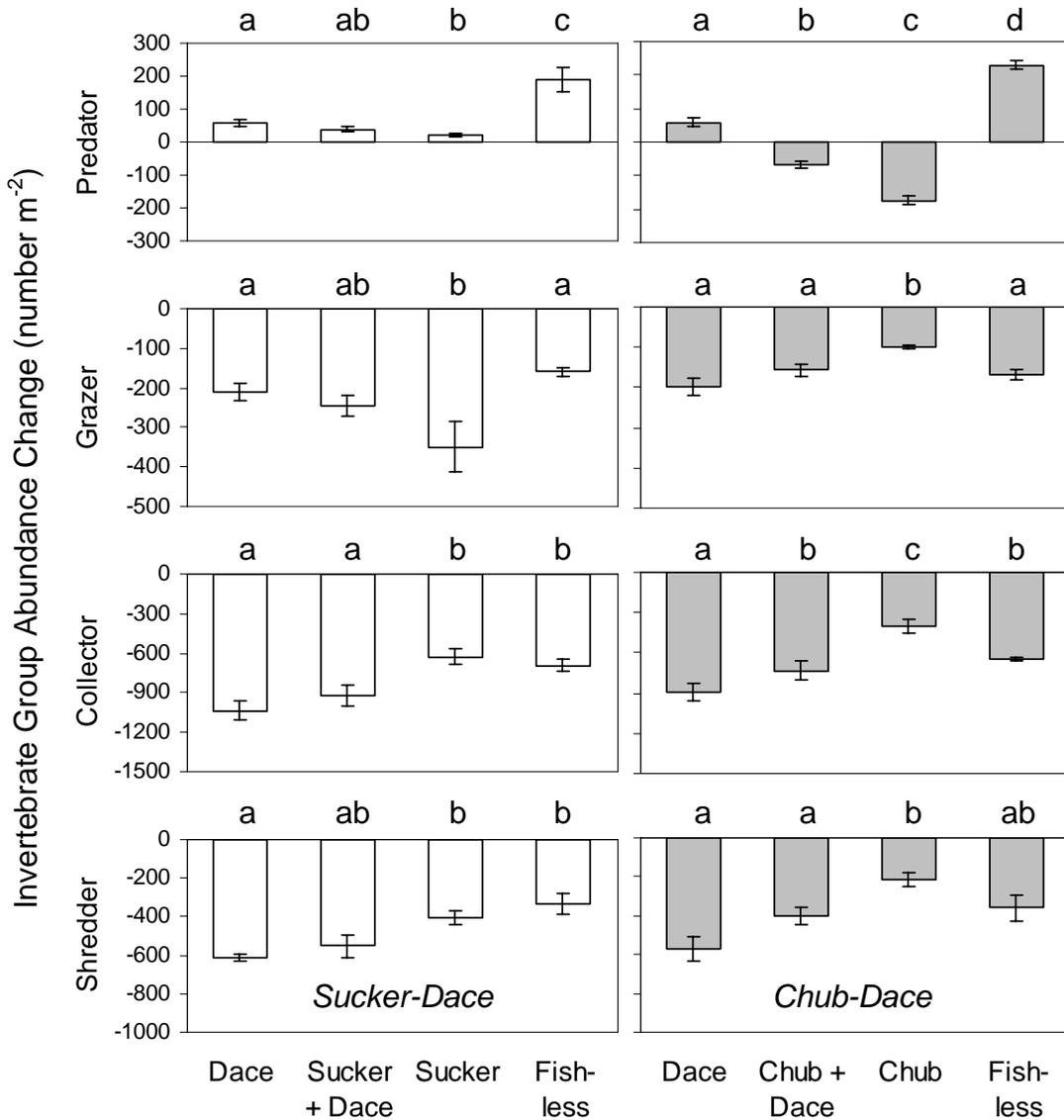
Figure 6. Change in mean (± SE) abundance of invertebrate functional feeding groups from three fish combination enclosures and a fishless enclosure in each experiment. Invertebrate groups include predators (top panels), grazers (middle-upper), collectors (middle-lower) and shredders (bottom). Each mean is the average of nine values: three invertebrate samples from each of three replicate enclosures per fish combination or fish exclusion. Significant differences ($P < 0.1$) for Tukey posthoc pairwise comparisons are designated with letters above columns; enclosures with the same letter are not significantly different.

Invertebrates were also diverse in the experiments, with 44 total taxa (41 insect taxa) identified, but most taxa were relatively rare. No taxon was unique to either experiment. Predators, with 15 taxa, were the most diverse functional feeding group, but collectors, shredders and grazers also had high diversity (11, 9 and 9 taxa, respectively). Richness (N) in enclosures at the start of the experiments averaged 37 taxa. Over the duration of the experiments, richness increased most in sucker controls and least in chub controls, but these changes were nominal and not statistically significant. Diversity (H') increased in all enclosures except for chub controls, and all enclosures increased in evenness (J') except for chub and sucker controls. Dace controls showed the greatest increases in diversity and evenness, and treatments in both experiments exhibited increases that were more similar to dace controls. Increases in diversity in dace controls were mostly due to increases in evenness as the most abundant invertebrate taxa, Chironomidae and Oligochaeta, were most reduced.

Biomass of Periphyton and Detritus

Fish combination enclosures had significant effects on the biomass of periphyton in both experiments (Sucker-Dace: $P = 0.008$; Chub-Dace: $P = 0.012$) (Figure 7). Periphyton biomass was decreased significantly more in sucker controls than in dace controls ($P < 0.001$) or sucker-dace treatments ($P = 0.012$). In chub controls, the biomass of periphyton was reduced significantly less than in chub-dace treatments ($P = 0.014$) or dace controls ($P < 0.001$). In both experiments, changes in the biomass of periphyton did not differ significantly in dace controls versus treatments (both $P > 0.1$). Periphyton biomass was much less reduced in fishless enclosures than in any of the fish combination enclosures (Figure 7).

In each experiment, fish combination enclosures also had significant effects on the biomass of detritus [FBOM (Sucker-Dace: $P = 0.007$; Chub- Dace: $P < 0.001$) and CBOM (Sucker-Dace: $P = 0.005$; Chub-Dace: $P < 0.001$)] (Figure 7). In sucker controls, the biomass of FBOM and CBOM were reduced significantly less than in dace controls
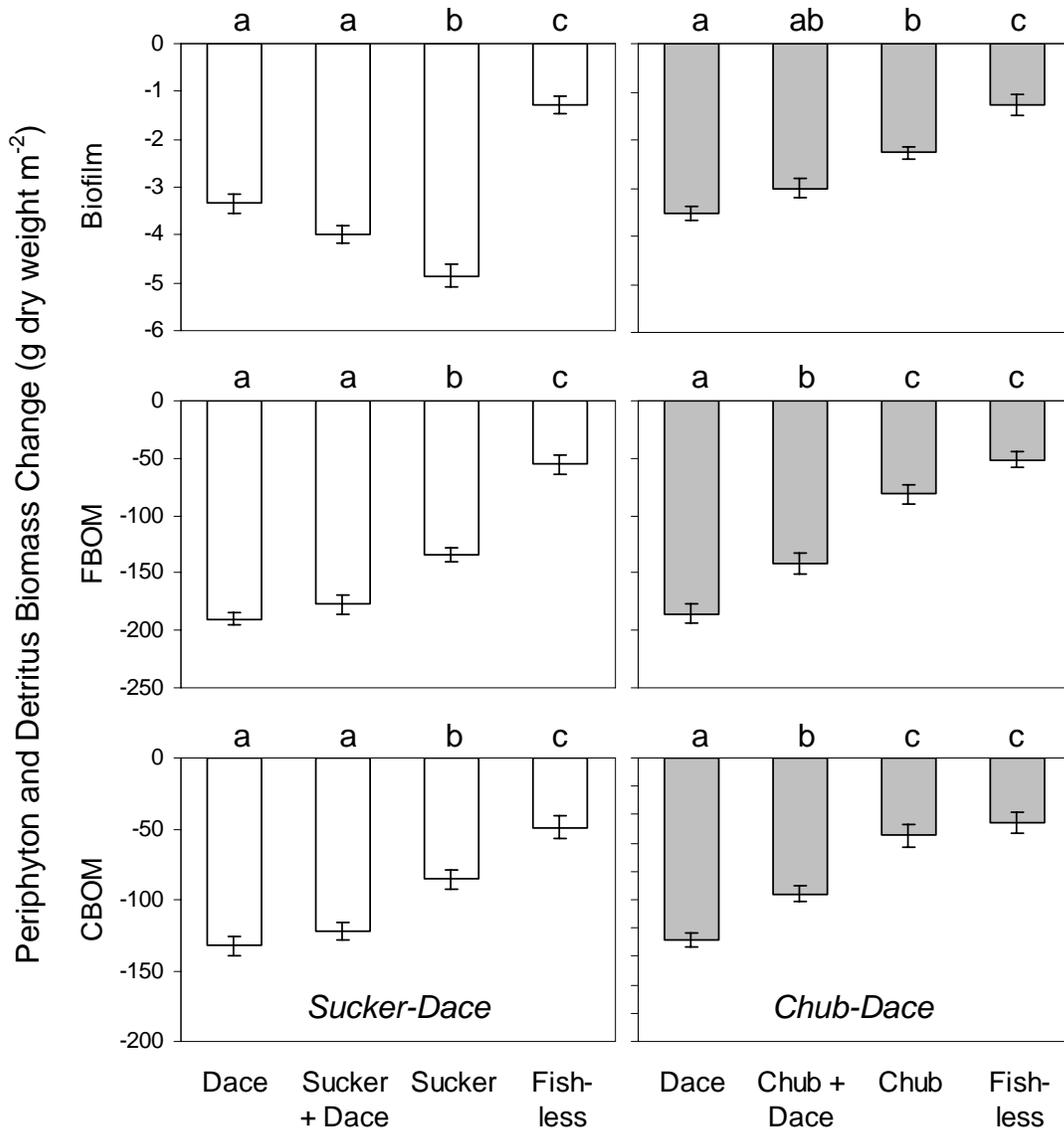
Figure 7. Change in mean (± SE) biomass of periphyton and detritus from three fish combination enclosures and a fishless enclosure in each experiment. Periphyton (top panels) comprised bacteria, algae and meiofauna, and detritus constituted fine benthic organic matter (FBOM; ≤ 1 mm) (middle) and coarse benthic organic matter (CBOM; > 1 mm) (bottom). Each mean is the average of nine values: three from each of three replicate enclosures per fish combination or fish exclusion. Significant differences ($P <$ 0.1) for Tukey posthoc pairwise comparisons are designated with letters above columns; enclosures with the same letter are not significantly different.

(both $P < 0.01$) or sucker-dace treatments (both $P < 0.05$), but changes in detritus biomass were not significantly different in sucker-dace treatments versus dace controls (both $P > 0.3$). Dace controls, chub controls and chub-dace treatments all differed significantly in changes in the biomass of FBOM and CBOM (all $P < 0.05$), with detritus biomass most decreased in dace controls and least in chub controls. In fishless enclosures, the biomass of FBOM and CBOM had reductions equivalent to that in chub controls but much less than in sucker or dace controls (Figure 7).

DISCUSSION

Results from both experiments conducted in Las Animas Creek suggested strong competition between non-native longfin dace and native Rio Grande sucker and Rio Grande chub, with the invasive species demonstrating stronger intraspecific competition relative to interspecific competition with the native fishes. In each experiment, the invasive fish grew more in treatment enclosures combined with either native fish species than in controls containing only the invasive species. In contrast, both native fishes gained weight in controls but lost weight in treatment enclosures. In addition, Rio Grande sucker and Rio Grande chub had greater mortality in treatment enclosures than in controls, whereas longfin dace had fewer deaths in treatment versus control enclosures.

Data in this study on the abundance of invertebrates and the biomass of periphyton and detritus provided indirect evidence of resource utilization by the three fish species. Longfin dace appeared to have the greatest effect on detritus biomass and the abundance of invertebrate collectors and shredders. Rio Grande sucker appeared to have a larger effect on periphyton biomass and invertebrate grazer abundance. Rio Grande chub appeared to have the strongest effect on invertebrate predator abundance and the weakest effect of the three fish species on the biomass of periphyton and detritus and the abundance of invertebrate grazers, collectors and shredders. Although ecosystem properties were not measured directly, changes in the abundance of invertebrates and the

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biomass of periphyton and detritus suggest that ecological changes in the flow of energy and the cycling of nutrients were caused by non-native longfin dace.

Competition between longfin dace and Rio Grande sucker may have been mediated directly through a reduction in the biomass of periphyton and detritus by longfin dace. Competition between longfin dace and Rio Grande chub may have been mediated indirectly through a bottom-up effect of reduced periphyton and detritus biomass by longfin dace that caused a reduction in the abundance of non-predatory invertebrates. Results from both experiments, however, were inconclusive because direct evidence of resource utilization was lacking, so it is possible that competition was also mediated partly through an interference mechanism. There is also a possibility that effects on fitness of the native fishes were caused by a limiting resource not affected by the invasive fish species.

Fitness of the Native Fishes

Viability (survival) and fecundity (reproduction) constitute the components of fitness in species, but growth has also been shown to be a positive surrogate of fitness in fishes (Hall et al. 1970). Increased growth generally produces higher viability and greater fecundity in species, and growth in fishes, which is indeterminate, is tightly coupled with resource utilization and is also positively related to fitness (Werner and Hall 1976, 1977). Data on fish in the experiments here, which included growth and mortality of fish competing interspecifically and intraspecifically, provide strong evidence that non-native longfin dace impacted fitness of native Rio Grande sucker and Rio Grande chub.

Longfin dace gained approximately 30% more weight in treatment enclosures with either of the native fishes than in controls. Both native fishes gained less weight per individual than longfin dace did in control enclosures; Rio Grande sucker grew less than 65%, and Rio Grande chub grew less than 35%, as much as longfin dace. Remarkably, Rio Grande sucker and Rio Grande chub lost weight in treatment enclosures with the invasive fish;

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sucker lost approximately 3% weight per individual and chub lost approximately 6%. Although many studies have reported a reduction in growth of a species from interspecific competition (e.g., Fausch and White 1986; Kohler 1992; Byers 2000; Forrester et al. 2006), few researchers have documented a loss of weight in a species by competing interspecifically (e.g., Shemai et al. 2007). Shemai et al. (2007) observed that non-native brown trout reduced the weight of native Rio Grande cutthroat trout in interspecific enclosures.

Longfin dace shares a more similar ecological niche with Rio Grande sucker than with Rio Grande chub (Minckley 1973; Lee et al. 1980; Sublette et al. 1990; Miller et al. 2005). It was therefore expected that longfin dace would have a greater effect on Rio Grande sucker than on Rio Grande chub in isolated pools, but impacts of non-native dace on the two native species did not differ significantly. The growth of each native fish in control versus treatment enclosures differed by approximately 0.8 and 0.9 g individual^{-1} for Rio Grande sucker and Rio Grande chub, respectively.

Mortality of Rio Grande sucker and Rio Grande chub was higher in treatment versus control enclosures. Approximately 10% fewer individuals of each native fish species survived in treatments with the invasive fish than in controls, providing further evidence that non-native longfin dace affected the fitness of native Rio Grande sucker and Rio Grande chub. Conversely, longfin dace had approximately 5% higher mortality in control enclosures than in treatments. Resetarits (1995, 1997) noted a similar interaction between different-sized competitors, with a smaller darter causing greater mortality of a larger sculpin.

Organization of the Invertebrate Assemblage

Total abundance of invertebrates changed considerably in both experiments. Longfin dace and Rio Grande sucker appeared to principally affect the invertebrate assemblage through consumption of periphyton and detritus, whereas Rio Grande chub appeared to

primarily affect invertebrates by consuming or displacing them. Rio Grande chub exhibited a relatively weak direct effect on the invertebrate assemblage compared to the strong indirect effects by Rio Grande sucker and longfin dace. Flecker (1992) documented a similar finding in a neotropical stream as invertivorous characids did not prey intensively on invertebrates, but resources were rapidly depleted by a grazing loricariid, which induced invertebrates to emigrate or deterred them from colonizing. The finding here of a weak effect by Rio Grande chub also agrees with several reports of weak effects of fish predation on stream invertebrates (e.g., Allan 1982; Holomuzki and Stevenson 1992), but it is contrary to many studies that found fish predators to produce strong effects (e.g., Flecker 1984; Gilliam et al. 1989; Power 1990, 1992).

Rio Grande chub is not an obligate invertivore, and other *Gila* species have been reported to also consume periphyton and detritus (Minckley 1973; Sublette et al. 1990; Miller et al. 2005). Even though it may prefer to feed on drifting invertebrates, Rio Grande chub in isolated pools with nominal flow might be forced to feed on alternate foods, such as periphyton and detritus, which may partly explain the finding here of strong competition between benthic longfin dace and water-column Rio Grande chub. Because Rio Grande chub is moreover a water-column feeder, its weak effect on benthic invertebrates may be partly explained by the disparate effects of drift-feeding versus benthivory in fish predation of benthic invertebrates (Dahl 1998a). Dahl (1998a) observed that benthivorous sculpin in a Swedish stream had much stronger effects on benthic invertebrates than drift-feeding trout did. It is also possible that interactions between Rio Grande chub and longfin dace involved some facilitation of access to invertebrates (Soluk and Collins 1988). Although it seems unlikely that longfin dace would have benefited Rio Grande chub much by displacing invertebrates into the water column, chub might have compelled invertebrates into the substrate, which could have subsidized dace and may partly explain why longfin dace grew more with Rio Grande chub than with Rio Grande sucker.

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Invertebrate taxa that were most abundant in the experiments appeared to be the most affected by the three fish species, which is common for generalist fish predators (Flecker 1984; Power 1990; Dahl 1998b) but rarer for omnivorous and herbivorous fishes (Gelwick and Matthews 1992; Bertrand and Gido 2007). Rio Grande sucker appeared to have the strongest effect on grazer taxa, primarily ephemeropterans, which agreed with a preference for periphyton in other streams (Swift-Miller et al. 1999). Collectors and shredders, principally dipterans and trichopterans, appeared to be most affected by longfin dace, which differed from a preference for periphyton in much of its native range (Schreiber and Minckley 1981; Grimm 1988). Except for the apparent negative effect on predatory invertebrates, Rio Grande chub appeared to have only a weak effect on benthic invertebrates relative to Rio Grande sucker and longfin dace, but other predatory fish have been shown to preferentially prey on invertebrate predators (Power 1990, 1992).

Fishless enclosures offered some perspective on the apparent effects of invertebrate predators and the three fish species on other invertebrate functional feeding groups in isolated pools in Las Animas Creek. In fishless enclosures, the abundance of invertebrate predators was greatly increased, which appeared to cause declines in the abundance of grazers, collectors and shredders that were comparable to the effects inferred for Rio Grande sucker and longfin dace. Other studies of invertebrate predators have not reported such strong effects on an invertebrate assemblage (e.g., Soluk 1993; Dahl and Greenberg 1997; Dahl 1998b). Invertebrate predator abundance declined only in fish combination enclosures with Rio Grande chub, and the apparent effect of Rio Grande chub on other invertebrate groups was weak compared to that of predatory invertebrates in fishless enclosures. It is possible that Rio Grande chub consumed invertebrate predators and indirectly relieved some pressure in enclosures imposed by predatory invertebrates on other invertebrate groups. Rio Grande chub, however, may also have displaced invertebrate predators from enclosures and indirectly facilitated immigration by other invertebrate groups, which could have elevated food availability for Rio Grande chub and misleadingly diminished its apparent effect on non-predatory invertebrates.

Utilization of Periphyton and Detritus

Periphyton and detritus biomass changed substantially in each experiment. Rio Grande sucker and longfin dace appeared to have strong effects on periphyton and detritus, respectively, whereas Rio Grande chub appeared to have weak effects. This outcome is consistent with other studies that found strong effects of herbivorous or omnivorous fish on periphyton and detritus (e.g., Gelwick and Matthews 1992; Flecker 1996; Taylor et al. 2006; Bertrand and Gido 2007). Taylor et al. (2006) noted that an abundant detritivorous fish in a speciose stream in the Andean piedmont profoundly affected ecological properties; removal of the detritivorous fish increased primary productivity and periphyton growth but decreased downstream nutrient transport. Longfin dace was also shown to be important in rapid cycling of nutrients in a nutrient-limited Sonoran Desert stream (Grimm 1988).

The strong effects of Rio Grande sucker and longfin dace on periphyton and detritus in the experiments here agreed with many other studies that emphasized the importance of 'bottom-up' versus 'top-down' processes in streams (e.g., Gelwick and Matthews 1992; Hunter and Price 1992; Flecker 1992, 1996). Other researchers have shown top-down effects to be important in small streams with a single fish predator (e.g., Power 1990; Flecker and Townsend 1994; McIntosh and Townsend 1996), so it seemed that Rio Grande chub, if it consumed more invertebrates than detritus or periphyton in the experiments, should have had a stronger effect than it did. The lack of a greater effect of Rio Grande chub on benthic invertebrates, however, may be related to other predictors of trophic cascades that were missing in Las Animas Creek. For instance, the invertebrate assemblage was not overly depauperate and the fish species were not highly specialized (Strong 1992).

The apparent consumption of periphyton and detritus by Rio Grande sucker and longfin dace emphasizes a resource overlap between these two species, providing evidence for exploitation as the mechanism of competition (Hart 1987; Holbrook and Schmitt 1989;

Byers 2000; Bohn and Amundsen 2001). Bohn and Amundsen (2001) described that a resource overlap for zooplankton between non-native vendace and native whitefish in a Scandinavian lake generated strong interspecific competition, which eventually culminated in a niche shift by the native species. Moreover, Byers (2000) noted that competition between an invasive and a native snail did not cause differences in resource utilization, but the non-native snail was much more efficient at converting resources to energy and growth. The mechanism of competition between longfin dace and Rio Grande chub could involve direct competition for periphyton or detritus. Alternatively, it might involve a negative indirect interaction through invertebrate grazers, collectors and shredders for periphyton and detritus in the food web (Hargrave et al. 2006), but data in the present study are inadequate to distinguish the influence of exploitation or interference (Schneider 1990; McIntosh et al. 1992).

Asymmetry of Fish Competition

Many invertebrate taxa and functional feeding groups were not affected symmetrically among treatment and control enclosures, which suggested that interspecific competition was extensive. The observed changes in abundance of most invertebrate taxa and functional feeding groups in treatments were asymmetrical; they were more comparable to the effects inferred from longfin dace than from the native fish species. Effects on periphyton and detritus were also asymmetrical among control and treatment enclosures. The observed changes in biomass of periphyton and detritus in treatments were likewise more similar to the effects observed in dace controls. It is possible that longfin dace reduced the consumption rate of resources by Rio Grande sucker and Rio Grande chub. Alternatively, longfin dace in treatment enclosures may have increased their own rate of resource consumption. Because longfin dace appeared to experience strong intraspecific competition in controls, dace in treatments might have been released from some stresses caused by strong intraspecific competition. These asymmetrical effects, overall, suggest that longfin dace were more effective than the native fishes at consuming resources.

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It was predicted that longfin dace and Rio Grande sucker would have a larger resource overlap than Rio Grande chub and longfin dace. It appeared, however, that dace affected chub more than sucker as evidenced by the greater mortality and greater weight loss of chub relative to sucker in treatment enclosures with non-native dace. The energy of resources exploited may be an important determinant in the effects of competition on fitness. For instance, longfin dace might have affected the rate of resource consumption by Rio Grande chub and Rio Grande sucker equally, but chub would be deprived of more energy by consuming fewer invertebrates than sucker would be by consuming less periphyton (Bohn and Amundsen 2001). Alternatively, longfin dace might share a resource evenly with Rio Grande sucker or Rio Grande chub, but dace might be better at converting energy from that resource into growth (Byers 2000). Longfin dace can exhibit protracted spawning periods and rapid growth rates, with young-of-year hatched in spring able to spawn in fall (Minckley and Barber 1971), which is consistent with a superior ability to convert energy.

Conclusion

Headwater streams are important to the conservation of native species in river systems because they can provide refuge from environmental disturbance and invasive species (Magoulick and Kobza 2003; Meyer et al. 2007). This study substantiated that invasive longfin dace severely impacted the capacity of isolated pools in Las Animas Creek to serve as refugia for native Rio Grande sucker and Rio Grande chub. Specifically, restoration of the native fish community to Las Animas Creek may require elimination of invasive longfin dace. Generally, if headwater streams can lose their capacity to function as refugia, there may be future problems in the management of native species in streams in arid and semi-arid lands (e.g., Rinne and Platania 1995; Calamusso and Rinne 1999). If a likely outcome of climate change is greater ecosystem contraction (i.e., intermittency) of small streams (Grimm and Fisher 1992; Stanley et al. 1997), which may involve strengthened biotic interactions (e.g., competition) with non-native species (Lodge 1993; Lake 2003), then many more freshwater ecosystems may be successfully

invaded by non-native species in the near future (Sala et al. 2000; Kolar and Lodge 2002; Marchetti et al. 2004; Olden et al. 2006).

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PRESENTATIONS

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